5

Terrestrial Animals

Key Findings

The following bullet points summarize the main findings of this chapter:

- The Intergovernmental Panel on Climate Change's (IPCC's) view of future species extinction relies on a narrow view of the literature that is highly selective and based almost entirely on model projections as opposed to real-world observations. The latter often contradict the former.

- Numerous shortcomings are inherent in the models used to predict the impact of climate on the health and distributions of animal species. Assumptions and limitations make those models unreliable in projecting the future in this regard.

- As in past species extinctions, future species losses are unlikely to be directly attributable to climate changes that act over long terms and to which species are well adapted. Species losses in the future are more likely to be attributable to the novel, relatively rapid twentieth and twenty-first century anthropogenic processes of habitat loss and the transportation-mediated dispersal of pathogens and predators (including man) into previously isolated populations.

- The planet's animal species have inherent abilities enabling them to cope with climate changes over a period of a few generations, a single generation, or even in real time.

- Research suggests amphibian populations will suffer little, if any, harm from projected CO_2-induced global warming, and they may even benefit from it.

- Enhanced plant productivity driven by elevated levels of atmospheric CO_2 tends to support greater abundance of soil microarthropods.

- Although some changes in bird populations and their habitat areas have been documented in the literature, linking such changes to CO_2-induced global warming remains elusive. Also, when there have been changes, they often are positive, as many species have adapted and are thriving in response to rising temperatures of the modern era.

- Published research indicates rising temperatures will not likely increase, and may decrease, plant damage from leaf-eating herbivores, as rising atmospheric CO_2 boosts the production of certain defensive compounds in plants that are detrimental to animal pests.

- Global warming is creating opportunities for butterflies to expand their populations and ranges, just the opposite of alarmist projections of range contractions and butterfly species demise in response to a CO_2-induced warming of Earth.

- The warming-induced extinctions of mammals that have been predicted to occur are highly unlikely to be realized in nature, and warming in fact opens new territories for mammal range expansions. In addition, rising atmospheric CO_2 concentrations may produce changes in the palatability of the trunk and branch tissues of certain trees that may protect them from being killed by hares and rabbits.

- The likely net effect of climate change on the spread of parasitic and vector-borne diseases is complex and at this time difficult to predict. Rising temperatures increase the mortality rates as well as the development rates of many parasites, and temperature is only one of many variables that influence the range of viruses and other sources of diseases.

- Polar bears have survived historic changes in climate that have exceeded those of the twentieth century or are forecast by computer models to occur in the future. In addition, some populations of polar bears appear to be stable despite rising temperatures and summer sea ice declines. The biggest threat they face is not from global warming, but commercial hunting by humans, which historically has taken a huge toll on polar bear populations.

- Studies of the effects of rising temperatures on reptiles find they often are able to tolerate a greater range of environmental conditions than they have been exposed to in the recent past, demonstrate abilities to thermo-regulate to achieve body temperatures close to their preferred temperatures, and often benefit from warmer temperatures.

- It appears earthworms and soil nematodes respond to increases in the air's CO_2 content, via a number of plant-mediated phenomena, in ways that further enhance the positive effects of atmospheric CO_2 enrichment on plant growth and development, while helping to sequester more carbon more securely in the soil and thereby reducing the potential for CO_2-induced global warming.

Introduction

The draft Summary for Policymakers from the Intergovernmental Panel on Climate Change's (IPCC) Working Group II contribution to the *Fifth Assessment Report* makes the following claims about the impact of climate change on species:

> In response to ongoing climate change, terrestrial and marine species have shifted their ranges, seasonal activities, migration patterns, and abundance, have demonstrated altered species interaction (*high confidence*). Increased tree mortality, observed in many places worldwide, has been attributed to climate change in some regions. While recent warming contributed to the extinction of many species of Central American amphibians (*medium confidence*), most recent observed terrestrial-species extinctions have not been attributed to recent climate change, despite some speculative efforts (*high confidence*). Natural climate change at rates much slower than current anthropogenic change has led to significant ecosystem shifts, including species emergences and extinctions, in the past million years (IPCC-II, 2014, p. 3).

While this language is somewhat more nuanced than past IPCC reports, the necessary qualifications and uncertainties are missing from this language appearing later in the same draft report:

> A large fraction of terrestrial and freshwater species faces increased extinction risk under projected climate change during and beyond the 21st century, especially as climate change interacts with other pressures, such as habitat modification, over-exploitation, pollution, and invasive species (*high confidence*). Extinction risk is increased under all RCP scenarios, with risk increasing with both magnitude and rate of climate change. Many species will be unable to move fast enough during the 21st century to track suitable climates under mid- and high-ranges rates of climate change (i.e., RCP4.5, 6.0, and 8.5) (*medium confidence*). See Figure SPM.5. Management actions can reduce, but not eliminate, risks to ecosystems and can increase ecosystem adaptability, for example through reduction of other stresses and habitat (Ibid., pp. 8–9).

These conclusions are overly alarmist and unsupported by scientific research. The primary error made by IPCC's authors is to ignore the growing anomaly between climate model simulations and real-world observations of global temperature. The world in fact is not warming as fast as IPCC predicts, the twentieth century warming was not as "unprecedented" as IPCC previously thought, transient climate response is likely to be less than once thought, the risk of damaging increases in drought or tropical cyclones is lower, and so on (Idso *et al.,* 2013a; Idso *et al.,* 2013b). All of these concessions and walk-backs have implications for the impacts of climate change on terrestrial animals, all of them seemingly positive, yet Working Group II's Summary for Policymakers makes no concessions. A large body of research thus must be treated with considerable caution because of the resulting exaggeration of species range shifts and erroneous climate projections at regional scales.

Even assuming IPCC climate models were unbiased and reasonably accurate at regional scales, the material presented in this chapter reveals IPCC's view of future species extinction relies on a narrow view of the literature that is highly selective. It is based almost entirely on "climate envelope" model projections that often contradict real-world observations. It is clear the SAR-based (species-area-relationship) extinction estimates pioneered by Thomas *et al.* (2005) exaggerate future extinction rates due to the inherent bias of structural errors (He and Hubbell, 2012) and by systematically disregarding any species that benefit from climate change (Stockwell, 2004). IPCC also improperly characterizes the adaptive responses (e.g., range shifts, phenotypic or genetic adaptations) of many species as supporting its model-based extinction claims. In reality such adaptive responses provide documentary evidence of species *resilience*, proving their ability to cope with present and future climate changes as they have so often done throughout the historic and geologic past.

The findings cited in this chapter make it clear that when confronted with climate change or other challenges, terrestrial animals ranging from amphibians and arthropods to insects, polar bears, and worms exhibit opportunistic and highly adaptive behaviors. Ranges do not suddenly shrink as wildlife passively endures changes to its habitat, as is often projected in model-based studies. Instead, the species fortify themselves against the possibility of extinction, behaving as resilient evolutionary survivors and colonizing new habitat as it becomes available, strengthening their populations against the myriad challenges associated with environmental change.

This chapter begins with a review and analysis of the IPCC-based species extinction claim, highlighting many of the problems inherent in the models on which such claims are based and examples from the paleoecological record where species responded to and survived climate changes similar to or greater than those forecast by IPCC. Model projections are then evaluated against real-world observations of how various animal species responded to what IPCC has called the unprecedented rise in atmospheric CO_2 and temperature of the twentieth and twenty-first centuries. Although there likely will be some changes in species population dynamics in the decades and centuries ahead, few if any species are likely to be driven even close to extinction by global warming. In several instances, real-world data indicate warmer temperatures and higher atmospheric CO_2 concentrations will be highly beneficial, favoring a proliferation of species. IPCC continues to ignore in its reports such positive externalities of rising temperature and atmospheric CO_2.

References

IPCC-II. 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability.* Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., and Hanson, C.D. (Eds.) Cambridge University Press, Cambridge, UK.

IPCC. 2014. Summary for Policymakers. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability.* Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Draft dated October 28, 2013.

Idso, C.D., Carter, R.M., and Singer, S.F. 2013a. (Eds.) *Climate Change Reconsidered II: Physical Science*. Chicago, IL: The Heartland Institute.

Idso, C.D., Carter, R.M., Singer, S.F., and Soon, W. 2013b. Scientific critique of IPCC's 2013 "Summary for Policymakers," *Policy Brief.* Nongovernmental International Panel on Climate Change (NIPCC), October.

5.1 The Extinction Hypothesis

- IPCC's view of future species extinction relies on a narrow view of the literature that is highly selective and based almost entirely on model projections as opposed to real-world observations. The latter often contradict the former.

5.1.1 Model Shortcomings

The species extinction hypothesis began to appear in the discussion of potential impacts of CO_2-induced global warming in the late twentieth and early twenty-first centuries. Thomas *et al*. (2004), for example, developed projections of future habitat distributions for more than a thousand plant and animal species. Using those projections, they produced estimates of extinction probabilities associated with climate change scenarios for the year 2050 promoted by IPCC (IPCC, 2007). Their ominous projections (the extinction of more than a million species if anthropogenic CO_2 emissions were not quickly and dramatically reduced) were widely disseminated to the popular media even before the research was published. The projections were typically portrayed as well-founded scientific predictions of what was bound to occur.

The 19 authors first determined the "climate envelopes" of 1,103 species, each envelope representing the current climatic conditions under which a given species was found in nature. Then, after selecting those species where the habitat area would be expected to decrease in response to an increase in temperature, they used an empirical power-law relationship that relates species number to habitat area size to determine extinction probability calculations.

At first blush, their procedure seems reasonable enough, all else being equal. But all else is rarely equal when something changes in the real world. Stockwell (2004) provided an entirely different analysis of the available data, noting most climate change effects research accentuates the "losers" while deprecating the "winners." Stockwell notes Thomas *et al.*'s approach to the issue "ignores species that are currently threatened with extinction by non-climatic factors, and which could therefore benefit from an expanded potential habitat and so escape extinction in the new CO_2/climate regime." As Stockwell describes it, "a CO_2- or climate-driven range expansion would clearly help species that are threatened with extinction due to increasing habitat loss attributable to expanding urbanization and agricultural activities; while it may help other species that are threatened with extinction by habitat fragmentation to cross geographical barriers that were previously insurmountable obstacles to them." Consequently, he continues, "by neglecting the many species that fall into these and other like categories, no decrease in extinctions is possible under Thomas *et al.*'s approach to the problem, even under [a] free dispersal scenario, with the result that a massive increase in extinctions is a foregone conclusion."

Stockwell further notes, "the no dispersal scenario also forces an unrealistic decrease in range with any climatic change that shifts habitat area without reducing it; while 'overfitting' reduces ranges even more, producing systematic errors on the order of 10–20%, particularly with smaller data sets, deficiencies in data sampling and modeling methods, and the inclusion of irrelevant variables (Stockwell and Peterson 2002a; 2002b; 2003)."

With respect to Bakkenes *et al*. (2002), one of the studies relied on by Thomas *et al.,* for example, Stockwell writes, "two independent climate variables adequately explain 93% of the variation in their dependent variable; while the use of more climate variables ends up incorporating more random variation than it does actual signal, leading to a contraction of the climate envelope and a systematic bias towards smaller predicted ranges." It should come as no surprise, therefore, as Stockwell continues, "that in this study and that of Peterson *et al*. (2002)—which comprise two of the six major studies on which the analysis of Thomas *et al*. is based—the use of only two climate variables by the two studies yields extinction percentages of 7% and 9%, while the four additional studies upon which Thomas *et al*. rely (which use from 3 to 36 independent variables) yield extinction percentages ranging from 20% to 34%, consistent with what would be expected from errors associated with statistical over-fitting."

Because these ecological models are so unreliable, the common-sense response should be to attempt to verify model-based projections with independent data. However, Stockwell notes, "their single attempt to do so with a real-world extinction supposedly caused by global warming (Pounds *et al*., 1999) has been satisfactorily explained by changes in local weather patterns due to upwind deforestation of adjacent lowlands (Lawton *et al*., 2001)." Stockwell concludes, "Thomas *et al*. have a dearth of pertinent hard data to support their contentions; and while the absence of evidence does not necessarily disprove a claim, the lack of any real extinction data to support the results of their analysis certainly suggests that the models they are using are not 'tried and true'."

Stockwell concludes, "Thomas *et al*. (2004) seek to create the impression of impending ecological disaster due to CO_2-induced global warming, claiming their results justify mandating reductions of greenhouse gas emissions," but their findings "are forced by the calculations, confounded with statistical bias, lack supporting real-world evidence, and are perforated with speculation." Stockwell concludes "their doctrine of 'massive extinction' is actually a case of 'massive extinction *bias*'."

It may be argued Thomas *et al*. provide a service to conservation by raising awareness of the potential for species extinction due to climate change, but promoting biased methods that are poorly developed and unsupported by evidence is not scientifically responsible. The discrepancy between the forecasts of future impacts that include large-scale range reduction has yet to be reconciled with the relatively few extinctions from quite large and rapid climate changes in the past (Moritz and Agudo, 2013).

Botkin *et al*. (2007) are highly critical of the application of such methods, particularly when the results are at variance with the evidence provided by the fossil record. And in another critique of the Thomas *et al*. paper, Dormann (2007) found it important to "review the main shortcomings of species distribution models and species distribution projections" such as those employed and derived by Thomas *et al*. He carefully analyzed three aspects of what he described as "problems associated with species distribution models."

The first of these aspects is general species distribution model issues, under which Dormann listed four major problems. The second is extrapolation issues, where he found five major problems; and the third is statistical issues, where he listed six major problems. The methods employed and findings claimed by studies such as Thomas *et al*., Dormann writes, "have been challenged for conceptual and statistical reasons" by many other researchers, including Buckley and Roughgarden (2004), Harte *et al*. (2004), Thuiller *et al*. (2004), Lewis (2006), and Botkin *et al*. (2007). Dormann thus concludes, "projections of species distributions are not merely generating hypotheses to be tested by later data" but instead are being presented as "predictions of tomorrow's diversity, and policy makers and the public will interpret them as forecasts, similar to forecasts about tomorrow's weather," which he clearly believes is unwarranted and unwise.

Detailed intercomparative studies have borne out these concerns about the quality of species' distribution models. Forecasts of the future geographic distribution of six species of Falco from northern Europe ranged from a contraction in 80% of the species to no net loss in any species, seriously hampering their efficacy in conservation practices (Rodriguez-Castaneda *et al*. 2012).

The most effective criticism has been of the method used to estimate extinction rates by reversing the species-area accumulation curve, a species-area relationship (SAR) used to estimate extinction rates before they are actually observed, the so-called "extinction debt" owing to reduction in habitat and population size during a climate change. Researchers He and Hubbell (2011) show Thomas *et al*. (2005) overestimate the extinction debt from habitat loss largely due to a sampling artifact.

Pereira *et al*. (2012) responded by claiming He and Hubbell's SAR estimates are themselves biased. Thomas and Williamson (2012) report extinction is caused by many factors, not just habitat loss, and species already have responded to climate change in a manner consistent with high future extinction risks. In reply, He and Hubbell (2012) show the Pereira *et al*. (2012) claims are not substantiated and the SAR method of Thomas *et al*. (2005) is not appropriate for estimating extinction rates caused by habitat loss of any kind, concluding, "this so-called backward SAR method is a method for estimating endemic species, not 'extinction debt.' The backward SAR method has nothing to do with, and does not measure, extinction debt." Subsequent debate has clarified the proofs and results are general and explain the widely recognized overestimation of extinction by the backward SAR method, which should not be used to estimate species extinction in practice (He and Hubbell, 2013).

Despite the multitude of problems associated with the Thomas *et al*. paper, the extinction hypothesis was revived by Parmesan (2006). In reviewing 866 papers addressing the subject of ecological and evolutionary responses to the global warming of the prior few decades, Parmesan raised new concerns about the ability of Earth's many species of plants and animals to maintain a viable foothold on the planet if temperatures continue to rise. But much of the evidence cited by Parmesan actually weighs *against* this concern.

Parmesan notes "most observations of climate-change responses have involved alterations of species' phenologies." She reports, for example, many species had exhibited "advancement of spring events," such that there was "a lengthening of vegetative growing season in the Northern Hemisphere," which is something most would consider a positive phenomenon. She also reports "summer photosynthetic activity increased from 1981–1991"—another positive response—and the growing season throughout the United States "was unusually long during the warm period of the 1940s," but "since 1996, growing season length has increased only in four of the coldest, most-northerly zones (42°–45° N latitude), not in the three warmest zones (32°–37° N latitude)."

The negativity Parmesan associates with these mostly positive warming-induced phenological changes arises from the possibility there may be "mismatches" across different trophic levels in natural ecosystems, such as between the time each year's new crop of herbivores appears and the time of appearance of the plants they depend on for food. Eleven plant-animal associations were studied intensively in this regard, and in seven of them, Parmesan states, "they are more out of synchrony now than at the start of the studies."

Of course there always will be winners and losers (some big and some small) in such animal-plant matchups during periods of climate change, and probably many "draws." In addition, the paucity of pertinent data at the time of the Parmesan study precluded a valid determination of which of the three alternatives is the most likely to predominate. As one example of a "big loser" in the face of recent global warming, Parmesan reports, "field studies have documented that butterfly-host asynchrony has resulted directly in population crashes and extinctions." But population extinctions are not species extinctions, and she acknowledges the local extinctions to which she referred merely resulted in "shifting [the] mean location of extant populations northward [in the Northern Hemisphere] and upward." Newer research conducted since the publication of Parmesan's study suggests there could be many more wins and draws than losses as species cope with and adapt to such trophic mismatches.

A second major biological response to global warming addressed by Parmesan is species migration, often said to lead to range restrictions that make it difficult for species to maintain the minimum viable population size required for their continued existence. For example, it is often claimed global warming will be so fast and furious that many species will not be able to migrate poleward in latitude or upward in altitude rapidly enough to avoid extinction, or if located on mountaintops they will run out of suitable new habitat to which they can flee when faced with rising temperatures. On this subject, Parmesan essentially rehashed the earlier findings of the meta-analyses of Root *et al*. (2003) and Parmesan and Yohe (2003), which predominantly portrayed species ranges as expanding in the face of rising temperatures, since warming provides an opportunity for species to expand their ranges at their cold-limited boundaries while often providing a much reduced impetus for them to retreat at the heat-limited boundaries of their ranges. An example of this phenomenon cited by Parmesan occurred in the Netherlands between 1979 and 2001, where she reports "77 new epiphytic lichens colonized from the south, nearly doubling the total number of species for that community."

Parmesan also reports "increasing numbers of researchers use analyses of current intraspecific genetic variation for climate tolerance to argue for a substantive role of evolution in mitigating negative impacts of future climate change," additionally noting the fossil record contains "a plethora of data indicating local adaptation to climate change at specific sites." In addition, she states, there is evidence many existing species during earlier periods of dramatic climate change "appeared to shift their geographical distributions as though tracking the changing climate." In both of these situations the outcomes were clearly positive.

The greatest push by Parmesan for a decisively negative consequence of global warming is her claim that "documented rapid loss of habitable climate space makes it no surprise that the first extinctions of entire species attributed to global warming are mountain-restricted species," "many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds *et al*., 1999, 2005)," and "among harlequin frogs in Central and South American tropics, an astounding 67% have disappeared over the past 20–30 years," citing Pounds *et al*. (2006) regarding the latter. Such claims subsequently were shown by several researchers to be incorrect (see Amphibians, Section 5.2), as all the extinctions and disappearances of the amphibian species to which Parmesan referred had nothing at all to do with "rapid loss of habitable climate space" at the tops of mountains. As Pounds *et al*. (2006) note, the loss of these species "is largest at middle elevations, even though higher-elevation species generally have smaller ranges." In addition, as noted in an earlier review of the subject by Stuart *et al*. (2004), many of the amphibian species declines "took place in seemingly pristine habitats," which had not been lost to global warming nor even modestly altered. The extinctions and species disappearances appeared not to have been due to rising temperatures *per se*, but to the fungal disease chytridiomycosis, which is caused by *Batrachochytrium dendrobatidis*, as noted by both Stuart *et al*. (2004) and Pounds *et al*. (2006).

The fallacy of the montane range restriction assumption was shown by Tingley *et al*. (2012) in a study of breeding ranges of birds across three elevational transects in the Sierra Nevada Mountains (USA). While rising temperature over the past century pushed species upslope, they found increased precipitation pulled them downslope, resulting in range shifts that were heterogeneous within species and among regions. Thus despite increasing temperature in montane environments, the highly variable precipitation regimes create highly heterogeneous responses by species at range margins.

Other studies have poked further holes in the model-based animal extinction hypothesis, some for similar reasons, others for new ones.

Noting "climate envelopes (or the climatic niche concept) are the current methods of choice for prediction of species distributions under climate change," Beale *et al*. (2008) state, "climate envelope methods and assumptions have been criticized as ecologically and statistically naive (Pearson and Dawson, 2003; Hampe, 2004)," and "there are many reasons why species distributions may not match climate, including biotic interactions (Davis *et al*., 1998), adaptive evolution (Thomas *et al*., 2001), dispersal limitation (Svenning and Skov, 2007), and historical chance (Cotgreave and Harvey, 1994)."

Beale *et al*. evaluated the degree of matchup of species distributions to environment by generating synthetic distributions that retained the spatial structure of observed distributions but were randomly placed with respect to climate. They report, "using data on the European distribution of 100 bird species, we generated 99 synthetic distribution patterns for each species," and "for each of the 100 species, we fitted climate envelope models to both the true distribution and the 99 simulated distributions by using standard climate variables." They determined the goodness-of-fit of the many distribution patterns, because, as they note, "there has been no attempt to quantify how often high goodness-of-fit scores, and hence ostensibly good matches between distribution and climate, can occur by chance alone."

The three U.K. researchers determined "species-climate associations found by climate envelope methods are no better than chance for 68 of 100 European bird species." And, they write, "because birds are perceived to be equally strongly associated with climate as other species groups and trophic levels (Huntley *et al*., 2004)," their results "cast doubt on the predictions of climate envelope models for all taxa." They further state, "many, if not most, published climate envelopes may be no better than expected from chance associations alone, questioning the implications of many published studies." The researchers conclude, "scientific studies and climate change adaptation policies based on the indiscriminate use of climate envelope methods irrespective of species sensitivity to climate may be misleading and in need of revision."

These results are not so surprising in view of the well-known ecological principle that critical life-history events and interspecies relationships often can be the major factor limiting the spread of a species. Correspondingly, seasonal climate and ecosystem productivity variables have been found to be more statistically significant determinants of range than the broader annual climate variables typically used in ecological niche models (Stockwell, 2006).

Nogues-Bravo (2009) states climate envelope models "are sensitive to theoretical assumptions, to model classes and to projections in non-analogous climates, among other issues." He reviewed the pertinent scientific literature to determine how appropriate existing models were for determining whether a species will be driven to extinction by hypothesized planetary warming. He explains, "the studies reviewed: (1) rarely test the theoretical assumptions behind niche modeling such as the stability of species climatic niches through time and the equilibrium of species with climate; (2) they only use one model class (72% of the studies) and one paleoclimatic reconstruction (62.5%) to calibrate their models; (3) they do not check for the occurrence of non-analogous climates (97%); and (4) they do not use independent data to validate the models (72%)."

Nogues-Bravo notes, "ignoring the theoretical assumptions behind niche modeling and using inadequate methods for hindcasting" may produce "a cascade of errors and naïve ecological and evolutionary inferences." He concludes, "there are a wide variety of challenges that [climate envelope models] must overcome in order to improve the reliability of their predictions through time."

Randin *et al*. (2009) focused their attention on the quality of species distribution models (SDMs). They note, "the mean temperature interpolated from local stations at a 20-meter resolution contains more variability than expressed by the mean temperature within a 50-km x 50-km grid cell in which variation in elevation is poorly represented." Or, as they describe elsewhere in their paper, "climatic differences along elevation gradients, as apparent at 25-m x 25-m resolution, allow plant species to find suitable climatic conditions at higher elevation under climate change," whereas "models at a 10' x 10' resolution [10 minutes of latitude x 10 minutes of longitude, which correspond to 16-km x 16-km cells in the Swiss Alps, where they carried out their analyses] reflect the mean climatic conditions within the cell, and thus provide imprecise values of the probability of occurrence of species along a thermal gradient."

In testing this "local high-elevation habitat persistence hypothesis," Randin *et al*. assessed "whether climate change-induced habitat losses predicted at the European scale (10 x 10' grid cells) are also predicted from local-scale data and modeling (25-m x 25-m grid cells)." For 78 mountain species modeled at both European and local scales, they found the "local-scale models predict persistence of suitable habitats in up to 100% of species that were predicted by a European-scale model to lose all their suitable habitats in the area."

Randin *et al*. suggest the vastly different results they obtained when using fine and coarse grid scales might help explain what they call the Quaternary Conundrum: "why fewer species than expected went extinct during glacial periods when models predict so many extinctions with similar amplitude of climate change (Botkin *et al*., 2007)." In addition, they note, "coarse-resolution predictions based on SDMs are commonly used in the preparation of reports by the Intergovernmental Panel on Climate Change," which are then used by "conservation planners, managers, and other decision makers to anticipate biodiversity losses in alpine and other systems across local, regional, and larger scales."

Willis and Bhagwat (2009) discuss other problems that arise from coarse model scales. In a "perspective" published in *Science* the two raised a warning flag, stating, "coarse spatial scales fail to capture topography or 'microclimatic buffering' and they often do not consider the full acclimation capacity of plants and animals," citing Botkin *et al*. (2007).

As an example of this model-based deficiency, Willis and Bhagwat cite Randin *et al*. (2009), noting for alpine plant species growing in the Swiss Alps, "a coarse European-scale model (with 16 km by 16 km grid cells) predicted a loss of all suitable habitats during the 21st century, whereas a model run using local-scale data (25 m by 25 m grid cells) predicted persistence of suitable habitats for up to 100% of plant species." The two Europeans note Luoto and Heikkinen (2008) "reached a similar conclusion in their study of the predictive accuracy of bioclimatic envelope models on the future distribution of 100 European butterfly species," finding "a model that included climate and topographical heterogeneity (such as elevational range) predicted only half of the species losses in mountainous areas for the period from 2051 to 2080 in comparison to a climate-only model."

Another problem was the models' failure to consider the capacity of plants and animals to acclimatize to warmer temperatures. Willis and Bhagwat note "many studies have indicated that increased atmospheric CO_2 affects photosynthesis rates and enhances net primary productivity—more so in tropical than in temperate regions—yet previous climate-vegetation simulations did not take this into account." They cite Lapola *et al*. (2009), who developed a new vegetation model for tropical South America, the results of which indicate "when the CO_2 fertilization effects are considered, they overwhelm the impacts arising from temperature," so "rather than the large-scale die-back predicted previously, tropical rainforest biomes remain the same or [are] substituted by wetter and more productive biomes."

"Another complexity," note Willis and Bhagwat, is the fact that "over 75% of the Earth's terrestrial biomes now show evidence of alteration as a result of human residence and land use," which has resulted in "a highly fragmented landscape" that has been hypothesized to make it especially difficult for the preservation of species. Nevertheless, they report Prugh *et al*. (2008) have "compiled and analyzed raw data from previous research on the occurrence of 785 animal species in >12,000 discrete habitat fragments on six continents," and "in many cases, fragment size and isolation were poor predictors of occupancy." They further note "this ability of species to persist in what would appear to be a highly undesirable and fragmented landscape has also been recently demonstrated in West Africa," where "in a census on the presence of 972 forest butterflies over the past 16 years, Larsen [2008] found that despite an 87% reduction in forest cover, 97% of all species ever recorded in the area are still present."

Suggitt *et al.* (2011) note "most multi-cellular terrestrial organisms experience climate at scales of millimeters to meters," yet "most species-climate associations are analyzed at resolutions of kilometers or more," in what is "commonly known as the 'bioclimate approach' or 'climate envelope' modeling." They write, "because individuals experience heterogeneous microclimates in the landscape, species sometimes survive where the average background climate appears unsuitable," which the vast majority of bioclimate studies do not consider in their analyses.

Suggitt *et al.* recorded temperatures in numerous microsites at two locations where the vegetation was relatively homogenous (the Lake Vyrnwy Royal Society for the Protection of Birds reserve in Wales, and High Peak in the Peak District National Park in England) in September 2007 and January 2008, and in numerous microsites within three habitat types (woodland, heathland, and grassland) in Skipwith Common in North Yorkshire, UK, in September 2008 and January 2009. The seven scientists report, "thermal differences between habitats, and slope and aspects, were of the same order of magnitude as projected increases in global average surface temperatures," and in some cases, microclimate temperature variations exceeded estimates of warming under all of IPCC's emissions scenarios, "which range from 1.1 to a 6.4°C rise in global mean temperatures (IPCC, 2007)."

Suggitt *et al.* add, "these large temperature differences provide opportunities for individual organisms that are able to move short distances to escape unfavorable microclimates," and, hence, "populations may shift microhabitats (slopes, aspects and vegetation density) in response to inter-annual variation in the climate." They state their results indicate "the incorporation of habitat and topographical information is essential for species that (a) have some level of flexibility in their habitat associations, and (b) are at least partially limited by temperature extremes." In the real world of nature, the "bioclimate approach" and "climate envelope" modeling are not adequate for describing how species will respond to future changes in climate.

Sears *et al.* (2011) analyzed how spatial heterogeneity can impact biological responses to thermal landscapes at scales more relevant to organisms than the (much larger) scales typically employed by standard climate envelopes. They examined the effects of topographic relief on the range of operative temperatures available for behavioral thermoregulation of animals within various parts of an area described by a given climate envelope. Their results indicated "empirical studies alone suggest that the operative temperatures of many organisms vary by as much as 10–20°C on a local scale, depending on vegetation, geology, and topography," and even this variation in abiotic factors "ignores thermoregulatory behaviors that many animals use to balance heat loads." Through a set of simulations of these phenomena, they "demonstrate how variability in elevational topography can attenuate the effects of warming climates." They found "identical climates can produce very different microclimates at the spatial scales experienced by organisms"; "greater topographic relief should decrease selective pressure on thermal physiology for organisms that use behavior to avoid thermal extremes in heterogeneous environments," citing Huey *et al.* (2003); and "topographic diversity should buffer the impacts of climate change by facilitating behavioral thermoregulation."

Sears *et al.* say well-known relationships in biophysical ecology show "no two organisms experience the same climate in the same way," and "changing climates do not always impact organisms negatively." They conclude, "when coupled with thermoregulatory behavior, variation in topographic features can mask the acute effect of climate change in many cases," rendering the climate envelope approach to assessing species responses to climate change rather useless if not downright deceptive.

Dobrowski (2011) writes, "the response of biota to climate change of the past is pertinent to understanding present day biotic response to anthropogenic warming," and "one such adaptive response garnering increased attention is the purported utilization of climatic refugia by biota." Historically, these refugia were "typically thought of as large regions in which organisms took refuge during glacial advances and retreats during the Pleistocene, which then acted as sources for colonization during more favorable climatic periods." But "in addition to these large-scale refugia," he writes, "there is compelling evidence that climatic refugia occurred at local scales during the Last Glacial Maximum and were also utilized during interglacial warm periods, including the current interglacial (Willis and Van Andel, 2004; Birks and Willis, 2008)."

Dobrowski notes, "modeling using global climate models (GCMs) and regional climate models (RCMs) is done at scales of tens to hundreds of kilometers, whereas research suggests that temperature varies at scales of < 1 km in areas of complex terrain (Urban *et al*., 2000; Fridley, 2009)." He reports, "Hijmans *et al.* (2005) showed that there can be temperature variation of up to 33°C within one 18-km raster cell." In addition, "GCMs and RCMs can simulate free-air conditions but fail to accurately estimate surface climate due to terrain features that decouple upper atmospheric conditions from boundary layer effects (Grotch and Maccracken, 1991; Pepin and Seidel, 2005)."

Dobrowski points out many researchers "have recently commented on the potential of topographically driven meso- or micro-climatic variation in mountain environments for providing refugia habitats for populations of species threatened by climate warming," citing Luoto and Heikkinen (2008), Randin *et al.* (2009), and Seo *et al.* (2009). And he notes these researchers "point to lower rates of predicted habitat loss and lower predicted extinction probabilities from species distribution models when using finely resolved climate data as compared with coarse scaled data," stating, "they suggest that this is evidence of 'local scale refugia' (Randin *et al*., 2009) or 'reserves to shelter species' (Seo *et al*., 2009)."

Dobrowski concludes, "microrefugia are likely to be found in terrain positions that promote the consistent decoupling of the boundary layer from the free-atmosphere," and "these terrain positions are likely to have climate states and trends that are decoupled from regional averages," which is "a requisite for microrefugia to persist through time." Thus, he concludes, "convergent environments (local depressions, valley bottoms, sinks, and basins) are primary candidates for microrefugia based on these criteria," which bodes well for the once-considered-impossible survival of many species of plants and animals in a possible further warming of the planet.

Lande (2009) writes, "the primary mechanisms of phenotypic adaptation are Darwinian evolution by natural selection on genetic variation, and phenotypic plasticity through environmental influence on individual development," further stating, "rapid phenotypic adaptation may be necessary to prevent [the] extinction of modern species subject to anthropogenic global warming, especially those [species] with long generations such as large-bodied vertebrates and perennial plants." Against this backdrop and while noting "genetic variance in plasticity within and/or among populations has commonly been observed (Scheiner, 1993, 2002)," Lande employed "quantitative genetic models of phenotypic plasticity to analyze the dynamics of phenotypic adaptation to a sudden extreme environmental change" that is "beyond the usual range of background environmental fluctuations."

Lande's model suggests, "during the first generation in the new environment the mean fitness suddenly drops and the mean phenotype jumps towards the new optimum phenotype by plasticity," after which "adaptation occurs in two phases." First, "rapid evolution of increased plasticity allows the mean phenotype to closely approach the new optimum," after which the new phenotype "undergoes slow genetic assimilation, with reduction in plasticity compensated by genetic evolution of reaction norm elevation in the original environment." Such findings suggest there is a sound observational and mechanistic basis for concluding Earth's flora and fauna are genetically capable of coping with the type of rapid CO_2-induced global warming IPCC contends will drive innumerable plant and animal species to extinction.

5.1.2 Paleoecological Records

- As in past species extinctions, future species losses are unlikely to be directly attributable to climate changes that act over long terms and to which species are well adapted. Species losses in the future are more likely to be attributable to the novel, relatively rapid twentieth and twenty-first century anthropogenic processes of habitat loss and the transportation-mediated dispersal of pathogens and predators (including man) into previously isolated populations.

Most of the world's major species "body types" were laid down during the Cambrian period 600 million years ago (Levinton, 1992). These species have dealt successfully through the ages with new pest enemies, new diseases, ice ages, and global temperature swings greater than that predicted to result from CO_2-induced global warming.

During the Paleocene-Eocene Thermal Maximum (PETM), some 56 million years ago, it is believed, large amounts of carbon were released to the ocean-atmosphere system and global temperatures may have risen by 5–8°C, although more recent climate modelling indicates changes in cloud properties and an increase in shortwave radiation played a much greater role in the warm PETM period than previously believed (Kiehl and Shields, 2013).

McInerney and Wing (2011) reviewed much of the scientific literature on the insights being sought by biologists concerned about potential species extincttions due to CO_2-induced global warming, and they give their assessment of the current status of the grand enterprise in which many scientists have been involved since the early 1990s, when the PETM and its significance first began to be recognized (Kennett and Stott, 1991; Koch *et al*., 1992).

Although there was a major extinction of benthic foraminifera in the world's oceans, the two researchers write, "most groups of organisms did not suffer mass extinction." In fact, they say, "it is surprising that cool-adapted species already living at higher latitudes before the onset of the PETM are not known to have experienced major extinctions," and "this absence of significant extinction in most groups is particularly interesting in light of the predictions of substantial future extinction with anthropogenic global warming." In addition, "low levels of extincttion in the face of rapid environmental change during the Quaternary pose a similar challenge to modeled extinctions under future greenhouse warming," citing Botkin *et al*. (2007). Finally, they observe, "rapid morphological change occurred in both marine and terrestrial lineages, suggesting that organisms adjusted to climate change through evolution as well as dispersal."

McInerney and Wing conclude by noting "research on the PETM and other intervals of rapid global change has been driven by the idea that they provide geological parallels to future anthropogenic warming." The many research results they review seem to suggest Earth's plants and animals, both on land and in the sea, may be much better equipped to deal with the environmental changes that may occur in response to anthropogenic CO_2 emissions than what many students of the subject have long believed.

Hof *et al*. (2011) present evidence demonstrating "recent geophysical studies challenge the view that the speed of current and projected climate change is unprecedented." In one such study, for example, they report Steffensen *et al*. (2008) showed temperatures in Greenland warmed by up to 4°C/year near the end of the last glacial period. They state this change and other rapid climate changes during the Quaternary (the last 2.5 million years) did not cause a noticeable level of broad-scale, continent-wide extinctions of species. Instead, these rapid changes appeared to "primarily affect a few specific groups, mainly large mammals (Koch and Barnosky, 2006) and European trees (Svenning, 2003)," so "few taxa became extinct during the Quaternary (Botkin *et al*., 2007)."

How were the bulk of Earth's species able to survive a climatic change that many today believe is unsurvivable? Hof *et al*. suggest "species may have used strategies other than shifting their geographical distributions or changing their genetic make-up." They note, for example, "intraspecific variation in physiological, phenological, behavioral or morphological traits may have allowed species to cope with rapid climatic changes within their ranges (Davis and Shaw, 2001; Nussey *et al*., 2005; Skelly *et al*., 2007)," based on "preexisting genetic variation within and among different populations, which is an important prerequisite for adaptive responses," noting "both intraspecific phenotypic variability and individual phenotypic plasticity may allow for rapid adaptation without actual microevolutionary changes." Hof *et al*. conclude, "species are probably more resilient to climatic changes than anticipated in most model assessments of the effect of contemporary climate change."

Indeed, as shown in the subsections below, model-based projections of animal extinctions in response to rising temperature and atmospheric CO_2 suffer a major loss of credibility when tested against real-world data. Although there likely will be some changes in species population dynamics, few if any species will be driven to extinction. In contrast, a number of studies indicate many animal species will benefit from a warming climate and rising atmospheric CO_2 concentrations, resulting in a proliferation, as opposed to extinction, of species.

Vegas-Vilarrubia *et al*. (2011) contend "current extinction estimates for the near-future should be revised in light of palaeoecological information, which shows that spatial reorganizations and persistence in suitable microrefugia have been more common than extinction during the Quaternary." As a result, they say, "an interesting consequence is the possibility of new unknown species combinations with no modern analogues."

The two phenomena that come into play in these ecosystem transformations are acclimation and adaptation, "with the first relying on phenotypic plasticity and the second involving genetic changes of potential evolutionary significance." Vegas-Vilarrubia *et al*. note "some authors propose that spatial reorganizations without extinction will be the dominant biotic response to the near-future global changes." But "it is also possible that ecosystems never attain equilibrium," they write, and "transient states perpetuate because of the recurrent action of environmental change." They note "one of the main lessons from this is that ecosystems may express their resilience when confronted with environmental shifts by attaining several possible equilibrium states, as manifested in changes in biodiversity and/or composition, without losing their ecological functions."

Vegas-Vilarrubia *et al.* cite the global warming that occurred at the end of the Younger Dryas (~13,000 to 11,500 years ago), which serves as one of the more powerful analogs of projected global warming "because both magnitude and rates of change parallel those predicted for the present century." This prior real-world transformation "seems to have consisted of ecological reorganizations and changes in community composition because of differential species migration patterns and rates," but they note, "so far, it has not been possible to associate large-scale extinctions to the Younger Dryas climatic reversal."

Mergeay and Santamaria (2012) continue that line of thinking in an editorial introducing nine papers in a special issue of *Evolutionary Applications.* The two special-issue editors note Shine (2012) opens the issue by "showing how evolution can rapidly modify ecologically relevant traits in invading as well as native species." Bijlsma and Loeschcke (2012) then "tackle the interaction of drift, inbreeding and environmental stress," and Angeloni *et al.* (2012) "provide a conceptual tool-box for genomic research in conservation biology and highlight some of its possibilities for the mechanistic study of functional variation, adaptation and inbreeding."

Van Dyck (2012) shows "an organism's perception of its environment is subject to selection, a mechanism that could reduce the initial impact of environmental degradation or alleviate it over the longer run." Urban *et al.* (2012) argue "certain consequences of global change can only be accounted for by interactions between ecological and evolutionary processes." And Lemaire *et al.* (2012) highlight "the important role of evolution in predator-prey interactions."

Focusing on eco-evolutionary interactions, Palkovacs *et al.* (2012) "review studies on phenotypic change in response to human activities" and "show that phenotypic change can sometimes cascade across populations, communities and even entire ecosystems." Bonduriansky *et al.* (2012) examine "non-genetic inheritance and its role in adaptation," dissecting "the diversity of epigenetic and other transgenerational effects." Finally, Santamaria and Mendez (2012) "build on the information reviewed in all previous papers to identify recent advances in evolutionary knowledge of particular importance to improve or complement current biodiversity policy."

"Overall," Mergeay and Santamaria (2012) conclude, "these nine papers offer compelling evidence for the role of evolutionary processes in the maintenance of biodiversity and the adaptation to global change."

Meylan *et al.* (2012) focused on "the role of hormonally mediated maternal effects in inducing phenotypic plasticity as a response to rising temperatures and extreme climatic events," citing Marquis *et al.* (2008) on lizards. The three researchers describe how the discovery of maternal androgens and glucocorticoids in egg yolks, together with the intra-clutch variation of these hormones (Groothuis and Schwabl, 2008), make it possible for the offspring phenotype to be "manipulated in response to environmental conditions experienced by the female (Weaver *et al.*, 2004)." This maternal effect can be considered a form of "intergenerational phenotypic (developmental) plasticity," which could prove crucial "in coping with unpredictable environments." They suggest "hormones are a critical link between the environment and the genome" because they "may mediate the expression of phenotypic variation, generate trait integration, shape multivariate trade-offs (Sinervo *et al.*, 2008) and either directly or indirectly shape phenotypic plasticity during ontogeny and later into adulthood (Lessells, 2008)."

Meylan *et al.* further state, "the hormonal cascades involved in organizational effects during development may be modulated by environmental stressors and the maternal response as given by the duration and magnitude of elevated glucocorticoids." They discuss "the phenotypic and population dynamic consequences of prenatal exposure to steroid hormones resulting in context-dependent expression of traits by the offspring," ultimately describing "how hormone-mediated maternal effects may enhance rapid adaptation to changing environmental conditions." Finally, the three ecologists write, "females exposed to abiotic stressors during reproduction may alter the phenotypes by manipulation of hormones to the embryos," and they conclude, "hormone-mediated maternal effects, which generate phenotypic plasticity, may be one avenue for coping with global change."

Clearly, Earth's life forms are well-endowed with complex change-management strategies, either through behavior or otherwise. More recent developments have sought to correct or augment the limitation of static, deterministic paradigms such as niche modeling and species area curves with more dynamic and stochastic paradigms—particularly exploring the consequences of "niche assembly" vs. "dispersal assembly" on extinction risk and biodiversity management (Stockwell, 2013). It is well-known that the composition of many communities is not ruled consistently by species' ecological niches or functional roles, and that they also incorporate stochastic processes (e.g. coastal fish metacommunities, see Mouillot, 2007). Recent work is beginning to redress the incomplete "niche-based" frameworks that have produced unrealistic and counterfactual estimates of extinction loss.

The most potent of the tools has been "unified neutral theory" (UNT, Hubbell, 2001), which provides a simple yet rigorous evaluation of the role of "dispersal assembly" in communities' richness and has provided deeper insights into extinction estimates than "niche assembly" alone might offer. It is clear the SAR-based extinction estimates pioneered by Thomas *et al.* (2005) exaggerate the extinction rates, due to the inherent bias of structural errors (He and Hubbell, 2012) and through disregarding the species that benefit from climate change (Stockwell, 2004). However, it is hypothesized that habitat reductions from any cause will increase the probability of extinction, as rarity usually precedes extinction, even if the effect is not immediately apparent. This is the basis for the notion of "extinction debt." This is a dilemma, for if every environmental change increases extinctions, why haven't all species gone extinct?

A recent application of the UNT simulations of habitat reductions has identified two distinctive species area curves: imminent extinctions from habitat loss and delayed total extinctions indicative of extinction debt. The lag times for relaxation of the community into a lower species richness following habitat loss are often very large, within the order of thousands of years (Halley and Sgardeli, 2014). This suggests much of the "extinction debt" from a specific climate disruption may be redeemed by environmental or physiological changes in the intervening period between when the extinction debt is incurred and when the population has dwindled to unsustainable levels.

Another UNT simulation of two types of colonizing dispersal events—the "volcanic island" and the "land bridge" (Rosindell and Harmon, 2013) shows the stark difference between the colonization of a virgin habitat that slowly builds up diversity, and the drastic reduction of biodiversity from the sudden connection of unrelated communities via a transportation corridor. As in past species extinctions, future species losses are unlikely to be directly attributable to climate changes that act over long terms and to which species are well adapted. Species losses in the future are more likely to be attributable to the novel, relatively rapid twentieth and twenty-first century anthropogenic processes of habitat loss and the transportation-mediated dispersal of pathogens and predators (including man) into previously isolated populations.

It is clear niche-model-based projections of extinctions are riddled with assumptions and limitations that make them an unreliable guide to the impact of climate change on species. The vast majority of the predicted extinctions likely will not occur. A significant body of real-world evidence suggests most of Earth's plants and animals will be able to easily adapt, survive, and even thrive in the face of projected climate change, even under the worst-case scenarios of CO_2-induced global warming predicted by IPCC. As shown hereafter and in Chapter 4 (see Section 4.4 on Extinction), far from being a detriment to the biosphere, the air's rising CO_2 content is enhancing vegetative productivity and fostering a great proliferation of plant and animal species all around the world, helping to protect them from other anthropogenic forces that might otherwise drive them to extinction, independent of whatever the planet's climate may do.

References

Angeloni, F., Wagemaker, C.A.M., Vergeer, P., and Ouborg, N.J. 2012. Genomic toolboxes for conservation biologists. *Evolutionary Applications* **5**: 130–143.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., and Latour, J.B. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* **8**: 390–407.

Beale, C.M., Lennon, J.J., and Gimona, A. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences USA* **105**: 14,908–14,912.

Bijlsma, R. and Loeschcke, V. 2012. Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications* **5**: 117–129.

Birks, H.J.B. and Willis, K.J. 2008. Alpine trees and refugia in Europe. *Plant Ecology and Diversity* **1**: 147–160.

Bonduriansky, R., Crean, A.J., and Day, D.T. 2012. The implications of nongenetic inheritance for evolution in changing environments. *Evolutionary Applications* **5**: 192–201.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R, Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Skjoldborg Hansen, A., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., and Stockwell, D.R.B. 2007. Forecasting the effects of global warming on biodiversity. *BioScience* **57**: 227–236.

Buckley, L.B. and Roughgarden, J. 2004. Biodiversity conservation: Effects of changes in climate and land use change. *Nature* **430**: 10.1038/nature02717.

Cotgreave, P. and Harvey, P.H. 1994. Associations among biogeography, phylogeny and bird species diversity. *Biodiversity Letters* **2**: 46–55.

Davis, A.J., Jenkinson, I.S., Lawton, J.H., Shorrocks, B., and Wood, S. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**: 783–786.

Davis, M.B. and Shaw, R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* **292**: 673–679.

Dobrowski, S.Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**: 1022–1035.

Dormann, C.F. 2007. Promising the future? Global change projections of species distributions. *Basic and Applied Ecology* **8**: 387–397.

Fridley, J.D. 2009. Downscaling climate over complex terrain: high finescale (< 1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). *Journal of Applied Meteorology and Climatology* **48**: 1033–1049.

Grotch, S.L. and Maccracken, M.C. 1991. The use of general circulation models to predict climatic change. *Journal of Climate* **4**: 283–303.

Groothuis, T.G.G. and Schwabl, H. 2008. Hormone-mediated maternal effects in birds: mechanisms matter but what do we know of them? *Philosophical Transactions of the Royal Society B* **363**: 1647–1661.

Halley, J.M. and Sgardeli, V. 2014. Extinction debt and the species-area relationship: a neutral perspective. *Global Ecology and Biogeography* **23**: 113–123.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* **13**: 469–471.

Harte, J., Ostling, A., Green, J.L., and Kinzig, A. 2004. Biodiversity conservation: Climate change and extinction risk. *Nature* **430**: 10.1038/nature02718.

He, F. and Hubbell, S.P. 2011. Species-area relationships always overestimate extinction rates from habitat loss. *Nature* **473**: 368–371.

He, F. and Hubbell, S.P. 2012. He and Hubbell reply. *Nature*: **482**: E5-E6.

He, F. and Hubbell, S.P. 2013. Estimating extinction from species-area relationships: why the numbers do not add up. *Ecology* **94**: 1905–1912.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.

Hof, C., Levinsky, I., Araujo, M.B., and Rahbek, C. 2011. Rethinking species' ability to cope with rapid climate change. *Global Change Biology* **17**: 2987–2990.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, 375pp.

Huey, R.B., Hertz, P.E., and Sinervo, B. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. *American Naturalist* **161**: 357–366.

Huntley, B., Green, R.E., Collingham, Y.C., Hill, J.K., Willis, S.G., Bartlein, P.J., Cramer, W., Hagemeijer, W.J.M., and Thomas, C.J. 2004. The performance of models relating species geographical distributions to climate is independent of trophic level. *Ecology Letters* **7**: 417–426.

IPCC, 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Parry, M.L., *et al.* (Eds.) Cambridge, UK: Cambridge University Press.

IPCC. 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom.

Kennett, J.P. and Stott, L.D. 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* **353**: 225–229.

Kiehl, J.T. and Shields, C.A. 2013. Sensitivity of the Palaeocene-Eocene Thermal Maximum climate to cloud properties. *Philosophical Transactions of the Royal Society A* **371**: 1471–2962.

Koch, P.L. and Barnosky, A.D. 2006. Late Quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution and Systematics* **37**: 215–250.

Koch, P.L., Zachos, J.C., and Gingerich, P.D. 1992. Correlation between isotope records in marine and continental carbon reservoirs near the Paleocene/Eocene boundary. *Nature* **358**: 319–322.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology* **22**: 1435–1446.

Lapola, D.M, Oyama, M.D., and Nobre, C.A. 2009. Exploring the range of climate biome projections for tropical South America: The role of CO_2 fertilization and seasonality. *Global Biogeochemical Cycles* **23**: 10.1029/ 2008GB003357.

Larsen, T.B. 2008. Forest butterflies in West Africa have resisted extinction ... so far (Lepidoptera: Papilionoidea and Hesperioidea). *Biodiversity and Conservation* **17**: 2833–2847.

Lawton, R.O., Nair, U.S., Pielke Sr., R.A., and Welch, R.M. 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* **294**: 584–587.

Lemaire, V., Bruscotti, S., Van Gremberghe, I., Vyverman, W., Vanoverbeke, J., and De Meester, L. 2012. Genotype x genotype interactions between the toxic cyanobacterium *Microcystis* and its grazer, the water flea *Daphnia*. *Evolutionary Applications* **5**: 168–182.

Lessells, C.M. 2008. Neuroendocrine control of life histories: what do we need to know to understand the evolution of phenotypic plasticity? *Philosophical Transactions of the Royal Society B* **363**: 1589–1598.

Levinton, J. 1992. The big bang of animal evolution. *Scientific American* **267**: 84–91.

Lewis, O.T. 2006. Climate change, species-area curves and the extinction crisis. *Philosophical Transactions of the Royal Society B* **361:** 163–171.

Luoto, M. and Heikkinen, R.K. 2008. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology* **14**: 483–494.

Marquis, O., Massot, M., and Le Galliard, J.F. 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. *Ecology* **89**: 2575–2583.

McInerney, F.A. and Wing, S.L. 2011. The Paleocene-Eocene Thermal Maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annual Review of Earth and Planetary Sciences* **39**: 489–516.

Mergeay, J. and Santamaria, L. 2012. Evolution and biodiversity: the evolutionary basis of biodiversity and its potential for adaptation to global change. *Evolutionary Applications* **5**: 103–106.

Meylan, S., Miles, D.B., and Clobert, J. 2012. Hormonally mediated maternal effects, individual strategy and global change. *Philosophical Transactions of the Royal Society B* **367**: 1647–1664.

Moritz, C. and Agudo, R. 2013. The future of species under climate change: resilience or decline? *Science* **341**: 504–508.

Mouillot, D. 2007. Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. *Journal of Applied Ecology* **44**: 760–767.

Nogues-Bravo, D. 2009. Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography* **18**: 521–531.

Nussey, D.H., Postma, E., Gienapp, P., and Visser, M.E. 2005. Selection on heritable phenotypic plasticity in a wild bird population. *Science* **310**: 304–306.

Palkovacs, E., Kinnison, M.T., Correa, C., Dalton, C.M., and Hendry, A. 2012. Ecological consequences of human-induced trait change: fates beyond traits. *Evolutionary Applications* **5**: 183–191.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**: 637–669.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

Pearson, R.G. and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**: 361–371.

Pepin, N.C. and Seidel, D.J. 2005. A global comparison of surface and free-air temperatures at high elevations. *Journal of Geophysical Research* **110**: 10.1029/ 2004JD005047.

Pereira, H.M., Borda-de-Água, L., and Santos Martins, I. 2012. Geometry and scale in species–area relationships. *Nature* **482**: E3–E4.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H., and Stockwell, D.R.B. 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* **416**: 626–629.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sanchez-Azofeifa, G.A., Still, C.J., and Young, B.E. 2006.

Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**: 161–167.

Pounds, J.A., Fogden, M.P.L., and Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature* **398**: 611–615.

Pounds, J.A., Fogden, M.P.L., and Masters, K.L. 2005. Responses of natural communities to climate change in a highland tropical forest. In: Lovejoy, T. and Hannah, L. (Eds.) *Climate Change and Biodiversity*, Yale University Press, New Haven, Connecticut, USA, pp. 70–74.

Prugh, L.R., Hodges, K.E., Sinclair, R.E., and Brashares, J.S. 2008. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences USA* **105**: 20,770–20,775.

Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W., and Guisan, A. 2009. Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology* **15**: 1557–1569.

Rodriguez-Castaneda, G., Hof, A., Jansson, R., and Harding, L. 2012. Predicting the fate of biodiversity using species' distribution models: enhancing model compare-ability and repeatability. *PloS ONE*. **7**: 1–10.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.

Rosindell, J.A. and Harmon L.J. 2013. A unified model of species immigration, extinction and abundance on islands. *Journal of Biogeography* **40**: 1107–1118.

Santamaria, L. and Mendez, P.F. 2012. Evolution in biodiversity policy—current gaps and future needs. *Evolutionary Applications* **5**: 202–218.

Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* **24**: 35–68.

Scheiner, S.M. 2002. Selection experiments and the study of phenotypic plasticity. *Journal of Evolutionary Biology* **15**: 889–898.

Sears, M.W., Raskin, E., and Angilletta Jr., M.J. 2011. The world is not flat: Defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology* **51**: 666–675.

Seo, C., Thorne, J.H., Hannah, L., and Thuiller, W. 2009. Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters* **5**: 39–43.

Sinervo, B., Clobert, J., Miles, D.B., McAdam, A.G., and Lancaster, L.T. 2008. The role of pleiotropy versus signaler-receiver gene epistasis in life history trade-offs: dissecting the genomic architecture of organismal design in social systems. *Heredity* **101**: 197–211.

Shine, R. 2012. Invasive species as drivers of evolutionary change: cane toads in tropical Australia. *Evolutionary Applications* **5**: 107–116.

Skelly, D.K., Joseph, L.N., Possingham, H.P., Freidenburg, L.K., Farrugia, T.J., Kinnison, M.T., and Hendry, A.P. 2007. Evolutionary responses to climate change. *Conservation Biology* **21**: 1353–1355.

Steffensen, J.P., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Fischer, H., Goto-Azuma, K., Hansson, M., Johnsen, S.F., Jouzel, J., Masson-Delmotte, V., Popp, T., Rasmussen, S.O., Rothlisberger, R., Ruth, U., Stauffer, B., Siggaard-Anderson, M.-L., Sveinbjornsdottir, A.E., Svensson, A., and White, J.W.C. 2008. High-resolution Greenland Ice Core data show abrupt climate change happens in few years. *Science* **321**: 680–684.

Stockwell, D.R.B. 2004. *Biased Towards Extinction*. Guest Editorial, *CO_2 Science* **7** (19): http://www.co2science.org/articles/ V7/N19/EDIT.php.

Stockwell, D.R.B. 2006. Improving ecological niche models by data mining large environmental datasets for surrogate models. *Ecological Modelling* **192**: 188–196.

Stockwell, D.R.B. 2013. A theory ready for extinction. *Quadrant Online*. http://quadrant.org.au/opinion/doomed-planet/2013/12/theory-fit-extinction/.

Stockwell, D.R.B. and Peterson, A.T. 2002a. Controlling bias during predictive modeling with museum data. In *Predicting Species Occurrences: Issues of Scale and Accuracy*. Scott, J.M., *et al*. (Eds.) Covello, CA: Island Press.

Stockwell, D.R.B. and Peterson, A.T. 2002b. Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**: 1–13.

Stockwell, D.R.B. and Peterson, A.T. 2003. Comparison of resolution of methods for mapping biodiversity patterns from point-occurrence data. *Ecological Indicators* **3**: 213–221.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., and Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* **306**: 1783–1786.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., and Thomas, C.D. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* **120**: 1–8.

Svenning, J.C. 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters* **6**: 646–653.

Svenning, J.C. and Skov, F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters* **10**: 453–460.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., and Conradt, L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–581.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., and Williams, S.E. 2004. Extinction risk from climate change. *Nature* **427**: 145–148.

Thomas, C.D. and Williamson, M. 2012. Extinction and climate change. *Nature* **482**: E4-E5.

Thuiller, W., Araújo, M.B., Pearson, R.G., Whittaker, R.J., Brotons, L., and Lavorel, S. 2004. Biodiversity conservation: Uncertainty in predictions of extinction risk. *Nature* **430**: 10.1038/nature02716.

Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C., and Beissinger, S.R. 2012. The push and pull of climate change causes heterogeneous changes in avial elevational ranges. *Global Change Biology* **18**: 3279–3290.

Urban, D.L., Miller, C., Halpin, P.N., and Sephenson, N.L. 2000. Forest gradient response in Sierran landscapes: the physical template. *Landscape Ecology* **15**: 603–620.

Urban, M.C., De Meester, L., Vellend, M., Stoks, R., and Vanoverbeke, J. 2012. A crucial step towards realism: responses to climate change from an evolving metacommunity perspective. *Evolutionary Applications* **5**: 154–167.

Van Dyck, H. 2012. Changing organisms in rapidly changing anthropogenic landscapes: the significance of the "Umwelt"-concept and functional habitat for animal conservation. *Evolutionary Applications* **5**: 144–153.

Vegas-Vilarrubia, T., Rull, V., Montoya, E., and Safont, E. 2011. Quaternary palaeoecoloogy and nature conservation: a general review with examples from the neotropics. *Quaternary Science Reviews* **30**: 2361–2388.

Weaver, I.C.G., Cervoni, N., Champagne, F.A., D'Alessio, A.C., Sharma, S., Seckl, J.R., Symov, S., Szyf, M., and Meaney, M.J. 2004. Epigenetic programming by maternal behavior. *Nature Neuroscience* **7**: 847–854.

Willis, K.J. and Bhagwat, S.A. 2009. Biodiversity and climate change. *Science* **326**: 806–807.

Willis, K.J. and Van Andel, T.H. 2004. Trees or no trees? The environments of central and eastern Europe during the last glaciation. *Quaternary Science Reviews* **23**: 2369–2387.

5.1.3 Other Studies

- The planet's animal species have inherent abilities enabling them to cope with climate changes over a period of a few generations, a single generation, or even in real time.

Results of other studies also suggest the model-based species extinction hypothesis is unlikely to occur. In a review paper published in *Current Biology*, for example, Erwin (2009) explored past epochs and the myriad nooks and crannies of Earth today, searching for the primary trigger of speciation. His conclusion? Warmth is the fire that fuels the process by which species originate, whereas cold tends to destroy what warmth produced.

Headquartered in the Department of Paleobiology at the National Museum of Natural History in Washington, DC (USA), Erwin writes, "some of the best evidence for a link between biodiversity and climate comes from latitudinal gradients in diversity, which provide an avenue to explore the more general relationship between climate and evolution." In reviewing that evidence, he notes, "among the wide range of biotic hypotheses, those with the greatest empirical support indicate that warmer climates [1] have provided the energetic foundation for increased biodiversity by fostering greater population size and thus increased extinction resistance, [2] have increased metabolic scope, [3] have allowed more species to exploit specialized niches as a result of greater available energy, and [4] have generated faster speciation and/or lower extinction rates." He states, "in combination with geologic evidence for carbon dioxide levels and changing areas of tropical seas, these observations provide the basis for a simple, first-order model of the relationship between climate through the Phanerozoic and evolutionary patterns and diversity," and "such a model suggests that we should expect greatest marine diversity during globally warm intervals," as is typically also found for terrestrial diversity.

Erwin notes "the three best-studied mass extinction events are associated with sharp changes in climate and support the contention that rapid shifts in climate can reduce global diversity," which sounds much like the mantra of IPCC regarding global warming. However, the climate shifts Erwin cites consist mostly of cooling, and it is not only the shift to cooling but stagnating in a cool state that bodes ill for biodiversity. As Erwin describes it, "the long interval of stagnant evolution during the Permo-Carboniferous glaciation is consistent with studies of modern-day latitudinal diversity that [indicate] rates of evolutionary innovation and diversification are higher in high-energy climates than in low-energy climates."

Further explaining this conceptual framework, Erwin notes "contemporary studies suggest a positive relationship between high-energy climates and [1] increased diversification rates, [2] increased number of niches because of increased metabolic scope, and [3] more specialized niches, and possibly because of [4] niche construction." He writes, "studies showing that the tropics are a cradle of diversity, pumping clade representatives into higher latitudes, as well as evidence of increased ordinal level originations in the tropics, and of the sudden appearance of several mammalian groups during the Paleocene-Eocene Thermal Maximum suggest an asymmetric pattern of innovations associated with high-energy climate regimes."

Erwin concludes, "there is an intriguing possibility that diversity does not track climate, but rather builds up during warm intervals but without falling by proportional amounts when climates turn cooler," with the result that "warmer climates may serve as an evolutionary diversification pump with higher diversity persisting [throughout following cooler periods], at least for a time."

Two generalizations clearly can be made: warmth typically begets speciation, and cold tends to lead to species extinctions.

Independent support for this thesis was provided in papers by Jaramillo *et al.* (2010) and Willis *et al.* (2010). Jaramillo *et al.* (2010) examined the Paleocene-Eocene Thermal Maximum (PETM), which occurred some 56.3 million years ago, at sites in Venezuela and Columbia. The PETM provides an interesting analog to the Current Warm Period, and it is postulated carbon dioxide rose rapidly in that era over a period of 10,000 to 20,000 years and global temperatures were elevated approximately 5 °C for 100,000 to 200,000 years.

The PETM was clearly identifiable in terms of temperature, where it was between 31 and 34 °C during the peak of global warmth. Using pollen and other organic materials, the authors were able to identify various plant species that existed during this period. In spite of the high temperatures and possibly less-moist conditions, the number of drought-tolerant plants did not increase, nor were moisture-requiring plants shown to decrease during the PETM. These facts lead the authors to speculate either rainfall or water use efficiency increased because of higher levels of atmospheric carbon dioxide, thereby compensating for the higher temperatures.

They also note the PETM brought a radical increase in diversity, measured in both absolute terms (number of species/taxa) and in evenness (relatively more even species percentages). This was achieved by addition of new taxa. The origination rate for new taxa during the PETM was two to six times higher than during the periods before and after, but extinction rates were not unusual. The species/taxa that originated, and the overall diversity, continued after the PETM. Thus the gains in plant species richness during the PETM were relatively persistent rather than transient.

It is believed tropical forests of today are currently growing in climates near the maximum temperature the plants can tolerate (~27.5 °C), and thus future global warming in tropical zones may stress plants and cause a reduction in forest growth, perhaps driving some species to extinction. However, Jaramillo *et al.* show temperatures of 31 to 34 °C seem not only to have been tolerated but to have caused a burst of speciation in the PETM, including major taxa that persist today. The high temperatures of the PETM were not detrimental to the tropical moist forests examined in this study.

Willis *et al.* (2010) identified past historical periods when climate was similar to that projected by global climate models for the next century or so, or in which the rate of temperature change was unusually rapid. These periods were examined for any climate-related extinctions.

The first period they examined was the Eocene Climatic Optimum (53–51 million years ago), when the atmosphere's CO_2 concentration exceeded 1,200 ppm and tropical temperatures were 5–10°C warmer than current values. Far from causing extinctions of the tropical flora (where the data are best), the four researchers report, "all the evidence from low-latitude records indicates that, at least in the plant fossil record, this was one of the most biodiverse intervals of time in the Neotropics." They also note "ancestors of many of our modern tropical and temperate plants evolved ... when global temperatures and CO_2 were much higher than present, ... indicating that they have much wider ecological tolerances than are predicted based on present-day climates alone."

The second period they examined consisted of two rapid-change climatic events in the Holocene—one at 14,700 years ago and one at 11,600 years ago—when temperatures increased in the mid- to high-latitudes of the Northern Hemisphere by up to 10°C over periods of less than 60 years. Many sites show evidence of rapid plant responses to rapid warming during these events. The authors note, "at no site yet studied, anywhere in the world, is there evidence in the fossil record for large-scale climate-driven extinction during these intervals of rapid warming." They report extinctions did occur due to the cold temperatures of the glacial epoch, when subtropical species in southern Europe were driven out of their ecological tolerance zone.

Willis *et al.* also make use of recent historical data, such as the 3°C rise in temperature at Yosemite Park over the past 100 years. Comparing surveys of mammal fauna conducted near the beginning and end of this period, they detected some changes but no local extinctions. Thus they determined for all the periods they studied, there were no detectable extinctions during very warm temperatures or very rapid warming.

D'Odorico *et al.* (2008) write, "recent climate change predictions indicate that, in addition to trends in the mean values of climate variables, an increase in interannual variability is expected to occur in the near future." Also noting "environmental fluctuations are usually believed to play a 'destructive role' in ecosystem dynamics," they explore the validity of this latter assumption in the context of current climate model predictions, asking, "Can environmental variability have only 'negative' effects on ecosystem dynamics?"

After lengthy mathematical analysis, D'Odorico *et al.* determined "opportunities for species existence/coexistence are found to increase with 'moderate' values of the variance of environmental fluctuations, while they decrease when these fluctuations are relatively strong." This outcome constitutes what has come to be known as the "intermediate disturbance hypothesis," which grew out of the work of Connell (1978), who, in the words of D'Odorico *et al.*, suggested "coral reefs and rain forests maintain high levels of diversity only in a non-equilibrium state," and Huston (1979), who noted "most communities have relatively high levels of diversity because environmental variability maintains them in a non-equilibrium state."

Noting numerous real-world indications (Chapin *et al.*, 1997; Steneck *et al.*, 2002; Bengtsson *et al.*, 2003; Elmqvist *et al.*, 2003; Bellwood *et al.*, 2004; Folke *et al.*, 2004) that "biodiversity may enhance ecosystem resilience," the four researchers provide a theoretical basis for this phenomenon, demonstrating the validity of the ecological equivalent of the common dictum of physical exercise gurus: no pain, no gain. This evidence suggests what IPCC considers unfavorable may in fact be just what is needed to increase the diversity and resilience of myriad terrestrial and aquatic ecosystems and propel them to higher levels of activity in the brave new world of our CO_2-enriched future.

In an overview of a symposium titled "Molecules to Migration: Pressures of Life," held in Africa on the Maasai Mara National Reserve of Kenya, Fuller *et al.* (2010) note the theoretical approach most commonly used to predict future species distributions in a CO_2-enriched and warmer world (the "climate envelope" approach) assumes "animals and plants can persist only in areas with an environment similar to the one they currently inhabit." This approach, they point out, "typically ignores the potential physiological capacity of animals to respond to climate change." They explain how "behavioral, autonomic, and morphological modifications such as nocturnal activity, selective brain cooling, and body color may potentially serve as buffers to the consequences of climate change."

The six scientists note all organisms "have the capacity to adapt to changing environmental conditions both by phenotypic plasticity within a life span and by microevolution over a few life spans." They note, "there is evidence that microevolution—that is, heritable shifts in allele frequencies in a population (without speciation)—has occurred in response to climate warming," citing Bradshaw and Holzapfel (2006, 2008). They also point out phenotypic plasticity "is likely to represent the first response of individual organisms." They report "adaptive changes in phenotype induced by climate change have been documented, for example, in the morphology and phenology of birds (Charmantier *et al.*, 2008) and mammals (Reale *et al.*, 2003; Linnen *et al.*, 2009; Maloney *et al.*, 2009; Ozgul *et al.*, 2009)."

Fuller *et al.* cite Pincebourde *et al.* (2009), who "showed that intertidal sea stars can behaviorally regulate their thermal inertia by increasing their rate of water uptake during high tide on hot days," which is "a response that affords protection against extreme aerial temperatures during subsequent low tides." Next they note "exposure of humans to hot conditions on successive days induces an increase in sweat capacity (Nielsen *et al.*, 1993)." They state, "other adaptations also ensue, including plasma volume expansion and decreased electrolyte content of sweat," and thus "a typical unacclimatized male, who can produce about 600 ml of sweat per hour, can double that output with heat acclimatization (Henane and Valatx, 1973)." This "phenotypic adaptation (in this case, heat acclimatization) can alter physiological tolerance (the risk of heat illness),” they note.

The Australian, South African, and U.S. scientists also cite several studies—Zervanos and Hadley (1973), Belovsky and Jordan (1978), Grenot (1992), Hayes and Krausman (1993), Berger *et al.* (1999), Dussault *et al.* (2004), Maloney *et al.* (2005), and Hetem *et al.* (2010)—of large herbivores that “increase nocturnal activity in the face of high diurnal heat loads.” They state “another adaptation that may enhance plasticity in response to aridity that is available to oryx and other artiodactyls, as well as members of the cat family (Mitchell *et al.*, 1987), is selective brain cooling,” in which cooling of the hypothalamus and the temperature sensors that drive evaporative heat loss “inhibits evaporative heat loss and conserves body water (Kuhnen, 1997; Fuller *et al.*, 2007),” which “is likely to be particularly valuable to animals under concurrent heat stress and dehydration.” Finally, they suggest maintaining genetic diversity for a trait such as fur or feather color that adapts various organisms to different thermal environments “may provide important plasticity for future climate change,” citing Millien *et al.* (2006), and “there is already evidence that, over the past 30 years as the climate has warmed, the proportion of dark-colored to light-colored Soay sheep has decreased on islands in the outer Hebrides,” citing Maloney *et al.* (2009).

Clearly, the planet’s animal species have inherent abilities enabling them to cope with climate changes over a period of a few generations, a single generation, or even in real time.

References

Bellwood, D.R., Houghes, T.P., Folke, C., and Nystrom, M. 2004. Confronting the coral reef crisis. *Nature* **429**: 827–833.

Belovsky, G.E. and Jordan, P.A. 1978. The time-energy budget of a moose. *Theoretical Population Biology* **14**: 76–104.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., and Nystrom, M. 2003. Reserves, resilience and dynamic landscapes. *Ambio* **32**: 389–396.

Berger, A., Scheibe, K.-M., Eichhorn, K., Scheibe, A., and Streich, J. 1999. Diurnal and ultradian rhythms of behavior in a mare group of Przewalski horse (*Equus ferus przewalskii*), measured through one year under semi-reserve conditions. *Applied Animal Behavior Science* **64**: 1–17.

Bradshaw, W.E. and Holzapfel, C.M. 2006. Climate change: evolutionary response to rapid climate change. *Science* **312**: 1477–1478.

Bradshaw, W.E. and Holzapfel, C.M. 2008. Genetic response to rapid climate change: it’s seasonal timing that matters. *Molecular Ecology* **17**: 157–166.

Chapin III, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., and Tilman, D. 1997. Biotic controls of the functioning of ecosystems. *Science* **277**: 500–504.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B., and Sheldon, B.C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**: 800–803.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* **199**: 1302–1310.

D’Odorico, P., Laio, F., Ridolfi, L., and Lerdau, M.T. 2008. Biodiversity enhancement induced by environmental noise. *Journal of Theoretical Biology* **255**: 332–337.

Dussault, C., Ouellet, J.P., Courtois, R., Huot, J., Breton, L., and Larochelle, J. 2004. Behavioral responses of moose to thermal conditions in the boreal forest. *Ecoscience* **11**: 321–328.

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, L., Walker, B., and Norberg, J. 2003. Response diversity and ecosystem resilience. *Frontiers in Ecology and Environment* **1**: 488–494.

Erwin, D.H. 2009. Climate as a driver of evolutionary change. *Current Biology* **19**: R575–R583.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C.S. 2004. Regime shifts, resilience and biodiversity in ecosystem management. *Annual Review of Ecology and Evolution Systems* **35**: 557–581.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R.S., Mitchell, D., and Maloney, S.K. 2010. Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology* **83**: 713–720.

Fuller, A., Meyer, L.C.R., Mitchell, D., and Maloney, S.K. 2007. Dehydration increases the magnitude of selective brain cooling independently of core temperature in sheep. *American Journal of Physiology* **293**: R438–R446.

Grenot, C.J. 1992. Ecophysiological characteristics of large herbivorous mammals in arid Africa and the Middle East. *Journal of Arid Environments* **23**: 125–155.

Hayes, C.L. and Krausman, P.R. 1993. Nocturnal activity of female desert mule deer. *Journal of Wildlife Management* **57**: 897–904.

Henane, R. and Valatx, J.L. 1973. Thermoregulatory changes induced during heat acclimatization by controlled hyperthermia in man. *Journal of Physiology* **230**: 255–271.

Hetem, R.S., Strauss, W.M., Fick, L.G., Maloney, S.K., Meyer, L.C., Shobrak, M., Fuller, A., and Mitchell, D. 2010. Variation in the daily rhythm of body temperature of free-living Arabian oryx (*Oryx leucoryx*): does water limitation drive heterothermy? *Journal of Comparative Physiology B* **180**: 10.1007/s00360–010–0480-z.

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**: 81–101.

Jaramillo, C., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M.J., de la Parra, F., Morón, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, F., Alvarán, M., Osorno, J., Crowley, J.L., Valencia, V., and Vervoort, J. 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. *Science* **330**: 957–961.

Kuhnen, G. 1997. Selective brain cooling reduces respiratory water loss during heat stress. *Comparative Biochemistry and Physiology A* **118**: 891–895.

Linnen, C.R., Kingsley, E.P., Jensen, J.D., and Hoekstra, H.E. 2009. On the origin and spread of an adaptive allele in deer mice. *Science* **325**: 1095–1098.

Maloney, S.K., Fuller, A., and Mitchell, D. 2009. Climate change: is the dark Soay sheep endangered? *Biological Letters* **5**: 826–829.

Maloney, S.K., Moss, G., Cartmell, T., and Mitchell, D. 2005. Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (*Connochaetes gnou*). *Journal of Comparative Physiology A* **191**: 1055–1064.

Millien, V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A.B., and Yom-Tov, Y. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters* **9**: 853–869.

Mitchell, D., Laburn, H.P., Nijland, M.J.M., and Zurovsky, Y. 1987. Selective brain cooling and survival. *South African Journal of Science* **83**: 598–604.

Nielsen, B., Hales, J.R.S., Strange, S., Christensen, N.J., Warberg, J., and Saltin, B. 1993. Human circulatory and thermoregulatory adaptations with heat acclimation and exercise in a hot, dry environment. *Journal of Physiology* **46**: 467–485.

Ozgul, A., Tuljapurkar, S., Benton, T.G., Pemberton, J.M., Clutton-Brock, T.H., and Coulson, T. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* **325**: 464–467.

Pincebourde, S., Sanford, E., and Helmuth, B. 2009. An intertidal sea star adjusts thermal inertia to avoid extreme body temperatures. *American Naturalist* **174**: 890–897.

Reale, D., McAdam, A.G., Boutin, S., and Berteaux, D. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society B* **270**: 591–596.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., and Tegner, M.J. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29**: 436–459.

Willis, K.J., Bennett, K.D., Bhagwat, S.A., and Birks, H.J.B. 2010. Perspective: 4 deg C and beyond: what did this mean for biodiversity in the past? *Systematics and Biodiversity* **8**: 3–9.

Zervanos, S.M. and Hadley, N.F. 1973. Adaptational biology and energy relationships of the collared peccary (*Tayassu tajacu*). *Ecology* **54**: 759–774.

5.2 Amphibians

- Research suggests amphibian populations will suffer little, if any, harm from projected CO_2-induced global warming, and they may even benefit from it.

Still *et al*. (1999) and Pounds *et al*. (1999) published a pair of papers in *Nature* dealing with the cause of major decreases in frog and toad populations in the highland forests of Monteverde, Costa Rica. Those diebacks—in which 20 of 50 local species went extinct locally, or were extirpated—had occurred over the prior two decades, a period described by IPCC as having experienced unprecedented warming. Holmes (1999), in a popular science article describing the mystery's putative solution, wrote the authors of the two reports made "a convincing case blaming global climate change for these ecological events." Then came the study of Lawton *et al*. (2001), who challenged this hypothesis, presenting "an alternative mechanism [of] upwind deforestation of lowlands" as the cause of the amphibian decline.

Lawton *et al*. began their analysis by noting the trade winds that reach the Monteverde cloud-forest ecosystem flow across approximately 100 km of lowlands in the Rio San Juan basin, and that deforestation proceeded rapidly in the Costa Rican part of the basin over the past century. By 1992, only 18 percent of the original lowland forest remained. The four scientists noted this conversion of forest to pasture and farmland altered the properties of the air flowing across the landscape. The reduced evapotranspiration that followed deforestation, for example, decreased the moisture content of the air mass, and regional atmospheric model simulations suggested there should be reduced cloud formation and higher cloud bases over such deforested areas, which would cause there to be fewer and higher-based clouds than otherwise would have been the case when the surface-modified air moved into the higher Monteverde region.

Thus there were two competing theories from which to choose a candidate mechanism for the environmental changes that had altered the Monteverde cloud-forest ecosystem: one that was global in nature (CO_2-induced warming) and one that was local (upwind lowland deforestation). Lawton *et al*. resolved the matter. Noting the lowland forests north of the San Juan River in southeastern Nicaragua had remained largely intact—providing a striking contrast to the mostly deforested lands in neighboring Costa Rica—they used satellite imagery to show "deforested areas of Costa Rica's Caribbean lowlands remain relatively cloud-free when forested regions have well-developed dry season cumulus cloud fields," noting further the prominent zone of reduced cumulus cloudiness in Costa Rica "lies directly upwind of the Monteverde tropical montane cloud forest." Consequently, they demonstrated by direct observation the effects predicted by the theory they espoused did indeed occur in the real world, alongside a "control" area identical in all respects but for the deforestation that produced the cloud effects.

Two years later, Nair *et al*. (2003) demonstrated the reduced evapotranspiration that followed prior and ongoing deforestation upwind of the Monteverde cloud forest decreased the moisture contents of the air masses that ultimately reached the tropical preserve, and regional atmospheric model simulations they conducted indicated there also should have been reduced cloud formation and higher cloud bases over these areas than there were before the deforestation began. Three years later, Ray *et al*. (2006) extended the work of Lawton *et al*. and Nair *et al*. while exploring in more detail the impact of deforestation in Costa Rican lowland and premontane regions on orographic cloud formation during the dry season month of March.

Ray *et al.* used the mesoscale numerical model of Colorado State University's Regional Atmospheric Modeling System to derive high-spatial-resolution simulations "constrained by a variety of ground based and remotely sensed observations," in order to "examine the sensitivity of orographic cloud formation in the Monteverde region to three different land use scenarios in the adjacent lowland and premontane regions," namely, "pristine forests, current conditions and future deforestation."

This observation-constrained modeling work revealed historic "deforestation has decreased the cloud forest area covered with fog in the montane regions by around 5–13% and raised the orographic cloud bases by about 25–75 meters in the afternoon." In addition, they write, their work suggests "further deforestation in the lowland and premontane regions would lead to around [a] 15% decrease in the cloud forest area covered with fog and also raise the orographic cloud base heights by up to 125 meters in the afternoon."

As additional cases of amphibian mass mortality were reported throughout the world, Parmesan (2006) and Pounds *et al*. (2006) pointed accusing fingers at atmospheric CO_2, this time claiming global warming was promoting the spread of *Batrachochytrium dendrobatidis* (*Bd*), a non-hyphal zoosporic fungus that was the immediate cause of the amphibian declines and triggering outbreaks of chytridiomycosis via what came to be known as the climate-linked epidemic hypothesis (CLEH).

Investigating this concept in the Penalara Natural Park in the Sierra de Guadarrama of Central Spain, Bosch *et al*. (2007) looked for relationships between 20 meteorological variables and the development of chytridiomycosis infection in the area's amphibian populations, focusing on "two time periods according to the lack (1976–1996) or presence (1997–2003) of observed chytrid-related mortalities." This work revealed "a significant association between change in local climatic variables and the occurrence of chytridiomycosis," leading them to conclude, "rising temperature is linked to the occurrence of chytrid-related disease."

Being careful not to be too adamant about what their data implied, however, Bosch *et al*. note "associations between climate and disease do not necessarily imply causation." They also state, "chytrid-related declines are probably the result of a complex web of interaction, and the effects of climate will be conditional on other factors such as host density, amphibian community composition, microbial competitors and zooplankton predators, to name but a few." To disentangle this network and break it down into its key components, they say it will be necessary "to collect seasonal data on amphibian densities, contemporary and historical measurements of the prevalence and intensity of infection, seasonal mortalities, and fine-scale meteorological conditions from a range of sites that represent altitudinal clines," and conduct "molecular epidemiological analyses."

Lips *et al*. (2008) evaluated data pertaining to population declines of frogs of the genus *Atelopus*, as well as similar data from other amphibian species, in Lower Central America and Andean South America, based on their own work and that of others recorded in the scientific literature. They sought to determine whether the documented population declines were more indicative of an emerging infectious disease or a climate-change-driven infectious disease, noting in this regard, "both field studies on amphibians (Briggs *et al*., 2005; Lips *et al*., 2006) and on fungal population genetics (Morehouse *et al*., 2003; Morgan *et al*., 2007) strongly suggest that *Bd* is a newly introduced invasive pathogen."

Lips *et al*. say their findings reveal "a classical pattern of disease spread across native populations, at odds with the CLEH proposed by Pounds *et al*. (2006)." Emphasizing the latter's "analyses and re-analyses of data related to the CLEH all fail to support that hypothesis," Lips *et al*. conclude their own analyses support "a hypothesis that *Bd* is an introduced pathogen that spreads from its point of origin in a pattern typical of many emerging infectious diseases," reemphasizing that "the available data simply do not support the hypothesis that climate change has driven the spread of *Bd* in our study area."

Although the four U.S. scientists make it clear disease dynamics are "affected by micro- and macro-climatic variables," and "such synergistic effects likely act on *Bd* and amphibians," their work clearly shows the simplistic scenario represented by the CLEH—which posits, in their words, that "outbreaks of chytridiomycosis are triggered by a shrinking thermal envelope"—paints an unrealistic picture of the role of global climate change in the much-more-complicated setting of real-world biology, where many additional factors may play even greater roles in determining amphibians' well-being.

Laurance (2008) tested the hypothesis, put forward by Pounds *et al*. (2006), that "the dramatic, fungal pathogen-linked extinctions of numerous harlequin frogs (*Atelopus* spp.) in upland rainforests of South America mostly occurred immediately following exceptionally warm years, implicating global warming as a likely trigger for these extinct-tions." He used "temperature data for eastern Australia, where at least 14 upland-rainforest frog species [had] also experienced extinctions or striking population declines attributed to the same fungal pathogen, and where temperatures [had] also risen significantly in recent decades." This work provided "little direct support for the warm-year hypothesis of Pounds *et al*." Instead, Laurance "found stronger support for a modified version of the warm-year hypothesis," where frog declines were likely to occur only following three consecutive years of unusually warm weather; and these declines were observed "only at tropical latitudes, where rising minimum temperatures were greatest."

Laurance states many researchers "remain unconvinced that ongoing disease-linked amphibian declines are being widely instigated by rising global temperatures or associated climatic variables, as proposed by Pounds *et al*." He notes, for example, "chytrid-linked amphibian declines have been documented on several continents and at varying times" and to date, "no single environmental stressor has been identified that can easily account for these numerous population crashes." He continues, "it stretches plausibility to argue that the chytrid pathogen is simply an opportunistic, endemic micro-parasite that has suddenly begun causing catastrophic species declines as a consequence of contemporary global warming."

Rohr *et al*. (2008) provided a rigorous test of the two competing hypotheses by evaluating "(1) whether cloud cover, temperature convergence, and predicted temperature-dependent *Bd* growth are significant positive predictors of amphibian extinctions in the genus *Atelopus* and (2) whether spatial structure in the timing of these extinctions can be detected without making assumptions about the location, timing, or number of *Bd* emergences." The five scientists report, "almost all of our findings are contrary to the predictions of the chytrid-thermal-optimum hypothesis," even noting "not all of the data presented by Pounds *et al*. (2006) are consistent with the chytrid-thermal-optimum hypothesis." They write, "there was no regional temperature convergence in the 1980s when extinctions were increasing, and that convergence only occurred in the 1990s when *Atelopus spp.* extinctions were decreasing, opposite to the conclusions of Pounds *et al*. (2006) and the chytrid-thermal-optimum hypothesis." On the other hand, they report, "there is a spatial structure to the timing of *Atelopus spp.* extinctions but that the cause of this structure remains equivocal, emphasizing the need for further molecular characterization of *Bd*."

Alford *et al*. (2009) quantified four movement characteristics of three groups of radio-tracked cane toads (*Bufo marinus*) at three places in Australia: a location where the toads had been established for some 50 years at the time of their sampling; a location where the first toads arrived about six months before sampling began in 1992 and 1993; and a location where sampling occurred for a period of 13 months, starting at the time of the toads' initial arrival in 2005. For all of the movement parameters they studied, "toads from the current invasion front differed dramatically from animals in the long-established population, while toads from the earlier invasion front were intermediate between these extremes."

The five researchers report "cane toads are now spreading through tropical Australia about 5-fold faster than in the early years of toad invasion." They state "the current invasion-front animals achieved these [high invasion speeds] by rarely reusing the same retreat site two days in succession, by travelling further each night when they did move, and by moving along straighter paths." Therefore, as they describe it, the toad invasion front "advances much more rapidly than would occur if the toads retained ancestral behaviors (less frequent relocation, with shorter movements, and fewer toads using straight paths)." And because "invasion-front toads in 1992 were more dispersive than origin-population toads in the same year, but … invasion-front toads have continued to evolve heightened dispersal ability and dispersed even more effectively in 2005 than they did in 1992," these observations suggest "as long as toads continue to invade suitable new habitat, dispersal ability will be selected upwards."

Alford *et al.* write the rapidity and magnitude of the shifts in cane toads "are truly remarkable," having been accomplished in only 50 generations (about 70 years), and they state "such a major shift over such a brief period testifies to the intense selective pressure exerted on frontal populations of range-shifting species." This development, in their words, "not only has implications for our understanding of the rates of invasion by non-native species, but also for the rate of range-shift in native taxa affected by climate change." The capacity for species to respond to changing environments may be underestimated when it is based on observations of individuals at the core of their range.

Further exploring this issue, Bustamante *et al.* (2010) exposed groups of Panamanian golden frogs (*Atelopus zeteki*) to varying dosages of zoospores of *Bd* and different temperatures and hydric environments to ascertain whether the frogs were susceptible to the pathogen and, if so, how environmental factors might affect the frogs' survival. These operations indicated "frogs exposed to a dosage of 100 *Bd* zoospores survived significantly longer than those that had been exposed to 10^4 or 10^6 zoospores." They also found "exposed frogs housed at 23°C survived significantly longer than those that were housed at 17°C," and "exposed frogs held in dry conditions survived significantly longer than those in wet conditions."

Since their study was conducted in a laboratory, Bustamante *et al.* acknowledge their results "do not directly test hypotheses about the relation between climate change and the decline of the frogs in the field," but they note their data nevertheless "do not support the contention that rising global temperatures are necessary to cause the death of amphibians infected with this pathogen, because the pathogen was just as lethal at 17°C as at 23°C, and frogs at the warmer temperature lived significantly longer than those at the cooler one." This result is inconsistent with the climate-linked epidemic hypothesis of Pounds *et al.* (2006)—and Bustamante was a coauthor of that paper.

Anchukaitis and Evans (2010) state "widespread amphibian extinctions in the mountains of the American tropics have been blamed on the interaction of anthropogenic climate change and a lethal pathogen." However, they note, "limited meteorological records make it difficult to conclude whether current climate conditions at these sites are actually exceptional in the context of natural variability," casting doubt once again on the contention modern global warming was the primary culprit in the demise of the Monteverde golden toad (*Bufo periglenes*).

Anchukaitis and Evans developed annual proxy records of hydroclimatic variability over the past century within the Monteverde Cloud Forest of Costa Rica, based on measurements of the stable oxygen isotope ratio ($\delta^{18}O$) made on trees lacking annual rings, as described in the papers of Evans and Schrag (2004) and Anchukaitis *et al.* (2008). That work revealed, "contrary to interpretations of the short instrumental record (Pounds *et al.*, 1999), no long-term trend in dry season hydroclimatology can be inferred from our $\delta^{18}O$ time series at Monteverde (1900–2002)." Instead, they found, "variability at the interannual scale dominates the isotope signal, particularly during the period of increased ENSO variance since the late 1960s," and they add, "there is no evidence of a trend associated with global warming." They emphasize "the extinction of the Monteverde golden toad appears to have coincided with an exceptionally dry interval caused by the 1986–1987 El Niño event," which they describe as "one of the longest driest periods in the last 100 years," based on their $\delta^{18}O$ chronology. In addition, they report, there is currently no consensus on how anthropogenic climate change might influence the El Niño Southern Oscillation, and "ENSO anomalies in the most recent decades are not beyond the range of natural variability during the instrumental period (Rajagopalan *et al*., 1997)."

Anchukaitis and Evans conclude their analysis suggests "the cause of the specific and well-documented extinction of the Monteverde golden toad was the combination of the abnormally strong ENSO-forced dryness and the lethality of the introduced chytrid fungus, but was not directly mediated by anthropogenic temperature trends, a finding from paleoclimatology that is in agreement with statistical reanalysis (Rohr *et al*., 2008; Lips *et al*., 2008) of the 'climate-linked epidemic hypothesis'." The latter two analyses also had revealed the chytrid-thermal-optimum hypothesis, as it alternatively has been described, to be devoid of merit. Consequently, even in the case of struggling amphibians, there are no real-world data indicating global warming is, or ever will be, responsible for driving them to extinction.

Noting "phenotypic plasticity, the capacity of a genotype to produce distinct phenotypes under different environmental conditions, is a common and powerful method of adaptation in nature," Orizaola and Laurila (2009) investigated variations in temperature-induced plasticity in larval life-history traits among populations of an isolated "meta-population" of pool frogs (*Rana lessonae*) in Central Sweden. They exposed larvae from three closely located populations to two temperatures (20 and 25°C) in the laboratory and then documented their growth and development responses at the two different temperatures. According to the two Swedish researchers, the results indicated "in general, larvae exposed to warmer temperature experienced higher survival and metamorphosed faster." They also found "differences among the populations in both trait mean values and in the plastic responses," and "among-family variation within populations was found in growth rate and time to metamorphosis, as well as in plasticity, suggesting that these traits have a capacity to evolve."

Orizaola and Laurila also report finding "strong population differentiation at a microgeographic scale in life-history characteristics and temperature-induced plasticity in [the] isolated amphibian meta-population." They report, in spite of "the near absence of molecular genetic variation within [the] meta-population, our study detected strong variation in trait means and plastic responses both among and within populations, possibly suggesting that natural selection is shaping life-history traits of the local populations." This phenomenon may be preparing pool frogs for still further temperature increases by providing them "ample phenotypic variation" to deal with a potentially warming environment.

Skelly *et al*. (2007) critique the use of the "climate-envelope approach" to predict extinctions, citing as their primary reason for doing so the fact that this approach "implicitly assumes that species cannot evolve in response to changing climate," when in numerous cases they can do so effectively. Noting "many examples of contemporary evolution in response to climate change exist," the group of seven scientists from the United States, Canada, and Australia report, "in less than 40 years, populations of the frog *Rana sylvatica* have undergone localized evolution in thermal tolerance (Skelly and Freidenburg, 2000), temperature-specific development rate (Skelly, 2004), and thermal preference (Freidenburg and Skelly, 2004)," and "laboratory studies of insects show that thermal tolerance can change markedly after as few as 10 generations (Good, 1993)." Since "studies of microevolution in plants show substantial trait evolution in response to climate manipulations (Bone and Farres, 2001)," they state, "collectively, these findings show that genetic variation for traits related to thermal performance is common and evolutionary response to changing climate has been the typical finding in experimental and observational studies (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001)."

Although evolution obviously will be slower among long-lived trees and large mammals, where long generation times are the norm, Skelly *et al*. say the case for rapid evolutionary responses among many other species "has grown much stronger (e.g., Stockwell *et al*., 2003; Berteaux *et al*., 2004; Hariston *et al*., 2005; Bradshaw and Holzapfel, 2006; Schwartz *et al*., 2006; Urban *et al*., 2007)." They write, "on the basis of the present knowledge of genetic variation in performance traits and species' capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as [with] other environmental changes (e.g., Grant and Grant, 2002; Stockwell *et al*., 2003; Balanya *et al*., 2006; Jump *et al*., 2006; Pelletier *et al*., 2007)." Frogs, as noted above, are no exception to this general rule.

Catenazzi *et al*. (2010) write, "climate change has been proposed as a driver of amphibian declines," but they note this hypothesis has been largely displaced by a competing theory built around the observation that the pathogen *Bd* has been "associated with amphibian declines throughout the world (Berger *et al*., 1998; Briggs *et al*., 2005; Lips *et al*., 2006)" in a manner indicating an introduced and subsequently spreading epidemic disease. They studied the recent collapse in anuran species richness and abundance in the Upper Manu National Park of Southeastern Peru.

Catenazzi *et al*. surveyed frogs in the Peruvian Andes in montane forests along a steep elevation gradient (1,200–3,700 m), using visual encounter surveys to sample stream-dwelling and arboreal species and leaf-litter plots to sample terrestrial-breeding species, in order to compare species richness and abundance among the wet seasons of 1999, 2008, and 2009. The U.S. and Peruvian researchers found there had been "a dramatic decline in species richness of amphibians"—a mean decline of 38% in the area of their study over the 10-year period—with stream-breeding species being "disproportionally represented among the missing taxa in 2008 and 2009." They state this result "is consistent with observations in other Neotropical (Lips, 1998) and Australian (Laurance *et al*., 1996; Williams and Hero, 1998) sites where the species richness and abundance of frogs have declined or frogs have been extirpated," noting "declines in these other areas are unequivocally linked to the introduction of *Bd* to naïve amphibian populations (Berger *et al*., 1998; Lips *et al*., 2006)."

Their results show "the geographic and elevational distribution of *Bd* extends to southern Peru," noting this extent is consistent with Lips *et al*.'s (2008) hypothesis of *Bd* spreading southward in a wave from a *Bd* introduction site in southwestern Ecuador. Alternatively, they suggest the *Bd* introduction site could be Cusco, which "receives more visitors than any other tourist destination in Peru." And, noting "frogs originating from many streams, ponds and lakes of the Bolivian-Peruvian Altiplano are sold live in the city for human consumption," they suggest this frog trade "could facilitate the spread of *Bd* over large areas in southern Peru."

Given the above observations, plus the fact that "*Bd* occurs in a wide range of land-cover types and microclimates," Catenazzi *et al*. say "it is unclear how climate change would increase the rate of spread or the virulence of such an opportunistic pathogen in frog populations." They conclude it hasn't. Despite decades of research and a general belief that the link between *Bd* arrival and population decline is well-resolved in regions such as Australia, there is no evidence the arrival of *Bd* coincided with amphibian population decline, because the present data are not adequate to determine whether *Bd* was present prior to initial sampling (Phillips *et al*., 2012). Phillips *et al*. (2012) conclude, "more generally, our discovery of a complete lack of evidence linking the arrival of *Bd* and the timing of population declines in north-eastern Australia points to the alarming ease with which paradigms can become established even in the absence of critical tests of those paradigms." An alternative explanation for the upturn in recorded fungal infections is not global warming, but human-mediated intensification of fungal disease dispersal, caused by transportation and modification of natural environments (Fisher *et al*., 2012).

In a nine-year study conducted in the Little Rock Creek Basin, located within the Selway-Bitterroot Wilderness just south of Hamilton, Montana (USA), McCaffery and Maxell (2010) "evaluated relationships among local climate variables, annual survival and fecundity, and population growth rates" in "a high-elevation population of a temperate pond-breeding frog species, the Columbia spotted frog (*Rana luteiventris*)." They monitored all life stages of the species and related the resulting demographic data to climate data collected at a nearby weather station. The two University of Montana biologists report "parameters that describe winter severity were negatively correlated with survival, transition, and breeding probabilities in this high-elevation *R. luteiventris* population," and there was "an increase in survival and breeding probability as severity of winter decreased."

"Contrary to much of what has been discussed in the literature," McCaffery and Maxell write, "these results suggest that under certain circumstances, a warming climate may be helpful to some amphibian populations, particularly those that live in harsh conditions at the edge of their thermal tolerances." As a case in point, they state their results "unambiguously demonstrate that earlier ending winters with lower snowpack in this system lead to higher survival rates, higher probabilities of breeding, and higher population viability." Thus, they conclude, "more generally, amphibians and other ectotherms inhabiting alpine or boreal habitats at or near their thermal ecological limits may benefit from the milder winters provided by a warming climate."

Additional studies show other real-world data that refute the contention global warming is driving amphibians to extinction. Berger *et al*. (2004), for example, found lower temperatures enhanced the development of chytridiomycosis in a study of eastern Australian frogs, and Seimon *et al*. (2007) determined glacial recession in the Peruvian Andes has been creating new amphibian habitats at recently deglaciated sites. Woodhams *et al*. (2010) note "amphibian skin peptides are one important defense against chytridiomycosis," and examining "the population-level variation in this innate immune defense [is important] to understand its relationship with disease dynamics." Briggs *et al*. (2010) note some amphibians with chytridiomycosis "develop only minor infections and suffer little or no negative effects." And Zukerman (2010) reports some of the most devastated populations of Australia's barred river frogs (*Mixophyes esiteratus*), tusked-frogs (*Adelotus sp.*), and several tree frog species (*Litoria sp.*), once thought to have been wiped out by the fungus, are now showing strong signs of recovery.

All in all, the above studies suggest amphibian populations will suffer little, if any, harm from projected CO_2-induced global warming, and they may even benefit from it.

References

Alford, R.A., Brown, G.P., Schwarzkopf, L, Phillips, B.L., and Shine, R. 2009. Comparisons through time and space suggest rapid evolution of dispersal behavior in an invasive species. *Wildlife Research* **36**: 23–28.

Anchukaitis, K.J. and Evans, M.N. 2010. Tropical cloud forest climate variability and the demise of the Monteverde golden toad. *Proceedings of the National Academy of Sciences, USA* **107**: 5036–5040.

Anchukaitis, K.J., Evans, M.N., Wheelwright, N.T., and Schrag, D.P. 2008. Stable isotope chronology and climate signal in neotropical montane cloud forest trees. *Journal of Geophysical Research* **113**: G03030.

Balanya, J., Oller, J.M., Huey, R.B., Gilchrist, G.W., and Serra, L. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science* **313**: 1773–1775.

Berger, L, Speare, R, Hines, H.B., Marantelli, G., Hyatt, A.D., McDonald, K.R., Skerratt, L.F., Olsen, V., Clarke, J.M., Gillespie, G., Mahony, M., Sheppard, N., Williams, C., and Tyler, M.J. 2004. Effect of season and temperature on mortality in amphibians due to chytridiomycosis. *Australian Veterinary Journal* **82**: 432–439.

Berger, L., Speare, R., Daszak, P., Green, D.E., Cunningham, A.A., Goggin, C.L., Slocombe, R., Ragan, M.A., Hyatt, A.D., McDonald, K.R., Hine, H.B., Lips, K.R., Marantelli, G., and Parkes, H. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rainforests of Australia and Central America. *Proceedings of the National Academy of Sciences USA* **95**: 9031–9036.

Berteaux, D., Reale, D., McAdam, A.G., and Boutin, S. 2004. Keeping pace with fast climatic change: can arctic life count on evolution? *Integrative and Comparative Biology* **44**: 140–151.

Bone, E. and Farres, A. 2001. Trends and rates of microevolution in plants. *Genetica* **112–113**: 165–182.

Bosch, J., Carrascal, L.M., Duran, L., Walker, S., and Fisher, M.C. 2007. Climate change and outbreaks of amphibian chytridiomycosis in a montane area of Central Spain: Is there a link? *Proceedings of the Royal Society B* **274**: 253–260.

Bradshaw, W.E. and Holzapfel, C.M. 2006. Evolutionary response to rapid climate change. *Science* **312**: 1477–1478.

Briggs, C.J., Knapp, R.A., and Vredenburg, V.T. 2010. Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. *Proceedings of the National Academy of Sciences, USA* **107**: 9695–9700.

Briggs, C.J., Vredenburg, V., Knapp, R.A., and Rachowicz, L.J. 2005. Investigating the population-level effects of chytridiomycosis, an emerging infectious disease of amphibians. *Ecology* **86**: 3149–3159.

Bustamante, H.M., Livo, L.J., and Carey, C. 2010. Effects of temperature and hydric environment on survival of the Panamanian Golden Frog infected with a pathogenic chytrid fungus. *Integrative Zoology* **5**: 143–153.

Catenazzi, A., Lehr, E., Rodriguez, L.O., and Vredenburg, V.T. 2010. *Batrachochytrium dendrobatidis* and the collapse of anuran species richness and abundance in the Upper Manu National Park, southeastern Peru. *Conservation Biology* **25**: 382–391.

Evans, M.N. and Schrag, D.P. 2004. A stable isotope-based approach to tropical dendroclimatology. *Geochimica et Cosmochimica Acta* **68**: 3295–3305.

Fisher, M.C., Briggs, C.J., Brownstein, J.S., Madoff, L.C., McCraw, S.L., and Gurr, S.J. 2012. Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**: 186–194.

Freidenburg, L.K. and Skelly, D.K. 2004. Microgeographical variation in thermal preference by an amphibian. *Ecology Letters* **7**: 369–373.

Good, D.S. 1993. Evolution of behaviors in *Drosophila melanogaster* in high-temperatures: genetic and environmental effects. *Journal of Insect Physiology* **39**: 537–544.

Grant, P.R. and Grant, B.R. 2002 . Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707–711.

Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T., and Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* **8**: 1114–1127.

Hendry, A.P. and Kinnison, M.T. 1999. The pace of modern life: measuring rates of contemporary micro-evolution. *Evolution* **53**: 637–653.

Holmes, R. 1999. Heads in the clouds. *New Scientist* (8 May): 32–36.

Jump, A.S., Hunt, J.M., Martinez-Izquierdo, J.A., and Peñuelas, J. 2006. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology* **15**: 3469–3480.

Kinnison, M.T. and Hendry, A.P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**: 145–164.

Laurance, W.F. 2008. Global warming and amphibian extinctions in eastern Australia. *Austral Ecology* **33**: 1–9.

Laurance, W.F., McDonald, K.R., and Speare, R. 1996. Epidemic disease and the catastrophic decline of Australian rain forest frogs. *Conservation Biology* **10**: 406–413.

Lawton, R.O., Nair, U.S., Pielke Sr., R.A., and Welch, R.M. 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* **294**: 584–587.

Lips, K.R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* **12**: 106–117.

Lips, K.R., Brem, F., Brenes, R., Reeve, J.D., Alford, R.A., Voyles, J., Carey, C., Livo, L., Pessier, A.P., and Collins, J.P. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences USA* **103**: 3165–3170.

Lips, K.R., Diffendorfer, J., Mendelson III, J.R., and Sears, M.W. 2008. Riding the wave: reconciling the roles of disease and climate change in amphibian declines. *PLoS (Public Library of Science) Biology* **6**(3): e72. doi:10.1371/journal.pbio.0060072.

McCaffery, R.M. and Maxell, B.A. 2010. Decreased winter severity increases viability of a montane frog population. *Proceedings of the National Academy of Sciences, USA* **107**: 8644–8649.

Morehouse, E.A., James, T.Y., Ganley, A.R.D., Vilgalys, R., Berger, L., Murphy, P.J., and Longcore, J.E. 2003. Multilocus sequence typing suggests the chytrid pathogen of amphibians is a recently emerged clone. *Molecular Ecology* **12**: 395–403.

Morgan, J.A.T., Vredenburg, V., Rachowicz, L.J., Knapp, R.A., Stice, M.J., Tunstall, T., Bingham, R.E., Parker, J.M., Longcore, J.E., Moritz, C., Briggs, C.J., and Taylor, J.W. 2007. Enigmatic amphibian declines and emerging infectious disease: population genetics of the frog-killing fungus *Batrachochytrium dendrobatidis*. *Proceedings of the National Academy of Sciences USA* **104**: 13,845–13,850.

Nair, U.S., Lawton, R.O., Welch, R.M., and Pielke Sr., R.A. 2003. Impact of land use on Costa Rican tropical montane cloud forests: sensitivity of cumulus cloud field characteristics to lowland deforestation. *Journal of Geophysical Research* **108**: 10.1029/2001JD001135.

Orizaola, G. and Laurila, A. 2009. Microgeographic variation in temperature-induced plasticity in an isolated amphibian metapopulation. *Evolutionary Ecology* **23**: 979–991.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**: 637–669.

Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S., and Coulson, T. 2007. The evolutionary demography of ecological change: linking trait variation and population growth. *Science* **315**: 1571–1574.

Phillips, B.L., Puschendorf, R., VanDerWal, J., and Alford, R.A. 2012. There is no evidence for a temporal link between pathogen arrival and frog extinctions in North-Eastern Australia. *PloS ONE* **7**: e52502.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sanchez-Azofeifa, G.A., Still, C.J., and Young, B.E. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**: 161–167.

Pounds, J.A., Fogden, M.P.L., and Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature* **398**: 611–615.

Rajagopalan, B., Lall, U., and Cane, M.A. 1997. Anomalous ENSO occurrences: An alternate view. *Journal of Climate* **10**: 2351–2357.

Ray, D.K., Nair, U.S., Lawton, R.O., Welch, R.M., and Pielke Sr., R.A. 2006. Impact of land use on Costa Rican tropical montane cloud forests: Sensitivity of orographic cloud formation to deforestation in the plains. *Journal of Geophysical Research* **111**: 10.1029/2005JD006096.

Rohr, J.R., Raffel, T.R., Romansic, J.M., McCallum, H., and Hudson, P.J. 2008. Evaluating the links between climate, disease spread, and amphibian declines. *Proceedings of the National Academy of Sciences USA* **105**: 17,436–17,441.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N., and O'Connor, R.J. 2006. Predicting extinctions as a result of climate change. *Ecology* **87**: 1611–1615.

Seimon, T.A., Seimon, A., Daszak, P., Halloy, S.R.P., Schloegel, L.M., Aguilar, C.A., Sowell, P., Hyatt, A.D., Konecky, B., and Simmons, J.E. 2007. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology* **13**: 288–299.

Skelly, D.K. 2004. Microgeographic countergradient variation in the wood frog, *Rana sylvatica*. *Evolution* **58**: 160–165.

Skelly, D.K. and Freidenburg, L.K. 2000. Effects of beaver on the thermal biology of an amphibian. *Ecology Letters* **3**: 483–486.

Skelly, D.K., Joseph, L.N., Possingham, H.P., Freidenburg, L.K., Farrugia, T.J., Kinnison, M.T., and Hendry, A.P. 2007. Evolutionary responses to climate change. *Conservation Biology* **21**: 1353–1355.

Still, C.J., Foster, P.N., and Schneider, S.H. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* **398**: 608–610.

Stockwell, C.A., Hendry, A.P., and Kinnison, M.T. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* **18**: 94–101.

Urban, M.C., Philips, B., Skelly, D.K., and Shine, R. 2007. The cane toad's (*Chaunus* [*Bufo*] *marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society of London B*: 10.1098/rspb.2007.0114.

Williams, S.E. and Hero, J.-M. 1998. Rainforest frogs of the Australian wet tropics: Guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society of London B* **265**: 597–602.

Woodhams, D.C., Kenyon, N., Bell, S.C., Alford, R.A., Chen, S., Billheimer, D., Shyr, Y., and Rollins-Smith, L.A. 2010. Adaptations of skin peptide defenses and possible response to the amphibian chytrid fungus in populations of Australian green-eyed treefrogs, *Litoria genimaculata*. *Diversity and Distributions* **16**: 703–712.

Zukerman, W. 2010. Fungus out! The frog resistance is here. *New Scientist* **2790** (10 December) http://www.newscientist.com/article/mg20827903.500-fungus-out-the-frog-resistance-is-here.html.

5.3 Arthropods

- Enhanced plant productivity driven by elevated levels of atmospheric CO_2 tends to support greater abundance of soil microarthropods.

Arthropods are invertebrate animals composed of a segmented body, jointed appendages, and an exoskeleton. A handful of studies have examined how these animals may be affected by Earth's rising atmospheric CO_2 concentration. One of the early emerging hypotheses is that if the productivity of the plants at the base of a food chain is enhanced by the aerial fertilization effect of extra CO_2, they could be expected to support greater animal populations at the other end, including arthropods.

Siemann (1998) studied the effects of both short- and long-term nitrogen fertilization on plant productivity and arthropod communities in an upland grass ecosystem in Minnesota. In both situations, plant productivity was enhanced; arthropods responded by increasing both their numbers and the number of their species, suggesting if atmospheric CO_2 enrichment tends to enhance plant productivity, it also will increase arthropod numbers and ecosystem species richness.

Rillig *et al.* (1999) confirmed this conclusion. In serpentine and sandstone grasslands in California, they found an approximate doubling of the air's CO_2 content significantly enhanced the masses of fungi living in the soil, resulting in large increases in the numbers of fungal-feeding microarthropods (108 and 39% increases in the sandstone and serpentine grasslands, respectively). Likewise, in a study of poplar tree cuttings in Michigan, Lussenhop *et al.* (1998) observed the fine roots of the trees in their approximately doubled CO_2 treatment supported twice as many microarthropods as the fine roots of the trees growing in ambient air. And in a multiple-microcosm study of mini-terrestrial ecosystems conducted in the United Kingdom, Jones *et al.* (1998) found a 53% increase in atmospheric CO_2 concentration produced an enhanced soil fungal population that supported 52% more soil microarthropods.

Sanders *et al.* (2004) studied effects of atmospheric CO_2 enrichment on the plant and arthropod communities of the understory of a closed-canopy sweetgum plantation (which reduces the light available to the understory between 70 and 95% during the growing season) in a study where the air's CO_2 content was increased by approximately 48%. They report total arthropod abundance did not differ between ambient and elevated CO_2 plots, nor did the abundances of detritivores, omnivores, or parasitoids. They conclude, "changes in plant community composition did not translate into differences in arthropod communities."

Sticht *et al.* (2006) investigated how elevated atmospheric CO_2 concentration (550 ppm as opposed to the ambient concentration of about 380 ppm) delivered via free-air CO_2 enrichment (FACE) technology interacted with two levels of nitrogen (N) fertilization (normal N and half-normal N) to influence the abundance and diversity of collembolans in a field planted to winter wheat at the Federal Agricultural Research Centre in Braunschweig, Lower Saxony, Germany, where the 45% increase in the air's CO_2 content increased aboveground wheat biomass production by approximately 14%. Invertebrate communities in general, and collembolans in particular, play an important role in maintaining soil fertility, as the authors say they "participate in organic matter decomposition and can stimulate nutrient mobilization and plant nutrient uptake (e.g. Wardle *et al*., 2004)."

The German researchers found "CO_2 enrichment enhanced the collembolan abundance by 58% under conventional N fertilization and by 100% under restricted N supply," and "under FACE conditions the collembolan diversity was higher (28 species) compared to ambient air conditions (23 species)." Sticht *et al*. conclude, "an increase in collembolan abundance and diversity can be expected as a result of enhanced quantity and changed quality of organic matter input into the soil associated with elevated atmospheric CO_2." And since this phenomenon "can stimulate nutrient mobilization and plant nutrient uptake," as they note, it is especially encouraging that its relative strength was greatest when nitrogen was most limiting in their experiment.

Enhanced plant productivity driven by elevated levels of atmospheric CO_2 tends to support greater abundance of soil microarthropods.

References

Jones, T.H., Thompson, L.J., Lawton, J.H., Bezemer, T.M., Bardgett, R.D., Blackburn, T.M., Bruce, K.D., Cannon, P.F., Hall, G.S., Hartley, S.E., Howson, G., Jones, C.G., Kampichler, C., Kandeler, E., and Ritchie, D.A. 1998. Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science* **280**: 441–443.

Lussenhop, J., Treonis, A., Curtis, P.S., Teeri, J.A., and Vogel, C.S. 1998. Response of soil biota to elevated atmospheric CO_2 in poplar model systems. *Oecologia* **113**: 247–251.

Rillig, M.C., Field, C.B., and Allen, M.F. 1999. Soil biota responses to long-term atmospheric CO_2 enrichment in two California annual grasslands. *Oecologia* **119**: 572–577.

Sanders, N.J., Belote, R.T., and Weltzin, J.F. 2004. Multitriphic effects of elevated atmospheric CO_2 on understory plant and arthropod communities. *Environmental Entomology* **33**: 1609–1616.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* **79**: 2057–2070.

Sticht, C., Schrader, S., Giesemann, A., and Weigel, H.-J. 2006. Effects of elevated atmospheric CO_2 and N fertilization on abundance, diversity and C-isotopic signature of collembolan communities in arable soil. *Applied Soil Ecology* **34**: 219–229.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., and Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629–1633.

5.4 Birds

- Although some changes in bird populations and their habitat areas have been documented in the literature, linking such changes to CO_2-induced global warming remains elusive. Also, when there have been changes, they often are positive, as many species have adapted and are thriving in response to rising temperatures of the modern era.

One of the great concerns associated with predictions of CO_2-induced global warming is the claim that the number of birds and their habitat areas will decline. Some estimates go so far as to suggest global warming could result in the extinction of several bird species. In the following subsections, such claims are examined through peer-reviewed studies conducted on birds in an effort to see how they have responded to what IPCC has called the unprecedented rise in atmospheric CO_2 and temperature of the late-twentieth and early twenty-first century.

Although some changes in bird populations and their habitat areas have been documented in the literature, linking such changes to CO_2-induced global warming remains elusive. Also, when there have been changes, they often are positive, as many species have adapted and are thriving in response to rising temperatures of the modern era.

5.4.1 Population Dynamics

How has modern warming impacted bird population dynamics? Several researchers have addressed this question for various bird species in many locations across the planet. This section summarizes what they have learned.

Schmidt *et al*. (2009) employed Bayesian hierarchical models to estimate the population size of trumpeter swans (*Cygnus buccinator*) based on aerial survey data collected by the U.S. Fish and Wildlife

Service throughout all known nesting habitats in the state of Alaska. These data collections were first made in 1968 and subsequently in 1975 and every five years thereafter through 2005. The results indicated "adult swan populations in Alaska increased at an average rate of 5.9% annually and cygnet production increased at 5.3% annually." The authors also found "cygnet production exhibited higher rates of increase at higher latitudes in later years," which they opine was "a response to warmer spring temperatures." The five researchers conclude, "trumpeter swan populations are increasing in Alaska, especially at northern latitudes," stating their study "represents one of the first to demonstrate a shift in breeding range of a bird possibly due to climate change." Hence, "for trumpeter swans, it appears that breeding range limits in Alaska have expanded" in response to the warming experienced there between 1968 and 2005.

White *et al.* (2011) analyzed how Great Cormorant numbers varied over the years in response to changes in sea surface temperature (SST) in the vicinity of Greenland's Disko Bay, using data obtained from the U.S. National Climate Data Center plus data for the number of breeding pairs of Great Cormorants in Disko Bay and adjacent areas they obtained from aerial and boat-based surveys described by Boertmann *et al.* (1996) and Boertmann (2006) for the period 1946–2005. According to the six scientists, population change rates of Great Cormorant colonies in the vicinity of Disko Bay "were significantly positively correlated with mean winter SST," adding, "populations increased during relatively warm years and decreased during relatively cold years," while also noting "the highest rates of population change correspond with periods of relatively high SST in recent years and during the 1960s." White *et al.* conclude, "taken together, the positive relationship between rates of population change in Cormorants and SST, the likely positive impact of Arctic warming on the preferred prey species of Cormorants, and the flexible food preferences and foraging strategies of Cormorants suggest that Cormorants are likely to benefit from a warming Arctic."

Grandgeorge *et al.* (2008) analyzed population sizes and phylogenetic and spatial structures of British and Irish seabirds based on "(1) presence or absence of the seabird species in the different counties of Britain and Ireland between 1875 to 1900 and 1968 to 1972, (2) seabird breeding censuses of Britain and Ireland from 1969 to 1970, 1985 to 1988 and 1998 to 2002, (3) at-sea abundance and distribution surveys of seabirds in the North Sea from 1980 to 1985 and 1990 to 1995, and (4) a bioenergetics model to estimate energy expenditures for 40 seabird species." With respect to population dynamics, their work revealed total seabird numbers "increased at an average rate of 1% per annum between 1969 and 2002, with a related increase of 115% in predicted total seabird predation." Also, "between 1875 and 1972 no seabird species was lost and there was an overall expansion in breeding range of the seabird population of Britain and Ireland, with the number of counties occupied increasing from 31 to 47."

The six scientists conclude, "the seabird community of Britain and Ireland has been remarkably resilient to environmental change in the 20th century." In fact, it "prospered during the 20th century" and "significantly raised ocean temperatures in the North Sea (Beaugrand, 2004)" may even have "created more favorable environmental conditions for some seabird species," citing Thompson (2006).

Lemoine *et al.* (2007) used data from the *Breeding Bird Atlas* of Lake Constance, which borders Germany, Switzerland, and Austria, to analyze the impact of land-use and climate changes on the region's abundance of Central European birds between the periods 1980–1981 and 1990–1992, and between 1990–1992 and 2000–2002. They found "the total number of [bird] species in the Lake Constance region increased from 141 species in 1980 to 146 species in 1990 and to 154 species in 2000," and "winter temperatures increased by 2.71°C and spring temperatures increased by 2.12°C over the 23 years from the first to the last census." These and other data led them to conclude, "increases in temperature appear to have allowed increases in abundance of species whose range centers were located in southern Europe and that may have been limited by low winter or spring temperature." In addition, they report "the impact of climate change on bird populations increased in importance between 1990 and 2000 and is now more significant than any other tested factor."

Seoane and Carrascal (2008) write, "it has been hypothesized that species preferring low environmental temperatures, which inhabit cooler habitats or areas, would be negatively affected by global warming as a consequence of the widely accepted increase of temperature during the last two decades." They note "this effect is assumed to be more intense at higher latitudes and altitudes because these areas seem to be changing more rapidly." They devised a study "to assess whether population changes agree with what could be expected under global warming (a decrease in species typical of cooler environments)," focusing on birds. Working in the Spanish portion of the Iberian Peninsula in the southwestern part of the Mediterranean Basin, the two researchers determined breeding population changes for 57 species of common passerine birds between 1996 and 2004 in areas without any apparent land-use changes. This work revealed, "one-half of the study species showed significant increasing recent trends despite the public concern that bird populations are generally decreasing," and "only one-tenth showed a significant decrease."

Seoane and Carrascal state, "the coherent pattern in population trends we found disagrees with the proposed detrimental effect of global warming on bird populations of western Europe." They are not the only ones to have reached this conclusion. They note, for example, "one-half of terrestrial passerine birds in the United Kingdom exhibited increasing recent trends in a very similar time period (1994–2004)," citing Raven *et al*. (2005), and they explain, "there is also a marked consistency between the observed increasing trends for forest and open woodland species in the Iberian Peninsula and at more northern European latitudes in the same recent years," citing Gregory *et al*. (2005). Likewise, they write, "Julliard *et al*. (2004a), working with 77 common bird species in France, found that species with large ecological breadth showed a tendency to increase their numbers throughout the analyzed period."

Seoane and Carrascal state, "bird species that inhabit dense wooded habitats show striking patterns of population increase throughout time." Noting "this is also the case with those bird species mainly distributed across central and northern Europe that reach their southern boundary limits in the north of the Iberian Peninsula," they theorize "these short- to medium-term population increases may be due to concomitant increases in productivity." In support of this notion they cite Julliard *et al*. (2004b) and the empirical observations of Myneni *et al*. (1997), Tucker *et al*. (2001), Zhou *et al*. (2001), Fang *et al*. (2003), and Slayback *et al*. (2003), whose work figured prominently in establishing the reality of the late twentieth-century warming- and CO_2-induced greening of the Earth phenomenon (see Section 4.2 on Biospheric Productivity), which has produced, in the words of the Spanish scientists, "an increase in plant growth or terrestrial net primary production in middle latitudes of the Northern Hemisphere since the 1980s, particularly in forest environments." It is clear the supposedly unprecedented warmth of the past two decades has not led to what Seoane and Carrascal call "the proposed detrimental effect of global warming on bird populations of western Europe."

Qian *et al*. (2009) compiled a comprehensive dataset of bird species richness in China based on pertinent scientific literature published over the past three decades for 207 localities, the vast majority of which were national nature reserves with a mean area of 3270 km^2, which dataset they analyzed for their relationships to 13 environmental variables. The authors observe, "of all environmental variables examined, normalized difference vegetation index [NDVI], a measure of plant productivity, is the best variable to explain the variance in breeding bird richness." Four of the 13 variables they tested explained 45.3% of the total species richness variance, with 21.2% being accounted for by NDVI, 12.5% by elevation range, and 11.6% by annual potential evapotranspiration and mean annual temperature together. They note the two most important predictors of their study (NDVI and elevation range) "have been found to be major predictors for breeding bird richness in other regions and the whole of the globe, indicating that the finding of [their] study at a smaller scale is to a large degree consistent with those of previous studies of breeding birds at larger scales."

In a major review of plant-animal interactions in 51 terrestrial ecosystems conducted 20 years earlier, McNaughton *et al*. (1989) found the biomass of plant-eating animals is a strongly increasing function of aboveground primary production, and in a subsequent review of 22 aquatic ecosystems, Cyr and Pace (1993) found the herbivore biomass of watery habitats also increases in response to increases in vegetative productivity. Thus it is abundantly clear greater plant productivity—both terrestrial and aquatic—leads to greater populations of plants and the animals that feed upon them, which should lead to greater ecosystem biodiversity and a reduced risk of extinction. Atmospheric CO_2 enrichment increases plant productivity (see Chapter 1), which supports more animal life, which leads to greater animal biodiversity, which is good for the planet and good for mankind.

A warmer climate has benefited birds on Australia's Heard Island, some 4,000 kilometers southwest of Perth. Over the last five decades of the twentieth century, as this sub-Antarctic island experienced a local warming of approximately 1°C, there were rapid increases in flora and fauna. The population of the King penguin, for example, "exploded from only three breeding pairs in 1947 to 25,000," and the Heard Island cormorant, listed previously as "vulnerable," increased to 1,200 pairs. Recovering from near extinction, fur seals now number 28,000 adults and 1,000 pups (Pockely, 2001).

Penguins in Antarctica also have fared well in warmer times. In response to dramatic warming observed on the western Antarctic Peninsula over the past several decades, the penguin population has become more diverse as chinstrap and gentoo penguins have begun to take up residence among the long-inhabiting Adelie penguin population (Smith *et al*., 1999). A study of penguin populations on the Ardley Peninsula of maritime Antarctica by Sun *et al.* (2000) found over the past 3,000 years the penguin population was lowest at 1,800–2,300 years BP, during a period of low temperature.

Huang *et al.* (2009) reported similar findings after evaluating paleo-evidence for penguin populations at Gardner Island in East Antarctica. According to the five researchers, penguins colonized the site shortly after it became ice-free 8,500 years ago. A pronounced population peak is evident in the data from about 4,700 to 2,400 BP, which corresponds closely to a substantially warmer period at this site. The authors document four other studies showing a penguin optimum roughly 3,000 to 4,000 years ago and coinciding with notably warm conditions. Together, these five studies encompass East Antarctica, the Ross Sea region, and the West Antarctic Peninsula. With all data currently available pointing to penguins having been most abundant during the warmest period of the Holocene several thousand years ago, it would seem reasonable to believe penguins will respond positively, not negatively, to any future warming.

Although global warming, regardless of its cause (natural or anthropogenic), appears to favor the population of many bird species, other human-related factors may offset such benefits and induce harm. For example, studies on the population dynamics of King penguins, *Aptenodytes patagonicus*, have been ongoing for many years. Recently, these fish-eating, top-of-the-food-chain predators have been used as indicator species for studies on the impacts of climate change in the southern hemisphere (Croxall *et al*., 2002; Tynan 1998). In many respects, penguins have become "polar bear equivalents" of the Antarctic ecosystem. It appears something other than global warming has had a major influence on their population in recent years.

Saraux *et al.* (2011) note "in 2007, the Intergovernmental Panel on Climate Change highlighted an urgent need to assess the responses of marine ecosystems to climate change. Because they lie in a high-latitude region, the Southern Ocean ecosystems are expected to be strongly affected by global warming. Using top predators of this highly productive ocean (such as penguins) as integrative indicators may help us assess the impacts of climate change on marine ecosystems."

Following that charge from IPCC, several reports have used data collected from penguins marked with flipper bands (Barbraud and Weimerskirch 2001; Jenouvrier *et al*., 2009) to predict impacts on the entire population from climate change scenarios modeled for the future. Flipper bands are metal markers attached to the upper part of the front flipper, where they are easily visible on land or in the water. Since penguins are birds that fly through the water, these "flippers" are actually wings and thus the sole source of a penguin's swimming power. Banding involves a single loop slipped over the upper, muscular section of one wing (equivalent to the human upper arm) and is meant to remain there for the life of the bird. These bands themselves, however, might have an influence on the data being collected on these penguins.

Research was conducted over a decade, in part to test the assumption that birds would adapt within a year at most to any negative effects of the metal flipper band (Barbraud and Weimerskirch 2001). Saraux *et al.* (2011) analyzed differences in reproduction and survival on 50 banded and 50 unbanded penguins over 10 years. The researchers evaluated annual and overall survival, arrival time at the breeding colony, laying dates, breeding success, success in chick rearing, duration of feeding trips ("foraging") and population growth.

They found the "banding of free-ranging king penguins (*Aptenodytes patagonicus*) impairs both survival and reproduction, ultimately affecting population growth rate." Over the 10-year period, banded birds were found to produce 39% fewer chicks and had a survival rate 16% lower than non-banded birds. Much of this effect appeared to be due to an increased time banded birds required to find sufficient food (both before and during the summer breeding season) and to their relatively late arrival at the breeding colony.

Saraux and colleagues write "one of our major findings is that responses of flipper-banded penguins to climate variability (that is, changes in sea surface temperature and in the Southern Oscillation index) differ from those of non-banded birds. We show that only long-term investigations may allow an evaluation of the impact of flipper bands and that every major life-history trait can be affected, calling into question the banding schemes still going on. In addition, our understanding of the effects of climate change on marine ecosystems based on flipper-band data should be reconsidered."

Another human-related activity with a significant impact on bird populations is the construction of wind farms. Pearce-Higgins *et al*. (2009) note "the displacement of birds away from turbines can result in individuals abandoning otherwise suitable habitat," and this "has been found to occur in a number of individual wind farm studies," citing Leddy *et al*. (1999), Larsen and Madsen (2000), Kowallik and Borbach-Jaene (2001), Hotker (2006), Hotker *et al*. (2006), and Larsen and Guillemette (2007). Pearce-Higgins *et al*. report, "some poorly sited wind farms have resulted in sufficient deaths to produce a population-level effect," citing Barrios and Rodriguez (2004, 2007), Everaert and Stienen (2006), Smallwood and Thelander (2007), Sterner *et al*. (2007), and Thelander and Smallwood (2007).

Pearce-Higgins *et al*. assessed the degree of occurrence of 12 widely distributed species of breeding birds within the vicinity of wind farm infrastructure (turbines, access tracks, and overhead transmission lines) on 12 wind farms located within unenclosed upland habitats (moorland, rough grassland, and blanket bog) in the United Kingdom, including most of the existing large upland wind farms in Scotland and northern England. The five UK scientists obtained "considerable evidence for localized reduction in breeding bird density on upland wind farms." After accounting for habitat variation, they report, "seven of the twelve species studied exhibited significantly lower frequencies of occurrence close to the turbines," and there was "equivocal evidence of turbine avoidance in a further two," and "no species were more likely to occur close to the turbines." Access tracks proved much less of a nuisance than turbines, and there was no evidence for consistent avoidance of overhead transmission lines. They conclude, "levels of turbine avoidance suggest breeding bird densities may be reduced within a 500-m buffer of the turbines by 15–52%, with buzzard (*Buteo buteo*), hen harrier (*Circus cyaneus*), golden plover (*Pluvialis apricaria*), snipe (*Gallinago gallinago*), curlew (*Numenius arquata*) and wheatear (*Oenanthe oenanthe*) most affected."

Pearce-Higgins *et al*. say their findings emphasize the need for a "strategic approach" to ensure wind farm development avoids areas with high densities of potentially vulnerable species, not only in the UK but also "across other similar windy semi-natural habitats in northwest Europe, southern South America, and central North America." Efforts should be made to "avoid high densities of potentially vulnerable open country species such as waders and raptors," they write. Their findings augment those of many others who have raised serious questions about the constructing of wind farms in inappropriate locations.

References

Barbraud, C. and Weimerskirch, H. 2001. Emperor penguins and climate change. *Nature* **411**: 183–186.

Barrios, L. and Rodriguez, A. 2004. Behavioral and environmental correlates of soaring bird mortality at on-shore wind turbines. *Journal of Applied Ecology* **41**: 72–81.

Barrios, L. and Rodriguez, A. 2007. Spatiotemporal patterns of bird mortality at two wind farms of Southern Spain. In: De Lucas, M., Janss, G.F.E. and Ferrer, M. (Eds.) *Birds and Wind Farms*. Quercus, Madrid, Spain, pp. 56–72.

Beaugrand, G. 2004. The North Sea regime shift: evidence, mechanisms and consequences. *Progress in Oceanography* **60**: 245–262.

Boertmann, D. 2006. Survey of Kittiwake colonies in Disko Bay and adjacent waters. Research Note, National Environmental Research Institute, Aarhus, Denmark.

Boertmann, D., Mosbech, A., Falk, K., and Kampp, K. 1996. Seabird colonies in western Greenland (60°–79°30'N. lat.). Research Note, National Environmental Research Institute, Aarhus, Denmark.

Croxall, J.P., Trathan, P.N., and Murphy, E.J. 2002. Environmental change and Antarctic seabird populations. *Science* **297**: 1510–1514.

Cyr, H. and Pace, M.L. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* **361**: 148–150.

Everaert, J. and Stienen, E.W.M. 2006. Impact of wind turbines on birds in Zeebrugge (Belgium). Significant effect on breeding tern colony due to collisions. *Biodiversity and Conservation* **16**: 3345–3359.

Fang, J., Piao, S., Field, C.B., Pan, Y., Guo, Q., Zhou, L., Peng, C., and Tao, S. 2003. Increasing net primary production in China from 1982 to 1999. *Frontiers in Ecology and the Environment* **1**: 293–297.

Grandgeorge, M., Wanless, S., Dunn, T.E., Maumy, M., Beaugrand, G., and Gremillet, D. 2008. Resilience of the British and Irish seabird community in the twentieth century. *Aquatic Biology* **4**: 187–199.

Gregory, R.D., van Strien, A.J., Vorisek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B., and Gibbons, D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **360**: 269.

Hotker, H. 2006. *The Impact of Repowering of Wind Farms on Birds and Bats*. Michael-Otto-Institut im NABU, Bergenhusen.

Hotker, H., Thomsen, K.-M., and Jeromin, H. 2006. *Impacts on Biodiversity of Exploitation of Renewable Energy Sources: The Example of Birds and Bats—Facts, Gaps in Knowledge, Demands for Further Research and Ornithological Guidelines for the Development of Renewable Energy Exploitation*. Michael-Otto-Institut im NABU, Bergenhusen.

Huang, T., Sun, L, Wang, Y., Liu, X., and Zhu, R. 2009. Penguin population dynamics for the past 8500 years at Gardner Island, Vestfold Hills. *Antarctic Science* **21**:571–578.

Jenouvrier, S., Caswell, H., Barbraud, C., Holland, M., Stroeve, J., and Weimerskirch, H. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences USA* **106**: 1844–1847.

Julliard, R., Jiguet, F., and Couvet, D. 2004a. Common birds facing global changes: what makes a species at risk? *Global Change Biology* **10**: 148–154.

Julliard, R., Jiguet, F., and Couvet, D. 2004b. Evidence for the impact of global warming on the long-term population dynamics of common birds. *Proceedings of the Royal Society B: Biological Sciences* **271**: S490–S492.

Kowallik, C. and Borbach-Jaene, J. 2001. Impact of wind turbines on field utilization by geese in coastal areas in NW Germany. *Vogelkundliche Berichte aus Niedersachen* **33**: 97–102.

Larsen, J.K. and Guillemette, M. 2007. Effects of wind turbines on flight behavior of wintering common eiders: Implications for habitat use and collision risk. *Journal of Applied Ecology* **44**: 516–522.

Larsen, J.K. and Madsen, J. 2000. Effects of wind turbines and other physical elements on field utilization by pink-footed geese (*Anser brachyrhynchus*): a landscape perspective. *Landscape Ecology* **15**: 755–764.

Leddy, K.L., Higgins, K.F., and Naugle, D.E. 1999. Effects of wind turbines on upland nesting birds in conservation reserve program grasslands. *Wilson Bulletin* **111**: 100–104.

Lemoine, N., Bauer, H.-G., Peintinger, M., and Bohning-Gaese, K. 2007. Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology* **21**: 495–503.

McNaughton, S.J., Oesterheld, M., Frank, D.A., and Williams, K.J. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341**: 142–144.

Myneni, R.C., Keeling, C.D., Tucker, C.J., Asrar, G., and Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**: 698–702.

Pearce-Higgins, J.W., Stephen, L., Langston, R.H.W., Bainbridge, I.P., and Bullman, R. 2009. The distribution of breeding birds around upland wind farms. *Journal of Applied Ecology* **46**: 1323–1331.

Pockely, P. 2001. Climate change transforms island ecosystem. *Nature* **410**: 616.

Qian, H., Wang, S., Li, Y., and Wang, X. 2009. Breeding bird diversity in relation to environmental gradients in China. *Acta Oecologica* **35**: 819–823.

Raven, M.J., Noble, D.G., and Baillie, S.R. 2005. *The Breeding Bird Survey 2004*. Thetford, UK: British Trust for Ornithology.

Saraux, C., Le Bohec, C., Durant, J.M., Viblanc, V.A., Gauthier-Clerc, M., Beaune, D., Park, Y-H., Yoccoz, N.G., Stenseth, N.C., and Le Maho, Y. 2011. Reliability of flipper-banded penguins as indicators of climate change. *Nature* **469**: 203–206.

Schmidt, J.H., Lindberg, M.S., Johnson, D.S., Conant, B., and King, J. 2009. Evidence of Alaskan trumpeter swan population growth using Bayesian hierarchical models. *Journal of Wildlife Management* **73**: 720–727.

Seoane, J. and Carrascal, L.M. 2008. Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences. *Global Ecology and Biogeography* **17**: 111–121.

Slayback, D., Pinzon, J., and Tucker, C. 2003. Northern hemisphere photosynthetic trends 1982–1999. *Global Change Biology* **9**: 1–15.

Smallwood, K.S. and Thelander, C. 2007. Bird mortality in the Altamont pass wind resource area, California. *Journal of Wildlife Management* **72**: 215–223.

Smith, R.C., Ainley, D., Baker, K., Domack, E., Emslie, S., Fraser, B., Kennett, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S., and Vernet M. 1999. Marine ecosystem sensitivity to climate change. *BioScience* **49**: 393–404.

Sterner D., Orloff, S., and Spiegel, L. 2007. Wind turbine collision research in the United States. In: De Lucas, M., Janss, G.F.E., and Ferrer, M. (Eds.) *Birds and Wind Farms.* Quercus, Madrid, Spain, pp. 81–100.

Sun, L., Xie, Z., and Zhao, J. 2000. A 3,000-year record of penguin populations. *Nature* **407**: 858.

Thelander, C.G. and Smallwood, K.S. 2007. The Altamont pass wind resource area's effect on birds: a case history. In: De Lucas, M., Janss, G.F.E., and Ferrer, M. (Eds.) *Birds and Wind Farms.* Quercus, Madrid, Spain, pp. 25–46.

Thompson, P.M. 2006. Identifying drivers of change: did fisheries play a role in the spread of North Atlantic fulmars? In Boyd, I.A., Wanless, S., and Camphuysen, C.J. (Eds.) *Management of Marine Ecosystems: Monitoring Change in Upper Trophic Levels*. Cambridge, UK: Cambridge University Press.

Tucker, C.J., Slayback, D.A., Pinzon, J.E., Los, S.O., Myneni, R.B., and Taylor, M.G. 2001. Higher northern latitude NDVI and growing season trends from 1982 to 1999. *International Journal of Biometeorology* **45**: 184–190.

Tynan, C.T. 1998. Ecological importance of the southern boundary of the Antarctic Circumpolar current. *Nature* **392**: 708–710.

White, C.R., Boertmann, D., Gremillet, D., Butler, P.J., Green, J.A., and Martin, G.R. 2011. The relationship between sea surface temperature and population change of Great Cormorants *Phalacrocorax carbo* breeding near Disko Bay, Greenland. *Ibis: The International Journal of Avian Science* **153**: 170–174.

Zhou, L., Tucker, C.J., Kaufmann, R.K., Slayback, D., Shabanov, N.V., and Myneni, R.B. 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research* **106**: 20.069–20,083.

5.4.2 Range Expansion

IPCC claims the increase in temperature predicted to result from the ongoing rise in the air's CO_2 content will be of such magnitude and speed that many species of plants and animals will not be able to migrate poleward in latitude or upward in elevation rapidly enough to avoid extinction as they are forced to seek cooler living conditions. There are many reasons for rejecting this contention, one of the most powerful being that increases in the air's CO_2 content generally enable plants to endure warmer weather, and as a result there is little or no need for them to shift the heat-limiting warm-temperature boundaries of their ranges as temperatures rise (see Section 3.13 and Section 4.2.3). At the cold-limiting cool-temperature boundaries of their ranges, warming provides opportunities for plants to push poleward and upward, resulting in expansions of their ranges and reductions in their risk of extinction.

This section reviews studies that suggest birds may respond in like manner, mimicking the respective shifts and non-shifts of the cold- and heat-limited boundaries of the ranges of the plants and associated herbivore life forms on which they depend for food.

Thomas and Lennon (1999) helped initiate extinction concerns about birds when they analyzed temporal trends in the spatial distributions of British birds over a 20-year period of global warming, looking for climate-induced changes in their breeding ranges. They found the northern margins of southerly species' breeding ranges shifted northward by an average of 19 km from 1970 to 1990, while the southern margins of northerly species' breeding ranges did not shift at all, in the mean. British birds thus expanded their ranges in the face of global warming, clearly a positive response that makes extinction less likely than it was before the warming.

Norment *et al*. (1999) analyzed bird surveys conducted along the Thelon River and its tributaries in the Canadian Northwest Territories from the 1920s through much of the 1990s, finding three bird species had expanded their breeding ranges southward, nine northward, and 16 were new to the area. The authors note the primarily northward range expansions may be explained by "a recent warming trend at the northern treeline during the 1970s and 1980s." Alternatively, they note the influx of new species may result from "increasing populations in more southerly areas." In either case, the birds appear to be faring quite well—even thriving—in the face of increasing temperatures in this forest-tundra landscape, which also appears to be the case in Norway (Saether *et al*., 2000).

Research suggests seabirds of Greenland are also likely to benefit from global warming. According to Wagner and Melles (2001), a significant number of seabirds inhabited the area around Liverpool Land, on the east coast of Greenland, during the Medieval Warm Period (900–1300 AD), yet there was little or no (inferred) bird presence for a several-hundred-year period prior to this time (Dark Ages Cold Period) and another significant absence of birds thereafter during the Little Ice Age, which marked "the coldest period since the early Holocene in East Greenland." As temperatures have risen over the past 100 years, seabirds once again have expanded their range to inhabit the area.

Kinzelbach (2004) explored the range history of the serin, a bird that "was a topic of particular interest to ornithologists of the 19th and 20th century" due to "the rapid expansion of its range in historical times." The author reexamined "all the sources of records of the serin in 16th century Europe, ... both those already known and some that have been newly discovered." The data confirmed the findings of Mayr (1926), that "north of 48°N there were no free-living populations of *Serinus serinus* in the 16th century." During that period, the serin's range was constrained, Kinzelbach reports, as it "was halted by colder periods of the Little Ice Age after 1585, only resuming a rapid expansion at the beginning of the 19th century," after which it was "able to expand its range from the Mediterranean region throughout large areas of Central Europe within a mere 200 years."

Brommer (2004) categorized birds of Finland as either northerly (34 species) or southerly (116 species) and quantified changes in their range margins and distributions from two atlases of breeding birds, one covering the period 1974–1979 and one for 1986–1989, to determine how the two groups of species responded to what he called "the period of the Earth's most rapid climate warming in the last 10,000 years," citing McCarthy *et al.* (2001). Southern species experienced a mean poleward advancement of their northern range boundaries of 18.8 km over the 12-year period, while the southern-range boundaries of the northern species remained essentially unaltered. Noting similar results had been obtained for birds in the United Kingdom (Thomas and Lennon, 1999) and other animals (primarily butterflies) elsewhere (Parmesan, 1996; Parmesan *et al.*, 1999), Brommer concludes, "in general, for Northern Hemisphere species, southerly range margins of species are less responsive to climate change than the northerly margins." This demonstrates once again the ranges of birds (and possibly other animals) in a warming world likely will increase, as their northern range boundaries expand poleward and upward while their southern range boundaries remain largely unaltered, which should render them less subject to extinction than they are currently or have been in the past.

For the portion of the United States east of the Rocky Mountains, Hitch and Leberg (2007) used data from the North American Breeding Bird Survey to evaluate shifts in the northern range boundaries of 26 species of birds with southern distributions and the southern range boundaries of 29 species of birds with northern distributions between the periods 1967–1971 and 1998–2002. They found the northern margins of the southern group of birds showed significant northward shifts that averaged 2.35 km per year for all species studied, which they describe as being "consistent with the results of Thomas and Lennon (1999) from Great Britain." Also in agreement with the observations on British birds, they determined "levels of warming do not appear to be so great [that] they are forcing birds to abandon the southernmost portions of their distributions."

Grandgeorge *et al.* (2008) analyzed population sizes and phylogenetic and spatial structures of British and Irish seabirds based on "(1) presence or absence of the seabird species in the different counties of Britain and Ireland between 1875 to 1900 and 1968 to 1972, (2) seabird breeding censuses of Britain and Ireland from 1969 to 1970, 1985 to 1988 and 1998 to 2002, (3) at-sea abundance and distribution surveys of seabirds in the North Sea from 1980 to 1985 and 1990 to 1995, and (4) a bioenergetics model to estimate energy expenditures for 40 seabird species." They found "a marked expansion in the breeding range of seabirds in Britain and Ireland between 1875 and 1972." In addition, they report total seabird numbers "increased at an average rate of 1% per annum between 1969 and 2002, with a related increase of 115% in predicted total seabird predation." Also, they state, "between 1875 and 1972 no seabird species was lost and there was an overall expansion in breeding range of the seabird population of Britain and Ireland, with the number of counties occupied increasing from 31 to 47."

The six scientists conclude, "the seabird community of Britain and Ireland has been remarkably resilient to environmental change in the 20th century." In fact, it "prospered during the 20th century," and "significantly raised ocean temperatures in the North Sea (Beaugrand, 2004)" may have "created more favorable environmental conditions for some seabird species," citing Thompson (2006).

Brommer (2008) notes a "population-level change expected under a climate-warming scenario is a poleward shift in the distribution of organisms," and he states many believe birds that "do not shift their range margin consist of species that are declining, and would therefore be of particular management concern." A few years earlier, Brommer (2004) had measured the range sizes and northern range margin locations of 116 bird species with a predominantly southern distribution in Finland, and of those species "the trend slope describing the change in their abundance for the period 1983–2005 was calculated for 53 species by Vaisanen (2006)." This, he notes, resulted in "the largest dataset available of the long-term trends in population numbers of Finnish birds that is comparable across species, because it has both been gathered and analyzed using the same procedures." Brommer (2008) determined the concomitant changes in the northern range margins of the 53 species.

The Finnish bird specialist found "species foraging in wet habitats had experienced strong range margin shifts as compared with other feeding ecologies." However, he found "no evidence that those feeding ecological groups that showed a relatively small shift in range margin had experienced low population growth or a population decline." Therefore, in discussing "the lack of correlation between the shift in range margin of the different feeding ecologies and the change in their mean abundance," Brommer states this real-world finding "is contrary to expected under a climate-change scenario, because, all else being equal, a clear range-margin shift should indicate a good capacity to track climatic change, which should result in a more positive trend in abundance if climate change is indeed the main driver of population-level change."

Maclean *et al.* (2008) analyzed counts of seven wading bird species—the Eurasian oystercatcher, grey plover, red knot, dunlin, bar-tailed godwit, Eurasian curlew, and common redshank—made at approximately 3,500 sites in Belgium, Denmark, France, Germany, Ireland, the Netherlands, and the United Kingdom on at least an annual basis since the late 1970s. They did this in order to determine what range adjustments the waders may have made in response to regional warming, calculating the weighted geographical centroids of the bird populations for all sites with complete coverage for every year between 1981 and 2000. They found "the weighted geographical centroid of the overwintering population of the majority of species has shifted in a northeasterly direction, perpendicular to winter isotherms," with overall 20-year shifts ranging from 30 to 119 km. In addition, they report, "when the dataset for each species was split into 10 parts, according to the mean temperature of the sites, responses are much stronger at the colder extremities of species ranges." They found, "at warmer sites, there was no palpable relationship between changes in bird numbers and changes in temperature." They conclude, "range expansions rather than shifts are occurring" as the planet warms.

Maclean *et al.* note the commonly used climate-envelope approach to predicting warming-induced species migrations "essentially assumes that as climate alters, changes at one margin of a species' range are mirrored by those at the other, such that approximately the same 'climate space' is occupied regardless of actual climate," whereas the evidence suggests "that this may not be the case: climate space can also change."

Maclean *et al.* further write, "it is actually not surprising that responses to temperature appear only to be occurring at the colder extremities of species ranges," for "it has long been known that it is common for species to be limited by environmental factors at one extremity, but by biological interactions at the other," citing Connell (1983) and Begon *et al.* (2005). They conclude it is likely "the warmer extremities of the species ranges examined in this study are controlled primarily by biotic interactions, whereas the colder margins are dependent on temperature."

In a model-based study, Jensen *et al.* (2008) state "global climate change is expected to shift species ranges polewards, with a risk of range contractions and population declines of especially high-Arctic species," citing the Arctic Climate Impact Assessment (ACIA, 2005). To evaluate this claim, they constructed species distribution models for the Svalbard-nesting pink-footed goose (*Anser brachyrhynchus*), in order to "relate their occurrence to environmental and climatic variables." They used the most parsimonious of the models to "predict their distribution under a warmer climate scenario," based on "mean May temperature, the number of frost-free months and the proportion of moist and wet moss-dominated vegetation in the area," the latter being "an indicator of suitable feeding conditions."

They found global warming "will have a positive effect on the suitability of Svalbard for nesting geese in terms of range expansion into the northern and eastern parts of Svalbard which are currently unsuitable." They also note this result does not even consider whether glaciers will decrease in size and expose still more potential nest sites. Thus they conclude by stating increased temperatures could help the population of pink-footed geese, as "elongation of the frost-free season in Svalbard may relax their dependence on the acquisition of body stores before arrival (so-called 'capital' breeding, *sensu* Drent and Daan, 1980), so that geese will have more time to acquire the necessary resources upon arrival and still breed successfully," noting "both factors are likely to have a positive effect on the population growth."

Zuckerberg *et al.* (2009) "used the New York State Breeding Birds Atlas, a statewide survey of 5,332 25-km^2 blocks surveyed in 1980–1985 and 2000–2005, to test several predictions that the birds of New York State are responding to climate change." They found "all bird species (n = 129) included in this analysis showed an average northward range shift in their mean latitude of 3.58 km." Citing a number of other studies, the researchers conclude, "the repeated pattern of a predicted northward shift in bird ranges in various geographic regions of the [Northern Hemisphere] provides compelling evidence that climate change is driving range shifts." This provides compelling evidence Earth's birds did precisely what they should have done, over the period of Zuckerberg *et al.*'s study, in order to maintain a strong presence on the planet in the face of the rising temperatures (natural or anthropogenic) of that period.

Hockey and Midgley (2009) write, "in the influential fourth assessment report of the Intergovernmental Panel on Climate Change, Rosenzweig *et al.* (2007) tested several thousand time-series data sets for changes in species behavior and geographic range consistent with climate change, reaching the conclusion that it is very likely that climate change is driving changes in natural biological systems." They note, "the use of such large data sets in meta-analyses may discourage the close inspection of observations and result in naively misattributing observed shifts to climate when other explanations may be more parsimonious."

To test this hypothesis, Hockey and Midgley "collated information about recent range changes in South African birds, specifically indigenous species that have colonized the Cape Peninsula, at the south-western tip of Africa in the Western Cape province, since the 1940s," where they state there have been "widespread anthropogenic changes of many kinds to the landscape, including urbanization, commercial afforestation and the introduction and spread of invasive alien trees, most of which occurred before climate change accelerated in the 1970s."

The two researchers found the colonization events "concur with a 'climate change' explanation, assuming extrapolation of Northern Hemisphere results and simplistic application of theory," but "on individual inspection, all but one may be more parsimoniously explained by direct anthropogenic changes to the landscape than by the indirect effects of climate change." Also, "no *a priori* predictions relating to climate change, such as colonizers being small and/or originating in nearby arid shrub-lands, were upheld."

The South African scientists state their work suggests "observed climate changes have not yet been sufficient to trigger extensive shifts in the ranges of indigenous birds in this region, or that *a priori* assumptions are incorrect." Either way, they continue, "this study highlights the danger of naive attribution of range changes to climate change, even if those range changes accord with the predictions of climate-change models," because "misattribution could distract conservationists from addressing pressing issues involving other drivers of biodiversity change such as habitat transformation, and obscure important lessons that might be learned from the dynamics that pertain to such changes."

Tyrberg (2010) compared fossil avifaunas of the Last Interglacial (LIG), about 130,000 to 117,000 years ago from multiple sites around the world to the modern avifaunas found in those locations. During much of this time interval, the globe was about 2°C warmer than it is today, and it was up to 10°C warmer in much of the Arctic. For fossil faunas, only species that still exist were included in the comparisons, because during the cold period of the last glacial, which followed the LIG, many species went extinct due to the cold, and climate tolerance can be determined reliably only for living species.

Based on the areal distributions of fossil avifaunas in different parts of the world, regions were delineated in which many of the identified species coexisted. If it was found the same sets of species share the same common ranges today, it was concluded the avifauna, as a whole, did not respond to any significant degree to the warmer temperatures of the LIG.

For sites that were about 2°C warmer during the LIG—including four sites in Florida, one in Alaska, two in Germany, and one in New Zealand—species present during the LIG were found to be the same as those that inhabit those regions today. At a site in Wales, however, where LIG temperatures were a full 4°C warmer than today, the fossil avifauna was similar to the current avifauna of Spain and Portugal, indicating the fossil avifauna had located themselves further northward during the LIG in response to the much greater warmth of that period. And in another exception to the study's primary findings of similar faunal structures, the LIG avifauna at a site in North Africa (which is now desert, with no birds present) was similar to that of the area south of the desert today, indicating—in light of the fact that during the LIG the Sahara desert received much more rainfall than it does currently—precipitation was the overriding factor determining both the current and fossil avifauna choice of territories.

Tyrberg concludes, "as for the effect of the generally warmer climate during the LIG it seems clear that differences on the order of 2°C or less, both on land and in sea-surface temperatures, are barely, if at all, detectable in the avifaunas."

Popy *et al.* (2010) employed data from two bird atlas surveys performed on a 1 km by 1 km grid (the first in 1992–1994 and the second in 2003–2005) in an alpine valley in the Italian Piedmont in search of evidence for an upward shift in the ranges of 75 bird species (68 of which were detected in both surveys) over this period, during which time the region's mean air temperature rose by 1.0°C. They found "the number of species whose mean elevation increased (n = 42) was higher than the number whose mean elevation decreased (n = 19), but the overall upward shift [29 m] was not significantly different from zero." In addition, they state even the 29-m increase was "smaller than would be expected from 'climatic envelope' models," as the "1.0°C increase in temperature would be equivalent to *c.* 200 m in elevation, based on an average gradient of -0.5°C per 100 m." In addition, they write, "at the European scale, no overall expansion or contraction of the distributions of the studied species was detected." Popy *et al.* conclude, "until a better understanding of the underlying mechanisms is achieved, predictions based only on 'climate envelope' models should be either validated or considered cautiously."

Using the same sampling techniques employed by Terborgh and Weske (1975) in 1969, and working at five of the nine localities studied by those earlier investigators, Forero-Medina *et al.* (2011) resampled bird communities at five elevations (690, 1310, 1570, 1970, and 2220 meters) within the Reserva Comunal El Sira on the Cerros del Sira massif in Peru some 41 years later, in 2010. They sought to determine what changes might have occurred in the elevations of the several species encountered at the two sampling times. Of the 55 species encountered in both sampling periods, 36 had moved up in elevation, 12 had moved down, and seven had not moved in either direction, resulting in an average upward shift of 49 meters for the 55 bird species over the 41-year period. They describe this change in elevation as being "significantly smaller" than the 152-meter increase one would have expected from the amount of warming experienced throughout the region between the times of the two studies.

In an attempt to determine to what extent tropical and subtropical birds from lower latitudes may have been making their way northwards in response to regional warming since the mid–1970s, Rappole *et al.* (2011) conducted a three-year field study on ranch land of the Welder Wildlife Refuge along a 30-km stretch of the Aransas River in southeastern Texas, which they say is located "at the northern end of the New World subtropics." Their findings indicate "range change is occurring at a rapid rate for tropical, subtropical, and warm desert birds in Texas." They report, "comparisons between former (1974) and current avian distributions for the region show significant breeding range extension of 40–220 km to the north, northeast or east for at least 68 species, many of which cross major biogeographic boundaries." They conclude "change in key parameters of habitat, e.g. seasonal food availability, as affected by factors related to climate change, e.g. mean annual precipitation, temporal distribution of precipitation (monthly means), or monthly means for nighttime-low temperatures during the breeding season, provide the most likely explanations for observed range extensions."

As for the single overriding "environmental factor associated with avian range shift in South Texas," Rappole *et al.* identify "change in mean annual temperature," as documented by Norwine and John (2007). They report the movement of this "large segment of the subtropical avian community into temperate habitats has not been met with a corresponding shift of temperate species as had been predicted by a number of models." Quite to the contrary, they continue, "the communities now overlap, creating, in effect, novel communities." These new communities possess a greater biodiversity than the ones that existed there prior to the arrival of the many new tropical and subtropical bird species.

The findings cited in this section make it clear that where confirmed regional warming over the time periods has been investigated, the vast majority of studies of bird range adjustments have revealed opportunistic poleward expansions of their cold-limited boundaries with little or no change in the locations of their (supposedly) heat-limited boundaries. This behavior is not a matter of massive range reductions or of bird species rushing, or even inching, toward extinction, as is often projected in model-based studies. Instead, the species are fortifying themselves against the possibility of extinction, behaving as resilient evolutionary survivors and colonizing new habitat as it becomes available, strengthening their populations against the myriad challenges associated with environmental change.

References

ACIA. 2005. *Arctic Climate Impact Assessment*. New York, NY: Cambridge University Press.

Beaugrand, G. 2004. The North Sea regime shift: evidence, mechanisms and consequences. *Progress in Oceanography* **60**: 245–262.

Begon, M., Townsend, C., and Harper, J. 2005. *Ecology: From Individuals to Ecosystems*. Oxford, UK: Blackwell.

Brommer, J.E. 2004. The range margins of northern birds shift polewards. *Annales Zoologici Fennici* **41**: 391–397.

Brommer, J.E. 2008. Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology. *Ornis Fennica* **85**: 109–117.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* **122**: 661–696.

Drent, R.H. and Daan, S. 1980. The prudent parent: energetic adjustment in avian breeding. *Ardea* **68**: 225–252.

Forero-Medina, G., Terborgh, J., Socolar, S.J., and Pimm, S.L. 2011. Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS ONE* **6**: e28535.

Grandgeorge, M., Wanless, S., Dunn, T.E., Maumy, M., Beaugrand, G., and Gremillet, D. 2008. Resilience of the British and Irish seabird community in the twentieth century. *Aquatic Biology* **4**: 187–199.

Hitch, A.T. and Leberg, P.L. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* **21**: 534–539.

Hockey, P.A.R. and Midgley, G.F. 2009. Avian range changes and climate change: a cautionary tale from the Cape Peninsula. *Ostrich* **80**: 29–34.

Jensen, R.A., Madsen, J., O'Connell, M., Wisz, M.S., Tommervik, H., and Mehlum, F. 2008. Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Global Change Biology* **14**: 1–10.

Kinzelbach, R.K. 2004. The distribution of the serin (*Serinus serinus* L., 1766) in the 16th century. *Journal of Ornithology* **145**: 177–187.

Maclean, I.M.D., Austin, G.E., Rehfisch, M.M., Blew, J., Crowe, O., Delany, S., Devos, K., Deceuninck, B., Gunther, K., Laursen, K., van Roomen, M., and Wahl, J. 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology* **14**: 2489–2500.

Mayr, E. 1926. Die Ausbreitung des Girlitz (*Serinus canaria serinus* L.). Ein BEitrag Zur Tiergeographie. *Journal of Ornithology* **74**: 571–671.

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., and White, K.S. (Eds.) 2001. *Climate Change 2001: Impacts, Adaptation, and Vulnerability*. Cambridge, UK: Cambridge University Press.

Norment, C.J., Hall, A., and Hendricks, P. 1999. Important bird and mammal records in the Thelon River Valley, Northwest Territories: Range expansions and possible causes. *The Canadian Field-Naturalist* **113**: 375–385.

Norwine, J. and John, K. 2007. Welcome to the Anthropocene: South Texas climate. In: Norwine, J. and John, K. (Eds.) *The Changing Climate of South Texas: 1900–2100*. Texas A & M University, Kingsville, Texas, USA, pp. 1–4.

Parmesan, C. 1996. Climate and species' range. *Nature* **382**: 765–766.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., and Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583.

Popy, S., Bordignon, L., and Prodon, R. 2010. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. *Journal of Biogeography* **37**: 57–67.

Rappole, J.H., Glasscock, S., Goldberg, K., Song, D., and Faridani, S. 2011. Range change among new world tropical and subtropical birds. In: Schuchmann, K.-L. (Ed.) *Tropical Vertebrates in a Changing World*. Bonner Zoologische Monographien No. 57: 151–167.

Rosenzweig, C., Casassa, G., Karoly, D.J., Imeson, A., Liu, C., Menzel, A., Rawlins, S., Root, T.L., Seguin, B., and Tryjanowski, P. 2007. Assessment of observed changes and responses in natural and managed systems. In Parry, M., *et al.* (Eds.) *Climate Change 2007: Impacts, Adaptation and Vulnerability.* Working Group II Contribution to the 4th Assessment Report of the Intergovernmental Panel on Climate Change, pp. 79–131. Cambridge, UK: Cambridge University Press.

Saether, B.-E., Tufto, J., Engen, S., Jerstad, K., Rostad, O.W., and Skatan, J.E. 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* **287**: 854–856.

Terborgh, J. and Weske, J.S. 1975. The role of competition in the distribution of Andean birds. *Ecology* **56**: 562–576.

Thomas, C.D. and Lennon, J.J. 1999. Birds extend their ranges northwards. *Nature* **399**: 213.

Thompson, P.M. 2006. Identifying drivers of change: did fisheries play a role in the spread of North Atlantic fulmars? In Boyd, I.A., Wanless, S., and Camphuysen, C.J. (Eds.) *Management of Marine Ecosystems: Monitoring Change in Upper Trophic Levels*. Cambridge, UK: Cambridge University Press.

Tyrberg, T. 2010. Avifaunal responses to warm climate: the message from last interglacial faunas. *Records of the Australian Museum* **62**: 193–205.

Vaisanen, R.A. 2006. Maalinnuston kannanvaihtelut Etela-ja Pohjois-Suomessa 1983–2005. *Linnut-vuosikirja* **2005**: 83–98.

Wagner, B. and Melles, M. 2001. A Holocene seabird record from Raffles So sediments, East Greenland, in response to climatic and oceanic changes. *Boreas* **30**: 228–239.

Zuckerberg, B., Woods, A.M., and Porter, W.F. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* **15**: 1866–1883.

5.4.3 Adaptation, Evolution, and Phenotypic Responses

Amid concerns of species extinctions in response to rising temperatures, observational data indicate birds are effectively coping with and adapting to various challenges to their existence, real or perceived, arising from global warming. This section examines adaptive responses pertaining to reproductive success, timing of spring arrival, and trophic mismatches. In brief, the findings discussed here provide ample reason to conclude birds likely will benefit from future global warming.

5.4.3.1 Reproductive Success

Concerns have been expressed that global warming may upset certain reproductive traits in birds, leading to downward trends in the populations of many species. However, as discussed below, birds are well-equipped to respond to warming, often adapting their breeding habits so their reproductive success is frequently higher at warmer temperatures.

Brown *et al*. (1999) studied a population of individually recognizable, color-banded Mexican jays in the Chiricahua Mountains of Arizona (USA) over the period 1971–1998 for trends in egg-laying dates and monthly minimum air temperatures. Over this 29-year period, they determined the date of first nest construction occurred 10.8 days earlier, and the date of first clutch came 10.1 days earlier. These changes were associated with significant upward trends in monthly minimum temperature in the study area; in many bird species “breeding is timed so as to have young in the nest when the principal food of the nestlings is at its peak.” With warmer minimum temperatures occurring earlier over their study period, they suggest this climatic trend could be producing an earlier abundance of such food, which would help explain the earlier egg-laying date.

The researchers also identified a second way in which earlier-occurring warmer night temperatures might lead to earlier breeding dates in birds: by alleviating thermal stresses on females on cold nights. Citing several studies that had revealed similar breeding trends in European birds, they suggest the “recognition of similar trends on both continents in very different environments is consistent with the interpretation that some avian populations are already responding to climate changes in the last 29 years or so.” These widespread changes are positive in nature, for not only are bird ranges increasing in size as air temperatures rise, the temporal availability of food needed to sustain important life processes is advancing in synchrony with the timing of egg-laying.

Visser *et al*. (2003) examined laying dates for 24 populations of great and blue tits (*Parus major* and *Parus caeruleus*, respectively) in six European countries from 1979 to 1998, during which time several (but not all) of the locations studied exhibited increases in near-surface air temperature. Results indicated “the phenological response to large-scale changes in spring temperature varies across a species’ range, even between populations situated close to each other.” They also report “this variation cannot be fully explained by variation in the temperature change during the pre- and post-laying periods.” Their results “show the value of replicating population studies across parts of a species’ range, as the effects of climate change may differ, even within a single species, on a small geographical scale.”

Halupka *et al*. (2008) documented various breeding parameters of reed warblers (long-lived passerine birds that winter in Africa but breed in the reed beds of marshlands in the Palaearctic) during 12 breeding seasons (1970–1973, 1980–1983, 1994, 2003, and 2005–2006) and compared trends in what they measured with concomitant trends in mean monthly temperatures. They found temperatures in the mean breeding season (April-August) increased significantly between 1970 and 2006, as did the mean temperature of each individual month of the breeding season, with the average temperature for the May-July period rising by 2°C. Egg-laying started three weeks earlier in 2005 and 2006 than in 1970 (as assessed by the first-egg date of the earliest pair of breeding birds), and the median first-egg date shifted forward by 18 days.

The end of egg-laying, however, did not change significantly in either direction, so there was a corresponding increase in the length of the egg-laying period, and with this longer laying period available to them, more birds were able to rear second broods. In the 1970s and 1980s, for example, the Polish researchers report, “only about 0–15% of individuals laid second clutches," but "between 1994 and 2006 up to 35% of birds reared second broods." In addition, they report, "during seasons with warm springs, early nests were better protected by being hidden in newly emerged reeds," and "as a result, these nests suffered fewer losses from predation." They conclude, "the studied population of reed warblers benefits from climate warming."

Based on bird-ringing records spanning 41 years (1964–2004), Husek and Adamik (2008) "documented shifts in the timing of breeding and brood size in a long-distance migrant, the red-backed shrike (*Lanius collurio*) from a central European population." They compared their results with the climatic history of the region over the same period. They determined temperatures in May increased significantly over the period of their study, and "in line with this increasing May temperature" there was "a 3- to 4-day shift towards earlier breeding." This pattern, they write, "is consistent with the results of similar studies on other long-distance migrating songbirds (e.g., Dunn, 2004)." In addition, they report, there was "an increase in brood size by approximately 0.3 nestlings since 1964." They state, "given that early broods are usually larger (Lack, 1968; this study) and that they have a higher nest success (Muller *et al*., 2005), this may have a positive effect on future population increases as the temperature continues to rise."

After observing two second clutches in a newly established population of tree swallows in the Shenandoah Valley of Virginia (USA), Monroe *et al.* (2008) monitored all late nests in the following two breeding seasons to see what they could learn about the phenomenon. This revealed, "among all females nesting in the early breeding rounds of 2006 and 2007, 5% of birds with successful first clutches later laid second clutches." The mean productivity for double-brooded females for 2006–2007 was 4.4 ± 1.3 fledglings from first clutches and 3.4 ± 0.8 from second clutches, so "double-brooded females significantly increased their total annual productivity compared to birds nesting only in the early rounds of breeding." The productivity of the double-brooded females was approximately 75 percent greater than that of the single-brooded females. Monroe *et al.* conclude, "in general, late summer and fall nesting among North American birds is underappreciated and may be increasing due to global warming," citing Koenig and Stahl (2007).

Dyrcz and Halupka (2009) examined long-term responses in the breeding performance of Great Reed Warblers living on fish ponds near Milicz in southwest Poland during various years from 1970 to 2007 (1970–1974, 1981–1984, 1997, and 2004–2007), over which period mean temperatures during the egg-laying months of the species (May–July) rose by 2.2°C, from 15.3 to 17.5°C. The two researchers found a "significant advancement in both earliest and annual median first-egg-laying dates" that "correlated with temperature increases early in the season." Latest first-egg-laying dates remained unchanged, as did several other breeding statistics, including clutch size, nest losses, and number of young per nest. Consequently—and contrary to a Bavarian population of Great Reed Warblers that also advanced its latest first-egg-laying date—the Polish bird population expanded its breeding season in response to regional warming, whereas the Bavarian birds merely shifted theirs, as documented by Schaefer *et al*. (2006).

Dyrcz and Halupka conclude, "the studied population does not benefit from climate warming (as found in Bavaria), but apparently does not suffer," reiterating "the Great Reed Warbler has adapted well ... by shifting the timing of breeding." The results of their study, they state, "do not confirm the prediction of Bairlein and Winkel (2000) that long-distance migrants would suffer due to climate change." In addition, they write, a comparison of their data with that of the Bavarian population "provides evidence that different populations of the same species can adapt in different ways to climate change," noting "this was also previously found for woodland species," citing Visser *et al*. (2002) and Sanz (2003).

Wesolowski and Cholewa (2009) investigated evidence for climate warming in Bialowieza National Park of East Poland over the period 1975–2007 to determine "whether local populations of four sedentary birds (*Sitta europaea, Poecile palustris, Cyanistes caeruleus, Parus major*) advanced their breeding phenology during that time, and how breeding phenology was affected by temperature variation during the period preceding egg laying." According to the authors, "mean yearly temperatures varied strongly across years, with a significant warming (~1°C) trend," and "in all species the onset of breeding was vary variable across years (up to 30 days), as birds started breeding earlier in springs with higher temperatures in the pre-laying period." They note the spring of 1990—when February and March were extremely warm with "mean temperatures +5°C higher than these months' averages, equivalent to the 'worst' IPCC warming scenario"—served as a natural experiment, showing "what would happen when the late winter/early spring period got substantially warmer." They found "all four species were able to react to this challenge by advancing the onset of breeding to unusually early dates that are usually found only in the Mediterranean populations."

The two researchers write, "the ability to react even in these extreme conditions shows that the range of phenotypic plasticity in these birds is far greater than normally observed, and suggests that there is still unexpressed potential in lay date flexibility." They therefore conclude, "local birds are already prepared to cope with envisaged warming, suggesting that there is no need for new response mechanisms." In addition, they state this phenomenon is "clearly noticeable among different groups of organisms in Bialowieza National Park (e.g. timing of bud burst in trees, Wesolowski and Rowinski, 2006, 2008; development of herbs on the forest floor, Falinski 2001, Sparks *et al*., 2009)," and they thus also conclude, "birds, trees and herbs in this primeval forest apparently 'read' environmental cues in a similar way and react to them in a comparable fashion," probably because "they have been exposed to the same vagaries of local climate over ages if not millennia, and there was plenty of time to match phenology of interacting species with one another."

Thomas *et al*. (2010) note "the timing of annual breeding is a crucial determinant of reproductive success, individual fitness, and population performance, particularly in insectivorous passerine birds," because "by synchronizing hatching with the narrow time window of maximal food abundance, parents can enhance their reproductive success through an increase in offspring growth rate and body condition, survival to fledging, and subsequent recruitment into the breeding population." They studied two populations of blue tits in northern Corsica (Muro and Pirio) to determine "how laying date is related to spring temperatures and vegetation phenology." These two factors were assumed to figure highly in determining the peak period of blue tit food abundance (caterpillars). They discovered "Blue Tits use a cue system that is context specific to fine-tune laying dates to match local conditions both on a spatial (habitat) scale and on a temporal (inter-annual) scale," and their "reliance on both temperature and phenology when breeding late in the season, as occurs in most populations where tits have been intensively studied north of the Mediterranean region, satisfactorily explains how these populations can advance breeding in response to rising spring temperatures while maintaining a relatively large variation in the onset of breeding on a local spatial scale."

Thomas *et al*. acknowledge, "if a single environmental feature [such as temperature] were responsible for the timing of breeding, climate change could cause a severe decline in breeding success, with negative demographic consequences." However, they state they "have not detected any consistent mismatch between Blue Tit breeding dates and caterpillar peak [abundance] dates over the 14 and 21 years for which they have data for Muro and Pirio, respectively." Their findings, they conclude, "offer some hope that breeding populations will respond well to global warming."

Barnagaud *et al*. (2011) note "deciphering the effects of climatic conditions on population dynamics is of major importance in understanding how organisms are likely to be affected by climate changes." Toward that end, they "used broad scale annual censuses of adult and young Black Grouse in the French Alps between 1990 and 2007 to test whether the breeding success of the species is affected by inter-annual climatic variation and long-term climate change," based on "annual counts of Black Grouse hens and chicks carried out by the French Mountain Galliforms Observatory on 58 counting sites," where "counts were performed on the same sites and areas from one year to another, with the same operators."

They note "the Alps are currently undergoing a significant global change in climatic conditions, with warmer temperatures and drier conditions, especially in winter, that reflect particularly well such large scale processes as the NAO [North Atlantic Oscillation]," citing Beniston *et al*. (1997), Giorgi *et al*. (1997), and Beniston (2005, 2006). They determined "the [current] optimal weather conditions for the reproduction of the Black Grouse in the French Alps correspond to average winter NAO values for the last 30 years," which suggests, they write, "the species has adapted to more frequent positive NAO anomalies in the last decades, i.e., to a warmer and drier climate."

Noting "neither the numbers of hens nor the breeding indexes have declined during the last 18 years," they further state "this result is consistent with recent reports (Storch, 2007) suggesting that the alpine populations of Black Grouse which declined during most of the twentieth century (Magnani, 1987) have stabilized in the past two decades, despite the climate warming threat." They point out "this absence of decline agrees with community-level studies showing lower-than-expected effects of climate change on alpine birds (Archaux, 2004)." The seven scientists also say their results indicate "Black Grouse have until now been able to track climatic trends towards a warmer and drier climate," and they "appear to be more threatened by declines in the availability of suitable areas and changes in habitat structure than by direct effects of climate warming on [their] reproduction." Thus, they conclude, "even a highly specialized mountain species can track rapid climate changes without decreasing its productivity, at least within the limits of current climate changes."

Weimerskirch *et al*. (2012) write, "in marine systems, wind is a major component of the environment, and climate change-induced alterations in oceanic wind regimes and strength have already occurred and are predicted to increase." With respect to what has "already occurred," they note "over the past fifty years, Southern Hemisphere westerlies have shifted poleward and increased in intensity," which could affect "the movement or distribution of wind-dependent species, such as migratory land birds or pelagic seabirds." The latter, the authors note, "rely extensively on wind to move at low costs between breeding and foraging sites," citing Weimerskirch *et al*. (2000) and Wakefield *et al*. (2009).

Weimerskirch *et al*. analyzed the possible influence of wind conditions over the Southern Ocean on the foraging ecology and life-history traits of the wandering albatross (*Diomedea exulans*), one of the most wide-ranging pelagic seabirds, employing data on the duration of their foraging trips and breeding success collected over the period 1966–2010, and foraging performance and body mass collected over the period 1989–2010, focusing on breeding birds from the Crozet Islands, which are situated in the windiest area of the Southern Ocean.

Over the period of time characterized by IPCC as having experienced unprecedented global warming, the foraging range of wandering albatrosses shifted poleward, as the wind also "strongly increased and shifted poleward," the four researchers report. As a result of this change, albatross "rates of travel and flight speeds have increased," a trend they say also has been found to have occurred in the southwestern Indian Ocean over the past 30 years by Peron *et al*. (2010). One important consequence of this change was a 22% decrease in the duration of albatross foraging trips between 1970 and 2008 (a drop from 12.4 to 9.7 days). And as a consequence of this change, they write, "breeding success has improved, and birds have increased in mass by more than one kilogram," a 10–12% increase in body weight for males and females alike.

The above-described real-world wind changes of the past half-century, in the words of Weimerskirch *et al*. (2012), "have affected positively the foraging efficiency and foraging range of wandering albatrosses, ultimately improving breeding success and reducing mortality risks, respectively." As can be estimated from their graph of the pertinent data, albatross breeding success rose from approximately 65% to 77% over the period studied.

References

Archaux, F. 2004. Breeding upwards when climate is becoming warmer: no bird response in the French Alps. *Ibis* **146**: 138–144.

Bairlein, F. and Winkel, W. 2000. Birds and climate change. In Lozan, J.L., Grassl, H., and Hupfer, P. (Eds.) *Climate of the 21st Century: Changes and Risks*. Hamburg, Germany: Wissenschaftliche Auswertungen, pp. 278–282.

Barnagaud, J.-Y., Crochet, P.A., Magnani, Y., Laurent, A.B., Menoni, E., Novoa, C., and Gimenez, O. 2011. Short-term response to the North Atlantic Oscillation but no long-term effects of climate change on the reproductive success of an alpine bird. *Journal of Ornithology* **152**: 631–641.

Beniston, M. 2005. Mountain climates and climatic change: an overview of processes focusing on the European Alps. *Pure and Applied Geophysics* **162**: 1587–1606.

Beniston, M. 2006. Mountain weather and climate: a general overview and a focus on climatic change in the Alps. *Hydrobiologia* **562**: 3–16.

Beniston, M., Diaz, S., and Bradley, R.W. 1997. Climatic change at high elevation sites: an overview. *Climatic Change* **36**: 233–251.

Brown, J.L, Shou-Hsien, L., and Bhagabati, N. 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proceedings of the National Academy of Science, U.S.A.* **96**: 5565–5569.

Dunn, P. 2004. Breeding dates and reproductive performance. *Advances in Ecological Research* **35**: 69–87.

Dyrcz, A. and Halupka, L. 2009. The response of the Great Reed Warbler *Acrocephalus arundinaceus* to climate change. *Journal of Ornithology* **150**: 39–44.

Falinski, J.B. 2001. Phytophenological atlas of the forest communities and species of Bialowieza National Park. *Phytocoenosis NS* **13**: 1–176.

Giorgi, F., Hurrell, J.W., and Marinucci, M.R. 1997. Elevation dependency of the surface climate change signal: a model study. *Journal of Climate* **10**: 288–296.

Halupka, L., Dyrcz, A., and Borowiec, M. 2008. Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. *Journal of Avian Biology* **39**: 95–100.

Husek, J. and Adamik, P. 2008. Long-term trends in the timing of breeding and brood size in the Red-Backed Shrike *Lanius collurio* in the Czech Republic, 1964–2004. *Journal of Ornithology* **149**: 97–103.

Koenig, W.D. and Stahl, J.T. 2007. Late summer and fall nesting in the Acorn Woodpecker and other North American terrestrial birds. *The Condor* **109**: 334–350.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. London, UK: Methuen.

Magnani, Y. 1987. *Reflexions sur la dynamique d'une population de Tetras lyre Tetrao tetrix L. des Alpes francaises*. In: Institut d'analyse des systemes biologiques et socio-economiques. Laboratoire de biometrie, Universite Claude Bernard Lyon I, Lyon.

Monroe, A.P., Hallinger, K.K., Brasso, R.L., and Cristol, D.A. 2008. Occurrence and implications of double brooding in a southern population of tree swallows. *The Condor* **110**: 382–386.

Muller, M., Pasinelli, G., Schiegg, K., Spaar, R., and Jenni, L. 2005. Ecological and social effects on reproduction and local recruitment in the red-backed shrike. *Oecologia* **143**: 37–50.

Peron, C., Authier, M., Barbraud, C., Delord, K., Besson, D., and Weimerskirch, H. 2010. Interdecadal changes in at-sea distribution and abundance of sub-antarctic seabirds along a latitudinal gradient in the Southern Indian Ocean. *Global Change Biology* **16**: 1895–1909.

Sanz, J.J. 2003. Large-scale effect of climate change on breeding parameters of pied flycatchers in Western Europe. *Ecography* **26**: 45–50.

Schaefer, T., Lebedur, G., Beier, J., and Leisler, B. 2006. Reproductive responses of two related coexisting songbird species to environmental changes: global warming, competition, and population sizes. *Journal of Ornithology* **147**: 47–56.

Sparks, T., Jaroszewicz, B., Krawczyk, M., and Tryjanowski, P. 2009. Advancing phenology in Europe's last remaining primeval forest: Are we in danger of underestimating the response to increasing temperatures? *Climate Research* **39**: 221–226.

Storch, I. 2007. Grouse: Status Survey and Conservation Action Plan 2006–2010. IUCN, Gland, Switzerland.

Thomas, D.W., Bourgault, P., Shipley, B., Perret, P., and Blondel, J. 2010. Context-dependent changes in the weighting of environmental cues that initiate breeding in a temperate passerine, the Corsican Blue Tit (*Cyanistes caeruleus*). *The Auk* **127**: 129–139.

Visser, M.E., Adriaensen, F., van Balen, J.H., Blondel, J., Dhondt, A.A., van Dongen, S., du Feu, C., Ivankina, E.V., Kerimov, A.B. de Laet, J., Matthysen, E., McCleery, R., Orell, M., and Thomson, D.L. 2003. Variable responses to large-scale climate change in European Parus populations. *Proceedings of the Royal Society of London B* **270**: 367–372.

Visser, M.E., Silverin, B., Lambrechts, M.M., and Tinbergen, J.M. 2002. No evidence for tree phenology as a cue for the timing of reproduction in tits *Parus* spp. *Avian Science* **2**: 1–10.

Wakefield, E., Phillips, R.A., Matthiopoulos, J., Fukuda, A., Higuchi, H., Marshall, G.J., and Trathan, P.N. 2009. Wind field and sex constrain the flight speeds of central-place foraging albatrosses. *Ecological Monographs* **79**: 663–679.

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A., and Costa, D.P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society B* **267**: 1869–1874.

Weimerskirch, H., Louzao, M. de Grissac, S., and Delord, K. 2012. Changes in wind pattern alter albatross distribution and life-history traits. *Science* **335**: 211–214.

Wesolowski, T. and Cholewa, M. 2009. Climate variation and bird breeding seasons in a primeval temperate forest. *Climate Research* **38**: 199–208.

Wesolowski, T. and Rowinski, P. 2006. Timing of bud burst and tree-leaf development in a multispecies temperate forest. *Forest Ecology and Management* **237**: 387–393.

Wesolowski, T. and Rowinski, P. 2008. Late leaf development in pedunculate oak *Quercus robur*: an antiherbivore defense? *Scandinavian Journal of Forest Research* **23**: 386–394.

5.4.3.2 Spring Arrival Dates

Changes in the date of spring migration arrival date of birds have been viewed by some as a fingerprint of climate change and possibly of species distress. Trends in this parameter should be evaluated with caution before making such a leap.

A case in point is the study of Mills (2005), who used data collected at Long Point Bird Observatory on the north shore of Lake Erie in Ontario, Canada over the period 1975–2000 to investigate whether there had been changes in the timing of spring and autumn migrations of 13 species of birds that might be viewed as ecological responses to global warming. He analyzed for trends in the day of first arrival in the spring, and in the days of first, second, and third quartile arrivals in the spring, as well as like departures in the autumn.

All 13 species exhibited earlier trends in the date of first arrival in the spring. When subjected to stringent thresholds of statistical analysis, however, only one species was considered to exhibit a definite trend. Spring quartile analyses were not nearly as universal. Only nine of the 13 species trended toward an earlier arrival date, and four trended toward a later arrival date. Of the nine that trended toward an earlier arrival date, only two were statistically significant, leaving the author to conclude, "most individuals of most species cannot conclusively be said to have migrated in 2000 earlier than their 1975 ancestors." Analysis of the quartile means revealed no significant phenological change by bird sex. With respect to autumn trends, five species showed delayed migration, two showed advanced migration, and six exhibited no trend.

Mills writes, "caution should be exercised in drawing broad conclusions about changes in migration phenology" with respect to global warming. He notes, for example, using first arrival dates to characterize migration systems "can be problematic because they are data from one tail of a distribution, they comprise a mostly male population and they may not correlate well with the balance of the migration period." He also notes "changes do not appear to be universal in spring, and change in that season is (a) considerably less than that suggested by [first arrival date] analysis and (b) both less complex and less common than that exhibited during autumn migration."

For studies that show a more conclusive link between temperature and date of bird migration, rather than considering such observations to be a sign of species in distress, an alternative and perhaps more correct interpretation is that such changes are simply a manifestation of the ability of birds to adapt or evolve in response to an environmental perturbation. Model-based claims of species decline typically do not account for adaptative or evolutionary responses, but because birds are winged creatures, it would be expected that under the threat of global warming they might take flight and migrate to cooler regions of the globe as an adaptive measure. Several studies of bird migration dates suggest they may be doing so.

Gordo and Sanz (2006) analyzed a large database of about 44,000 records they assembled from observations at more than 1,300 sites throughout Spain during the period 1944–2004 in a study of the migratory behavior for five trans-Saharan bird species: *Ciconia ciconia* or white stork, *Cuculus canorus* or cuckoo, *Apus apus* or swift, *Hirundo rustica* or barn swallow, and *Luscinia megarhynchos* or nightingale. This phenomenon previously had been proposed by the country's Instituto Nacional de Meteorologia as "a potential bioindicator of the timing of seasons," the current study of which the two Spanish researchers describe as "the most complete and thorough analysis available for the Mediterranean region."

Gordo and Sanz report "spring arrival dates have tended to advance since the mid–1970s," and "individuals arrived earlier in warmer years," noting "the earlier arrivals related to higher temperatures should be due to the advancement of the spring course in the Iberian Peninsula and consequently the presence of ecological suitable conditions for an early colonization of first breeders." They found "current arrival dates are similar or even seem to be a bit later to those occurring at the beginning of the study period." According to Gordo and Sanz, "the advance in arrival date recorded over the last few decades should be better interpreted as a trend towards re-establishing the timing of migration after an anomalous period of delayed arrivals during the 1970s–1980s," which suggests birds have been adapting to temperature changes throughout the Mediterranean region, where temperatures were likely warmer in the mid–1940s than they were throughout the 1990s and during the first years of the twenty-first century.

Studying the skylark (*Alauda arvensis*), which is migratory in Eastern and Northern Europe but resident in areas with milder winters (such as the UK), Askeyev *et al.* (2009) analyzed the dates of their spring arrival in the Volga-Kama region of the Tatarstan Republic of Russia, using "one of the longest extant records of bird migration in the world," which runs from 1811 to 2008, with sporadic missing years in the first half of the record. They report March temperatures rose about 5.2°C over their study period, but 3.7°C (~70%) of that warming occurred over the final three decades of the nearly two-century-long interval. They also found a corresponding inflection point in the rate-of-advancement of skylark spring arrival-date that was approximately 15 times greater (0.368 day per year) than it was over the study period's first 17 decades (0.024 day per year).

Plotting arrival-date as a function of temperature, they found the inflection point occurred at a mean March temperature of –3.5°C, suggesting a mean rate of advancement of spring arrival-date of 0.5 day per °C for mean March temperature increases below a negative 3.5°C, and a mean rate of advancement of arrival-date of 3.4 days per °C for mean March temperature increases above –3.5°C. That represents close to a seven-fold increase in the rate of advancement of spring arrival-date upon exceeding this biological "tipping point" temperature.

Askeyev *et al*. conclude, "the nonlinear nature of the relationship between first arrival and temperature suggests that above a critical temperature threshold a much more rapid change in first arrival date will occur." This observation suggests regardless of whether "tipping points" occur in the realm of climatology, they do in fact occur, and in some cases already have occurred, to the benefit of certain of Earth's birds—the hotter it gets, the better they do what they need to do to deal with the evolving situation.

Van Buskirk *et al*. (2012) state, "phenological responses to climate change are well-documented in plants and animals," and "it is widely assumed that much of the shift in phenology is due to facultative changes in the activities or physiologies of individuals induced by environmental conditions, known as phenotypic plasticity." However, they write, "phenotypic plasticity is not the only mechanism that can produce population responses to climate change," noting "gradual or sudden shifts in the selection regime can be triggered by environmental change, and these in turn can alter the genetic composition of populations." They point out "rapid evolved responses to climate change are widely anticipated by evolutionary biologists (Bradshaw and Holzapfel, 2001; Davis *et al*., 2005; Gienapp *et al*., 2008; Hoffman and Willi, 2008; Hoffmann and Sgro, 2011), and already have been observed in a few cases (Umina *et al*., 2005; Bradshaw and Holzapfel, 2008)."

Between June 1961 and August 2006, Van Buskirk *et al*. operated 35 mist nets for five to six days a week on a 10-ha study area on the Powdermill Nature Reserve in Pennsylvania (USA), in order to obtain the data needed to estimate the magnitude of temperature-induced phenotypic plasticity in spring arrival date of 27 species of birds in eastern North America, by recording the effects of annual variation in spring temperature on the behavior of thousands of individuals. They hypothesized that if phenotypic plasticity could not account for the totality of observed shifts in migration phenology over this period, what remained unaccounted for could be attributed, at least partly, to microevolutionary change.

The three researchers report "for 2441 individuals detected in multiple years, arrival occurred earlier during warm years, especially in species that migrate short distances," but the change in phenology predicted "under a model of pure phenotypic plasticity" fell far short of the change in arrival date they observed, explaining only 13–25% of the climate-induced trend in phenology. Although they acknowledge their approach to the problem "probably underestimates the full scope of plasticity," Van Buskirk *et al*. say their data suggest "part of the response to environmental change [warming] has been caused by microevolution." They also conclude "the estimated evolutionary rates [0.016 haldanes] are plausible."

The three scientists write, "rapid genetic response to climate change is widely seen as a critical component of the kind of adaptation that will be required of many organisms," especially in a world that warms as suggested by the models employed by IPCC. In addition, "the contribution of plasticity will allow individuals to adjust their phenotype to short-term environmental fluctuations, which are projected to increase under most scenarios of climate change." That's good news for birds.

References

Askeyev, O.V., Sparks, T.H., and Askeyev, I.V. 2009. Earliest recorded Tatarstan skylark in 2008: non-linear response to temperature suggests advances in arrival dates may accelerate. *Climate Research* **38**: 189–192.

Bradshaw, W.E. and Holzapfel, C.M. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academies of Science USA* **98**: 14,509–14,511.

Bradshaw, W.E. and Holzapfel, C.M. 2008. Genetic responses to rapid climate change: it's seasonal timing that matters. *Molecular Ecology* **17**: 156–166.

Davis, M.B., Shaw, R.G., and Etterson, J.R. 2005. Evolutionary responses to changing climate. *Ecology* **86**: 1704–1714.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A., and Merila, J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology* **17**: 167–178.

Gordo, O. and Sanz, J.J. 2006. Climate change and bird phenology: a long-term study in the Iberian Peninsula. *Global Change Biology* **12**: 1993–2004.

Hoffmann, A.A. and Sgro, C.M. 2011. Climate change and evolutionary adaptation. *Nature* **470**: 479–485.

Hoffmann, A.A. and Willi, Y. 2008. Detecting genetic responses to environmental change. *Nature Reviews Genetics* **9**: 421–432.

Mills, A.M. 2005. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* **147**: 259–269.

Umina, P.A., Weeks, A.R., Kearney, M.R., McKechnie, S.W., and Hoffmann, A.A. 2005. Rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science* **308**: 691–693.

Van Buskirk, J., Mulvihill, R.S., and Leberman, R.C. 2012. Phenotypic plasticity alone cannot explain climate-induced change in avian migration timing. *Ecology and Evolution* **2**: 2430–2437.

5.4.3.3 Trophic Mismatches

Another concern about the potential effects of global warming is that, as the world warms, mismatches may occur among various life cycle stages of plants, the insects that feed on them, and numerous species of animals, such as birds, that feed on insects and provide them as food for their young, a situation that could spell disaster for some species. This concept has been said by Visser and Both (2005) to constitute an "insufficient adjustment" to climate change. This section investigates the validity of such concerns, finding trophic mismatches are a non-problem in most instances.

Bauer *et al.* (2010) examined the effect of 47 years of warming (1961–2007) on the time of leafing-out of dominant English oak trees (*Quercus robur*) at four research sites in the Czech Republic located in full-grown, multi-aged floodplain forests that had been under no forestry management. The researchers also evaluated the time of appearance of the two most abundant species of caterpillars in the floodplain forests—the winter moth (*Operophtera brumata*) and the tortrix moth (*Tortrix viridana*)—and the first and mean laying dates of two of the ecosystem's most common birds: great tits (*Parus major*) and collared flycatchers (*Ficedula albicollis*).

According to the researchers, "mean annual temperature showed a significant increase of 0.27–0.33°C per decade, with approximately the same magnitude of change during spring at all sites." They also found, "on average (all four sites), the bud burst date for English Oak has advanced by 7.9 days and full foliage by 8.9 days, with approximately the same shifts being recorded for the peak of the beginning and end of frass for herbivorous caterpillars," the observational variable they used to characterize the caterpillars' presence. Last, they determined "the first laying date of Great Tits has advanced by between 6.2 to 8.0 days," and "the mean laying date has advanced by 6.4 to 8.0 days." Similarly, the "Collared Flycatcher first laying date has advanced by 8.5 to 9.2 days over the past 47 years, and the mean laying date by 7.7 to 9.6 days."

Bauer *et al.* state "trends in the timing of reproduction processes of both bird species are coherent with the trends in development of English Oak and with peak herbivorous caterpillar activity." In this specific food chain, the common shifting of the different organisms' phenological stages toward the beginning of the year "does not appear to have led to mistiming in the trophic food chain."

Citing Visser *et al.* (1998, 2006) and Visser (2008), Matthysen *et al.* (2011) note "the increasing mismatch between great tit *Parus major* laying dates and their caterpillar food supply in the Netherlands has rapidly become a classic example of a lack of adaptation to climate change." However, they report, "other populations of the same bird species have subsequently been shown to advance their laying dates much more strongly" in order to match the earlier spring growth of vegetation that typically occurs during periods of extended warming, citing Cresswell and McCleery (2003) and Charmantier *et al.* (2008).

Matthysen *et al.* "studied the breeding cycle of two sympatric and closely related species, the blue tit *Cyanistes caeruleus* and the great tit *Parus major,* in a rich oak-beech forest," where they had collected data on the breeding biology of the birds from 1979 to 2007 in a 12-hectare plot provided with nest boxes inside the Peerdsbos forest near Antwerp, Belgium. Both bird species were shown to have "advanced their mean first-egg dates by 11–12 days over the last three decades," and "the time from first egg to fledging has shortened by 2–3 days, through a decrease in laying interruptions, incubation time and nestling development time."As a consequence, they write, "the average time of fledging has advanced by 15.4 and 18.6 days for blue and great tits, respectively, and variance in fledging dates has decreased by 70–75%." Most important, they note, "indirect estimates of the food peak suggest that both species have maintained synchronization with the food supply," and "analyses of within-individual variation show that most of the change can be explained by individual plasticity in laying date, fledging date and nest time." Matthysen *et al.* emphasize "synchronization of the nestling period with the food supply not only depends on first-egg dates but also on additional reproductive parameters including laying interruptions, incubation time and nestling growth rate." As a result of adjustments in these several related phenomena, they report, "both of our study species have been able to maintain synchrony with their food supply in the face of global warming."

Vatka *et al*. (2011) further investigated the possibility global warming may lead to trophic mismatches between the times when birds of temperate and boreal regions require an abundance of food to feed their new hatchlings and the times when that food is available in its greatest abundance, as in the cases of great tits, blue tits, and pied flycatchers in the Netherlands, which require a timely abundance of caterpillars to feed their young (Visser *et al*., 1998; Visser *et al*., 2006; Both *et al*., 2009). Vatka *et al*. note, "the same has not happened with great tits in England (Cresswell and McCleery, 2003) nor with great tits and collared flycatchers in the Czech Republic (Bauer *et al*., 2010)." They describe yet a third type of food supply-and-demand response to warming they recently observed and documented.

Working with data collected in northern Finland over the period 1975–2009 within coniferous, deciduous, and mixed forests of varying ages—including young stands, swamps, and clear cuttings—the three Finnish scientists studied "changes in the timing of breeding in the willow tit (*Poecile montanus*), and the timing of its caterpillar food resource in relation to warming springs," using "generalized linear mixed effect models to study the importance of synchrony between the timing of breeding in willow tits and the caterpillar food availability on the breeding success, measured as nestling survival rate and mean nestling weight." In contrast to prior no change results and poorer synchrony findings, Vatka *et al*. report they not only "found no signs of emerging asynchrony" but that synchrony actually improved during the study, and it had moderate positive effects on breeding success. The observed improvement in synchrony mirrors results from the coal tit in the Netherlands, the authors add, citing Both *et al*. (2009).

Reed *et al*. (2013) studied a wild population of great tits (*Parus major*) in the Netherlands in relation to the phenology of their food supply, noting "great tits rely on caterpillars to feed their chicks and strive to match their breeding time with the pronounced seasonal peak in caterpillar biomass, which enhances offspring survival." The researchers studied this by "using almost four decades of individual-level life-history data from a great tit population." They report warmer springs had indeed "generated a mismatch between the annual breeding time and the seasonal food peak, intensifying directional selection for earlier laying dates." However, they found inter-annual variation in population mismatch had not affected population growth, and they "demonstrated a mechanism contributing to this uncoupling, whereby fitness losses associated with mismatch are counter-acted by fitness gains due to relaxed competition." The team of Dutch, French, Norwegian, and U.S. scientists states their findings imply "natural populations may be able to tolerate considerable maladaptation driven by shifting climatic conditions without undergoing immediate declines." They conclude, "our results imply that considerable directional selection might be demographically tolerable on decadal time scales without immediate population declines, effectively buying time for microevolution to restore adaptation."

Burthe *et al*. (2012) "compared phenological trends for species from four levels of a North Sea food web over 24 years [1983–2006] when sea surface temperature (SST) increased significantly," starting with primary producers (phytoplankton), primary consumers (zooplankton), and secondary consumers (sandeels), and finally focusing on five seabird predators—the common guillemot (*Uria aalge*), razor bill (*Alca torda*), European shag (*Phalacrocorax aristotelis*), black-legged kittiwake (*Rissa tridactyla*), and Atlantic puffin (*Fratercula arctica*)—all of which are seabirds that prey on current-year sandeels (*Ammodytes marinus*). The nine researchers say they found "little consistency in phenological trends between adjacent trophic levels, no significant relationships with SST, and no significant pairwise correlations between predator and prey phenologies," which they take as evidence "trophic mismatching is occurring." Yet in spite of the supposed trophic mismatches discovered over the course of their research, Burthe *et al*. report, "to date, there is no evidence that these changes are impacting on the breeding success of any of the seabird species."

Although much remains to be learned about this topic, it is clear trophic mismatches, thought to be initiated by global warming, need not produce negative responses from bird populations. Many bird species may not be affected at all, and others may even benefit from such a climate change.

References

Bauer, Z., Trnka, M., Bauerova, J., Mozny, M., Stepanek, P., Bartosova, L., and Zalud, Z. 2010. Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. *International Journal of Biometeorology* **54**: 99–111.

Both, C., van Asch, M., Bijlsma, R.G., van den Burg, A.B., and Visser, M.E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* **78**: 73–83.

Burthe, S., Daunt, F., Butler, A., Elston, D.A., Frederiksen, M., Johns, D., Newell, M., Thackeray, S.J., and Wanless, S. 2012. Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Marine Ecology Progress Series* **454**: 119–133.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B., and Sheldon, B.C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**: 800–803.

Cresswell, W. and McCleery, R. 2003. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology* **72**: 356–366.

Matthysen, E., Adriaensen, F., and Dhondt, A.A. 2011. Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus, Parus major*). *Global Change Biology* **17**: 1–16.

Reed, T.E., Grotan, V., Jenouvrier, S., Saether, B.-E., and Visser, M.E. 2013. Population growth in a wild bird is buffered against phonological mismatch. *Science* **340**: 488–491.

Vatka, E., Orell, M., and Rytkonen, S. 2011. Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. *Global Change Biology* **17**: 3002–3009.

Visser, M.E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B-Biological Sciences* **275**: 649–659.

Visser, M.E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for yardstick. *Proceedings of the Royal Society B* **272**: 2561–2569.

Visser, M.E., Holleman, L.J.M., and Gienapp, P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**: 164–172.

Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M., and Lessells, C.M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society B-Biological Sciences* **265**: 1867–1870.

5.4.3.4 Other Responses

Additional adaptive or evolutionary responses to warming, not discussed in the prior subsections, have been identified in the literature for birds, each of which suggests birds are adequately suited to withstand any of the temperature changes predicted to accompany the future rise in atmospheric CO_2.

In regard to the challenges migratory animals may face due to potential changes in climate, Dias *et al*. (2011) write, "existing phenotypic plasticity *per se* may allow, within certain limits, the persistence of species and populations (even if in suboptimal circumstances), gaining time for selection to act, or for more favorable environmental conditions to be restored," noting "there is strong evidence that recent climate changes may have already impacted migratory behavior" as it pertains to birds, citing Fiedler (2003) and Newton (2008).

Dias *et al*. evaluated individual flexibility in the migration strategies of a highly pelagic seabird, the Cory's shearwater (*Calonectris diomedea*). They deployed leg-mounted geolocators weighing approximately 3.6 grams at the end of the breeding seasons of 2006, 2007, and 2008, recovering them in the early stages of the subsequent breeding seasons, to track the migration of 57 of the birds that spent the breeding season at Selvagem Grand Island (30°02' N, 15°52' W). The five researchers report 14 birds that were tracked for more than one non-breeding season "showed a remarkable capacity to change winter destinations between years," with some shifting all the way from the South Atlantic to the North Atlantic, and from the Atlantic Ocean to the Indian Ocean. They found individual birds "also showed flexibility in stopover behavior and migratory schedule." Dias *et al*. conclude Cory's shearwaters are in a good position "to face the consequences of a changing environment," adding, "whether Cory's shearwaters are unusual in this respect, or whether future analyses will reveal that flexibility in migration strategies is a more general trait of marine migratory fauna is something that repeated tracking of individuals in coming years should clarify."

According to Forero-Medina *et al*. (2011), "the tropics contain most of the world's species at risk of extinction (Pimm and Jenkins, 2010), yet few studies evaluate the response of tropical species to climate disruption other than through modeling (Jetz *et al*., 2007; Marini *et al*., 2009; La Sorte and Jetz, 2010)." Using the same sampling techniques employed by Terborgh and Weske (1975) in 1969, and working at five of the nine localities studied by those earlier investigators, Forero-Medina *et al*. (2011) resampled bird communities at five elevations (690, 1310, 1570, 1970, and 2220 meters) within the Reserva Comunal El Sira on the Cerros del Sira massif in Peru 41 years later in 2010, seeking to determine what changes might have occurred in the elevations of the several species encountered at the two sampling times. Of the 55 species encountered in both sampling years, the four researchers report 36 had moved up in elevation, 12 had moved down, and seven had not moved in either direction, resulting in an average upward shift of 49 meters for the 55 bird species over the 41-year period. They describe this change in elevation as "significantly smaller" than the 152-meter increase one would have expected from the amount of warming experienced throughout the region between the times of the two studies.

Forero-Medina *et al.* note more than one mountain had been involved in the initial study of Terborgh and Weske (1975), and "the same bird species exhibited different elevation ranges on different mountains, indicating considerable flexibility in the occupancy of habitat and independence of temperature (Diamond, 1970; Terborgh, 1985)." Therefore, they write, "the limited upward elevational shifts reported here are unlikely to be simple responses to increased temperature *per se*." Instead, they suggest, "birds are likely responding to gradual changes in the nature of the habitat or availability of food resources through their dependence on long-lived elements of the ecosystem (trees), and how the species' competitors respond." They note "the rate of migration of trees is less (45%) than that predicted from the temperature increase of the region," and "similar lags in the response of trees may be occurring at the Sira, accounting for the lag in response of birds."

Put another way, Forero-Medina *et al.* conclude, "instead of being directly dependent on temperature, birds may be responding to gradual changes in the nature of their habitat or availability of food resources, and presence of competitors," so "endothermy [the ability of certain animals to control their body temperature] may provide birds with some flexibility to temperature changes and allow them to move less than expected."

Van Buskirk *et al.* (2010) write, "recent climate change has caused comparatively rapid shifts in the phenology and geographic distributions of many plants and animals," but "there is debate over the degree to which populations can meet the challenges of climate change with evolutionary or phenotypic responses in life history and morphology," which for a warming climate includes a reduction in body size. They devised an experimental strategy to explore the issue further, studying the body sizes of birds captured in mist-nets and traps between June 1961 and November 2006 at the Powdermill Nature Reserve, a field station operated by the Carnegie Museum of Natural History in Pennsylvania (USA) at a location broadly representative of bird communities in the Appalachian region of eastern North America. At this location, 35 mist nets were operated five to six days per week during spring and autumn migrations. A reduced number of nets was used during summer, and birds for winter banding were caught in wire traps when the temperature was below freezing.

The three researchers report migrating birds captured at the banding station "have steadily decreasing fat-free mass and wing chord since 1961, consistent with a response to a warmer climate" and confirming "phenotypic responses to climate change are currently underway in entire avian assemblages," where "size was negatively correlated with temperature in the previous year, and long-term trends were associated with the direction of natural selection acting on size over the winter." In addition, they note, "species undergoing the strongest selection favoring small wing chord showed the most rapid long-term declines in wing [size]," which suggests "phenotypic changes are therefore in line with the prevailing selection regime." Noting "in summer, 51 of 65 breeding species had negative slopes of mass against year, 20 of 26 wintering species had negative slopes, 60 of 83 spring migrants had negative slopes, and 66 of 75 autumn migrants had negative slopes," Van Buskirk *et al.* state their results "offer compelling evidence that climate change has already produced observable adaptive shifts in morphology, behavior, and phenology of a great many species," which suggests these birds have evolved a capacity for rapid phenotypic shifts to optimum body mass in response to climate fluctuations.

Additional support for this thesis comes from Carey (2009), who notes "organisms living today are descended from ancestors that experienced considerable climate change in the past," and thus suggests, "species that persist into future climates may be able to do so in part owing to the genetic heritage passed down from ancestors who survived climate changes in the past." She also states, "if climate change were the only new challenge facing birds, one might imagine that many species could become adapted to new conditions and survive with existing population variability and the genetic information that their ancestors used to survive past climate change."

Karell *et al.* (2011) theorize "global climate warming changes the environment of most organisms and is expected to lead to a change in selection pressures with micro-evolutionary consequences that allow the adaptation of organisms to the new environment and thereby long-term population persistence." They further note, "microevolution in response to climate change has been demonstrated in invertebrate populations (Umina *et al*., 2005; Balanya *et al*., 2006)," but "these studies lack information on the mechanisms and selective factors linking particular genotypes to climate."

Karell *et al*. explored "the links between climate change and alteration of the selective regime on a highly heritable phenotypic trait, plumage coloration in the tawny owl (*Strix aluco*), a common bird of prey throughout the temperate regions of Europe." They used data from 1981 to 2008 in a 250-km^2 study area in Southern Finland dominated by mixed forests, agricultural areas, and small freshwater courses, where "plumage coloration was scored using a semi-continuous ordinal scale (range from 4 (grey) to 14 reddish-brown)) on all breeding individuals on each encounter ($N = 1116$ records of 491 individuals) using a standardized and repeatable scoring that shows coloration is independent of age and sex." In addition, they scored museum skin specimens collected between 1915 and 1980; and they extracted the data on all records of adult ringed and recaptured tawny owls in Finland to which color morph (grey or brown) had been assigned during 1961–2008. Finally, they write, "measures of temperature and snow depth from the time window that correlated best with annual tawny owl survival were selected as covariates for further modeling."

The five Finnish researchers determined "brown individuals had lower survival than grey ones as snow cover became deeper" and there was a "lower survival for brown individuals compared with grey ones in cold temperatures," as cooler conditions would be expected to promote a deeper snow cover. Thus they report as snow depth decreased over time in response to warming, "there was a time trend in survival of the color morphs from 1981–2008, in which survival of the grey morph was fairly stable across years, whereas survival of brown individuals improved dramatically towards the end of the time series." They also report this phenotypic change was present on a larger nationwide scale—the increase of the brown morph occurred "all over Finland, involving thousands of individuals," such that "the survival propensities of the morphs have equalized in recent, mild winters."

Karell *et al*. remark the phenotypic change they documented "is unlikely to be caused by genetic drift, because drift is only a major force for changing allele frequencies in small populations." Therefore, "given the strong genetic underpinning of tawny owl morphs," they say they consider the observed phenotypic trend in the proportion of the brown morph as "indicative for a shift in gene frequencies." Hence, they conclude, to the best of their knowledge, the results of their study constitute "the first empirical evidence of climate-driven change in selection on a heritable trait," providing a whole new perspective on the potential of Earth's fauna to withstand the challenges of global warming.

Gremillet *et al*. (2012) state little auks (*Alle alle*) are the most numerous seabirds in the North Atlantic, with an estimated population of 40 to 80 million individuals, citing Stempniewicz (2001), and they consume up to 24% of local plankton production, citing Karnovsky and Hunt (2002). The researchers also note the "little auk field metabolic rate is 70% higher than predicted by body mass, and they have very limited capacity to store fat." Consequently, they say, little auks "are predicted to be particularly sensitive to altered feeding conditions," citing Harding *et al*. (2009). More specifically, they write, the recent work of Karnovsky *et al*. (2010) "showed a very strong link between summer SST [sea surface temperature] within the foraging areas of little auks, species composition of local zooplankton communities, and dietary preferences of the birds, whereby colder water contained more larger copepods, which were also preferentially fed upon by little auks," so "birds had to feed on smaller, less profitable copepod species in warmer water." As a result of these observations, they hypothesize "higher SSTs would modify little auk diet, foraging effort, provisioning rates, breeding success and adult survival," which they presume would significantly decline in response to warming.

In an integrative study of the behavior, physiology, and fitness of colonies of little auks at three sites of significantly different temperature—Kap Hoegh, East Greenland (70°43'N, 22°38'W), Hornsund, West Spitsbergen (77°00'N, 15°22'E), and Kongsfjorden, West Spitsbergen (79°01'N, 12°25' E)—Gremillet *et al*. evaluated the effects of ocean warming on little auks across the Greenland Sea over the period 2005–2007. They noted "comparing the ecophysiology of little auks from different colonies subject to contrasting SST regimes at one moment in time" would allow them to "simulate the effect that increasing water temperatures might have on this Arctic species across the 21st century."

"During the study period," the researchers write, "little auks maintained their fitness despite contrasting ocean surface temperatures and copepod availability across the Greenland Sea." Gremillet *et al*. write, "contrary to our hypothesis, the birds responded to a wide range of sea surface temperatures via plasticity of their foraging behavior, allowing them to maintain their fitness levels," indicating "they are successful at dealing with the influence of current climate change in the Arctic." In the concluding sentence of their abstract, the team of nine scientists from eight countries (Canada, Denmark, France, Ireland, Norway, Poland, South Africa, and the United States) writes, "predicted effects of climate change are significantly attenuated by such plasticity, confounding attempts to forecast future effects of climate change using envelope models."

According to Smit *et al*. (2013), "one of the main predictions of bioclimatic envelope models is that populations near the climatic extremes of species' distributions, where thermoregulatory costs are presumably high, are performing sub-optimally and are at greater risk of extinction," citing Thomas *et al*. (2004). However, Smit *et al*. suggest, "if populations are physiologically adapted (genetic variation across generations and/or plastic adjustments) to their respective climates, species may be capable of maintaining high levels of performance throughout their geographic ranges," citing Chown *et al*. (2010) and Glanville *et al*. (2012).

Smit *et al*. investigated the effects of air temperature (T_A) on body temperature (T_B) and the behavior of an arid-zone endotherm, the White-Browed Sparrow-Weaver (*Plocepasser mahali*) at two sites 100 km apart, in the southern Kalahari Desert of South Africa, over two consecutive summer seasons. The four researchers found a relatively large variation in T_B that occurred both within and between populations, suggesting "an arid-zone passerine responds differently to prevailing weather conditions in two locations over its range, and that it also responds to seasonal changes in weather conditions." This further suggests "a species' current range may not be an accurate representation of its climatic tolerance."

"Taken together with the data of Glanville *et al*. (2012)," Smit *et al*. explain, this result "suggests that the thermal physiology of endotherms is far more flexible than previously thought, and could potentially contribute to the adaptation of populations under changing climatic conditions," citing Boyles *et al*. (2011)." They conclude, "when predicting species' responses to climate change, their sensitivity (sensu Williams *et al*., 2008) should be resolved at the population, rather than species, level."

References

Balanya, J., Oller, J.M., Huey, R.B., Gilchrist, G.W., and Serra, L. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science* **313**: 1773–1775.

Boyles, J.G., Seebacher, F., Smit, B., and McKechnie, A.E. 2011. Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology* **51**: 676–690.

Carey, C. 2009. The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B* **364**: 3321–3330.

Chown, S.L., Hoffmann, A.A., Kristensen, T.N., Angilletta, M.J., Stenseth, N.C., and Pertoldi, C. 2010. Adapting to climate change: a perspective from evolutionary physiology. *Climate Research* **43**: 3–15.

Diamond, J.M. 1970. Ecological consequences of island colonization by Southwest Pacific birds, I. Types of niche shifts. *Proceedings of the National Academy of Sciences USA* **67**: 529–536.

Dias, M.P., Granadeiro, J.P., Phillips, R.A., Alonso, H., and Catry, P. 2011. Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings of the Royal Society B* **278**: 1786–1793.

Fiedler, W. 2003. Recent changes in migration behavior of birds: a compilation of field observations and ringing data. In: Berthold, P., Gwinner, E., and Sonnenschein, E. (Eds.) *Avian Migration*. Springer, Berlin, Germany, pp. 21–38.

Forero-Medina, G., Terborgh, J., Socolar, S.J., and Pimm, S.L. 2011. Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS ONE* **6**: e28535.

Glanville, E.J., Murray, S.A., and Seebacher, F. 2012. Thermal adaptation in endotherms: climate and phylogeny interact to determine population-level responses in a wild rat. *Functional Ecology* **26**: 390–398.

Gremillet, D., Welcker, J., Karnovsky, N.J., Walkusz, W., Hall, M.E., Fort, J., Brown, Z.W., Speakman, J.R., and Harding, A.M.A. 2012. Little auks buffer the impact of current Arctic climate change. *Marine Ecology Progress Series* **454**: 197–206.

Harding, A.M.A., Egevang, C., Walkusz, W., Merkel, F., Blanc, S., and Gremillet, D. 2009. Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behavior, and energy consumption. *Polar Biology* **32**: 785–796.

Jetz, W., Wilcove, D.S., and Dobson, A.P. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* **5**: 3157.

Karell, P., Ahola, K., Karstinen, T., Valkama, J., and Brommer, J.E. 2011. Climate change drives microevolution in a wild bird. *Nature Communications*: 10.1038/ ncomms1213.

Karnovsky, N., Harding, A.M.A., Walkusz, V., Kwasniewski, S., Goszczko, I., Wiktor, J., Routti, H., Bailey, A., McFadden, L., Brown, Z., Beaugrand, G., and Gremillet, D. 2010. Foraging distributions of little auks (*Alle alle*) across the Greenland Sea: Implications of present and future climate change. *Marine Ecology Progress Series* **415**: 283–293.

Karnovsky, N.J. and Hunt Jr., G.L. 2002. Estimation of carbon flux to dovekies (*Alle alle*) in the North Water. *Deep Sea Research II* **49**: 5117–5130.

La Sorte, F.A. and Jetz, W. 2010. Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B Biological Sciences* **277**: 3401–3410.

Marini, M.A., Barbet-Massin, M., Lopes, L.E., and Jiguet, F. 2009. Predicted climate-driven bird distribution changes and forecasted conservation conflicts in a neotropical savanna. *Conservation Biology* **23**: 1558–1567.

Newton, I. 2008. *The Migration Ecology of Birds.* Academic Press, London, United Kingdom.

Pimm, S.L. and Jenkins, G.L. 2010. Extinctions and the practice of preventing them. In: Sodhi, N.S. and Ehrlich, P.R. (Eds.) *Conservation Biology for All.* Oxford University Press, Oxford, United Kingdom, pp. 181–198.

Smit, B., Harding, C.T., Hockey, P.A.R., and McKechnie, A.E. 2013. Adaptive thermoregulation during summer in two populations of an arid-zone passerine. *Ecology* **94**: 1142–1154.

Stempniewicz, L. 2002. *Alle alle* little auk. *The Journal of the Birds of the Western Palearctic*. Oxford University Press, Oxford, United Kingdom. *BWP Update* **3**: 175–201.

Terborgh, J. 1985. The role of ecotones in the distribution of Andean birds. *Ecology* **66**: 1237–1246.

Terborgh, J. and Weske, J.S. 1975. The role of competition in the distribution of Andean birds. *Ecology* **56**: 562–576.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Barend, F., Erasmus, N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., and Williams, S.E. 2004. Extinction risk from climate change. *Nature* **427**: 145–148.

Umina, P.A., Weeks, A.R., Kearney, M.R., McKechnie, S.W., and Hoffmann, A. 2005. A rapid shift in a classical clinal pattern in *Drosophila* reflecting climate change. *Science* **308**: 691–693.

Van Buskirk, J., Mulvihill, R.S., and Leberman, R.C. 2010. Declining body sizes in North American birds associated with climate change. *Oikos* **119**: 1047–1055.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffman, A.A., and Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* **6**: 2621–2626.

5.5 Insects

- Published research indicates rising temperatures will not likely increase, and may decrease, plant damage from leaf-eating herbivores, as rising atmospheric CO_2 boosts the production of certain defensive compounds in plants that are detrimental to animal pests.

Included among the many animal-related concerns over global warming is the worry there will be an increase in the intensity of herbivore pressure on plants. This section reviews research that has been conducted on this topic, beginning with research regarding aphids and then moths, and then regarding specific kinds of vegetation (herbaceous plants, woody plants, and other plants.

5.5.1 Aphids

We begin our survey of the effects of rising temperature and CO_2 levels on aphids with Ma *et al.* (2004), who conducted detailed experiments on the impacts of high temperature, period of exposure, and developmental stage on the survival of the aphid *Metopolophium dirhodum*, which they say “is the most abundant of the three cereal aphid species in Germany and central European countries.” This protocol revealed “temperatures over 29°C for 8 hours significantly reduced survival, which decreased generally as the temperature increased.” The researchers also determined “exposing aphids to 32.5°C for 4 hours or longer significantly reduced survival,” and “mature aphids had a lower tolerance of high temperatures than nymphs.” Ma *et al.* conclude, “global warming may play a role in the long-term changes in the population abundance of *M. dirhodum*.” Specifically, “an increase in TX [daily average temperature] of 1°C and MaxT [maximum daily temperature] of 1.3°C during the main period of the aphid population increase would result in a 33% reduction in peak population size,” and “an increase in TX of 2°C and MaxT of 2.6°C would result in an early population collapse (74% reduction of population size)."

Adler *et al*. (2007) examined the effects of long-term experimental warming on an aphid-sagebrush (*Obtusicauda coweni-Artemisia tridentata*) interaction out-of-doors in the field at the Rocky Mountain Biological Laboratory, Colorado (USA), where five of ten 3-m x 10-m plots in an ungrazed montane meadow were warmed by overhead infrared heaters that provided a continuous heat flux of 22 W/m^2 to the plots ever since 1993. Working at this facility for three consecutive years (1996–1998), they determined how warming affected aphid density, and they used additional observations, manipulative experiments, and chemical analyses to explore some of the mechanisms that might mediate potential effects of warming on aphid density.

The four researchers report, "in no year did we find support for the prediction that warming increased aphid abundance or population growth." They found "warming decreased aphid density on sagebrush in one year, tended to decrease aphids in a second year, and had no effect in a third year." In the first of these years (1997), "there were over 3 times as many aphids per stalk in control compared to warmed plots," and "the proportion of stems infested was almost twice as high." Furthermore, "in enclosures that excluded predators, warming decreased aphid population growth by an amount consistent with observed field density differences," and in a separate snow-manipulation experiment in unheated plots, they found "the timing of snowmelt did not affect aphid density." Adler *et al*. conclude, "long-term studies within a natural community context may provide counterexamples to the prediction that warming will increase herbivore pressure on plants."

Much more research has been conducted on the direct and indirect response of aphids to rising atmospheric CO_2. Docherty *et al*. (1997), for example, grew beech and sycamore saplings in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm, while groups of three sap-feeding aphid species were allowed to feed on the saplings. Overall, the elevated CO_2 had few significant effects on aphid feeding and performance. There was, however, a non-significant tendency for elevated CO_2 to reduce the individual weights and population sizes of the aphids, suggesting future increases in the air's CO_2 content might reduce aphid feeding pressures on beech and sycamore saplings, and possibly other plants as well.

Whittaker (1999) reviewed the scientific literature on population responses of herbivorous insects to atmospheric CO_2 enrichment, concentrating on papers resulting from relatively long-term studies. The only herbivorous insects found to exhibit population increases in response to elevated CO_2 exposure were those classified as phloem feeders; specifically, aphids. Although this finding appeared to favor aphids over plants, additional studies came to different conclusions.

Newman *et al*. (1999) grew tall fescue plants for two weeks in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm before inoculating them with aphids (*Rhopalosiphum padi*). After nine additional weeks of differential CO_2 exposure, the plants were harvested and their associated aphids counted. Although elevated CO_2 increased plant dry matter production by 37%, this did not result in similar increases in aphid colonization. The plants grown in air of elevated CO_2 concentration contained far fewer aphids than the plants grown in ambient air.

Percy *et al*. (2002) grew the most widely distributed tree species in all of North America—trembling aspen—in 12 30-m-diameter FACE rings in air maintained at ambient CO_2 and O_3 concentrations, ambient O_3 and elevated CO_2 (560 ppm during daylight hours), ambient CO_2 and elevated O_3 (46.4–55.5 ppb during daylight hours), and elevated CO_2 and O_3 over each growing season from 1998 through 2001. Throughout the experiment they assessed a number of the young trees' growth characteristics and the responses of the sap-feeding aphid *Chaitophorus stevensis*, which they say "infests aspen throughout its range." By itself, elevated CO_2 did not affect aphid abundance, but it increased the densities of natural enemies of the aphids, which over the long term would tend to reduce aphid numbers. Also, by itself, elevated O_3 did not affect aphid abundance, but it had a strong negative effect on natural enemies of aphids, which over the long term would tend to increase aphid numbers. When both trace gases were applied together, elevated CO_2 completely counteracted the reduction in the abundance of natural enemies of aphids caused by elevated O_3. Hence, elevated CO_2 tended to reduce the negative impact of aphids on trembling aspen in this study.

Holopainen (2002) reviewed the scientific literature addressing the joint effects of elevated concentrations of atmospheric O_3 and CO_2 on aphid-plant interactions. Compiling the results of 26 pertinent studies, Holopainen found atmospheric CO_2 enrichment increased aphid performance in six studies, decreased it in six studies, and had no significant impact on it in the remaining 14 studies. Similar results were found for aphid-plant interactions in the presence of elevated O_3 concentrations.

Newman (2003) reviewed the scientific literature on aphid responses to concurrent increases in atmospheric CO_2 and air temperature and also investigated the subject via the aphid population model of Newman *et al.* (2003). He concluded when the air's CO_2 concentration and temperature are both elevated, "aphid population dynamics will be more similar to current ambient conditions than expected from the results of experiments studying either factor alone." The only general conclusion that can be drawn, Newman states, is "insect responses to CO_2 are unlikely to all be in the same direction." Nevertheless, "the lack of a simple common phenomenon does not deny that there is some overriding generality in the responses by the system."

Awmack *et al.* (2004) conducted a two-year study at the Aspen FACE site near Rhinelander, Wisconsin (USA) of the individual and combined effects of elevated CO_2 (+200 ppm) and O_3 (1.5 x ambient) on the performance of *Cepegillettea betulaefoliae* aphids feeding on paper birch trees, in what they call "the first investigation of the long-term effects of elevated CO_2 and O_3 atmospheres on natural insect herbivore populations." At the individual scale, they report, "elevated CO_2 and O_3 did not significantly affect [aphid] growth rates, potential fecundity (embryo number) or offspring quality." At the population scale, "elevated O_3 had a strong positive effect," but "elevated CO_2 did not significantly affect aphid populations."

In comparing their results with those of prior related studies, the three scientists report "the responses of other aphid species to elevated CO_2 or O_3 are also complex." In particular, they note "tree-feeding aphids show few significant responses to elevated CO_2 (Docherty *et al.*, 1997), while crop-feeding species may respond positively (Awmack *et al.*, 1997; Bezemer *et al.*, 1998; Hughes and Bazzaz, 2001; Zhang *et al.*, 2001; Stacey and Fellowes, 2002), negatively (Newman *et al.*, 1999) or not at all (Hughes and Bazzaz, 2001), and the same species may show different responses on different host plant species (Awmack *et al.*, 1997; Bezemer *et al.*, 1999)." In summarizing their observations, they state "aphid individual performance did not predict population responses to CO_2 and O_3," and they conclude, "elevated CO_2 and O_3 atmospheres are unlikely to affect *C. betulaefoliae* populations in the presence of natural enemy communities."

In a study of a different aphid (*Chaitophorus stevensis*) conducted at the same FACE site, Mondor *et al.* (2004) focused on pheromones, which they note "are utilized by insects for several purposes, including alarm signaling," and which in the case of phloem-feeding aphids induces high-density groups of them on exposed leaves of trembling aspen trees to disperse and move to areas of lower predation risk. In this experiment the four treatments were: control (367 ppm CO_2, 38 ppb O_3), elevated CO_2 (537 ppm), elevated O_3 (51 ppb), and elevated CO_2 and O_3 (537 ppm CO_2, 51 ppb O_3). Within each treatment, several aspen leaves containing a single aphid colony of 25 ± 2 individuals were treated in one of two ways: (1) an aphid was prodded lightly on the thorax so as to not produce a visible pheromone droplet, or (2) an aphid was prodded more heavily on the thorax and induced to emit a visible pheromone droplet, after which, in the words of the scientists, "aphids exhibiting any dispersal reactions in response to pheromone emission as well as those exhibiting the most extreme dispersal response, walking down the petiole and off the leaf, were recorded over 5 min."

Mondor *et al.*'s observations were striking. They found the aphids they studied "have diminished escape responses in enriched carbon dioxide environments, while those in enriched ozone have augmented escape responses, to alarm pheromone." They report, "0% of adults dispersed from the leaf under elevated CO_2, while 100% dispersed under elevated O_3," indicating the effects of elevated CO_2 and elevated O_3 on aphid response to pheromone alarm signaling are diametrically opposed. Elevated O_3 (which is detrimental to vegetation) helped aphids escape predation and therefore live to do further harm to the leaves they infest, but elevated CO_2 (which is beneficial to vegetation) made it more difficult for aphids to escape predation and thereby provided an additional benefit to plant foliage. Mondor *et al.* state this phenomenon may be of broader scope than what is revealed by their specific study, noting other reports suggest "parasitoids and predators are more abundant and/or efficacious under elevated CO_2 levels (Stiling *et al.*, 1999; Percy *et al.*, 2002), but are negatively affected by elevated O_3 (Gate *et al.*, 1995; Percy *et al.*, 2002)."

Chen *et al.* (2004) grew spring wheat from seed to maturity in high-fertility well-watered pots out-of-doors in open-top chambers (OTCs) maintained at atmospheric CO_2 concentrations of 370, 550, and 750 ppm. Approximately two months after seeding, 20 apterous adult aphids (*Sitobion avenae*) from an adjacent field were placed on the wheat plants of each of 25 pots in each OTC, and 15 pots were left as controls. At subsequent five-day intervals, both apterous and alate aphids were counted. About one month later, 10 alate morph fourth instar nymphs were introduced onto the plants of each of nine control pots, and for the next two weeks the number of offspring laid on those plants were recorded and removed daily to measure reproductive activity. At the end of the study, the wheat plants were harvested and their various growth responses determined.

The scientists found the introduced aphid populations increased after infestation, peaked during the grain-filling stage, and declined a bit as the wheat matured. On the final day of measurement, aphids in the 550 ppm CO_2 treatment were 32% more numerous than those in ambient air, and aphids in the 750 ppm treatment were 50% more numerous. Alate aphids also produced more offspring on host plants grown in elevated CO_2: 13% more in the 550 ppm treatment, and 19% more in the 750 ppm treatment.

As for the wheat plants, Chen *et al*. report "elevated CO_2 generally enhanced plant height, aboveground biomass, ear length, and number of and dry weight of grains per ear, consistent with most other studies." With respect to aboveground biomass, for example, the 550 ppm treatment displayed an increase of 36%, and the 750 ppm treatment displayed an increase of 50%, in the case of both aphid-infested and non-infested plants.

Chen *et al*. comment, "aphid infestation caused negative effects on all the plant traits measured ... but the negative effects were smaller than the positive effects of elevated CO_2 on the plant traits." They conclude, "the increased productivity occurring in plants exposed to higher levels of CO_2 more than compensate for the increased capacity of the aphids to cause damage." In this experiment, therefore, both the plant and the insect that feeds on it were benefited by the applied increases in atmospheric CO_2 concentration.

Chen *et al*. (2005) grew transgenic cotton plants for 30 days in well-watered and fertilized sand/ vermiculite mixtures in pots set in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 370, 700, and 1,050 ppm. A subset of aphid-infected plants was additionally supplied with predatory ladybugs, and three generations of cotton aphids (*Aphis gossypii*) were subsequently allowed to feed on some of the plants. Based on measurements made throughout this complex set of operations, Chen *et al*. found "plant height, biomass, leaf area, and carbon:nitrogen ratios were significantly higher in plants exposed to elevated CO_2 levels," and "more dry matter and fat content and less soluble protein were found in *A. gossypii* in elevated CO_2." They also found "cotton aphid fecundity significantly increased ... through successive generations reared on plants grown under elevated CO_2"; "significantly higher mean relative growth rates were observed in lady beetle larvae under elevated CO_2"; and "the larval and pupal durations of the lady beetle were significantly shorter and [their] consumption rates increased when fed *A. gossypii* from elevated CO_2 treatments." Chen *et al.* say their study "provides the first empirical evidence that changes in prey quality mediated by elevated CO_2 can alter the prey preference of their natural enemies," and in this particular case, they found this phenomenon could "enhance the biological control of aphids by lady beetle."

According to Auad *et al*. (2012), the yellow sugarcane aphid—first called *Chaitophorus flavus*, but later changed to *Sipha flava*—"has an extensive geographic range that includes all the Americas and Hawaii," and it "is not only a serious pest of sugarcane, but it infests corn, sorghum, wheat, and several other grasses." They note "plant injury caused by this aphid is often severe and is associated with the release of an unidentified toxin followed by leaf chlorosis (Breen and Teetes, 1986; Webster, 1990)." In Brazil, where Auad *et al*. reside, the four scientists report elephant grass (*Pennisetum purpureum*)—one of the most widely used grasses for dairy cattle forage—"is being compromised by *S. flava* attack." The four Brazilian researchers investigated the "effects of elevated CO_2 alone and in combination with elevated temperature on the interactions of *S. flava* and one of its hosts," *P. purpureum*.

Auad *et al*. discovered "the combination of elevated CO_2 and high temperature significantly decreased the duration of nymphal stadia" and "the longevity and reproductive success of *S. flava*," such that "adults produced fewer nymphs in an environment with elevated CO_2 and high temperature than an environment with elevated CO_2 and lower fluctuating temperatures."

The four researchers conclude "*S. flava* populations will significantly decrease under future climatic conditions when both the concentration of atmospheric CO_2 and temperature are projected to increase."

Klaiber *et al*. (2013) "used a model system comprised of Brussels sprout (*Brassica oleraceae* var. *gemmifera*) and a specialized herbivorous insect, the cabbage aphid (*Brevicoryne brassicae*) to test for the effects of various periods of exposure to an elevated (2 x ambient) CO_2 concentration on key plant functional traits and on host plant location behavior by the insect, assessed as plant colonization rates." With respect to plant/herbivore interactions, the four Swiss scientists say, "doubling the ambient CO_2 concentration had a marked effect on plant colonization by winged aphids particularly when plants were exposed to CO_2 for longer periods." After an exposure of only two weeks, for example, there was no difference in colonization rate, whereas after six and 10 weeks "elevated CO_2 led to a respective 15 and 26% reduction of colonization rates" by the cabbage aphid. The authors also note plant volatile emissions, which have been linked to attracting insects, were significantly reduced at the higher CO_2 concentration. Klaiber *et al*. conclude, "in agro-ecosystems, reduced crop plant colonization by an herbivorous pest insect under elevated CO_2 might be advantageous."

It appears the ongoing rise in the air's CO_2 content will likely not have a major impact on aphid-plant interactions, although the scales appear to be tipped in favor of plants over aphids. It is also possible both plants and aphids will benefit from atmospheric CO_2 enrichment, but with plants benefiting more.

References

Adler, L.S., De Valpine, P., Harte, J., and Call, J. 2007. Effects of long-term experimental warming on aphid density in the field. *Journal of the Kansas Entomological Society* **80**: 156–168.

Auad, A.M., Fonseca, M.G., Resende, T.T., and Maddalena, I.S.CP. 2012. Effect of climate change on longevity and reproduction of *Sipha flava* (Hemiptera: Aphididae). *Florida Entomologist* **95**: 433–444.

Awmack, C.S., Harrington, R., and Leather, S.R. 1997. Host plant effects on the performance of the aphid *Aulacorthum solani* (Homoptera: Aphididae) at ambient and elevated CO_2. *Global Change Biology* **3**: 545–549.

Awmack, C.S., Harrington, R., and Lindroth, R.L. 2004. Aphid individual performance may not predict population responses to elevated CO_2 or O_3. *Global Change Biology* **10**: 1414–1423.

Bezemer, T.M., Jones, T.H., and Knight, K.J. 1998. Long-term effects of elevated CO_2 and temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. *Oecologia* **116**: 128–135.

Bezemer, T.M., Knight, K.J., and Newington, J.E., *et al.* 1999. How general are aphid responses to elevated atmospheric CO_2? *Annals of the Entomological Society of America* **92**: 724–730.

Breen, J.P. and Teets, G.L. 1986. Relationships of the yellow sugarcane aphid (Homoptera: Aphididae) density to sorghum damage. *Journal of Economic Entomology* **79**: 1106–1110.

Chen, F., Ge, F., and Parajulee, M.N. 2005. Impact of elevated CO_2 on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Leis axyridis*. *Environmental Entomology* **34**: 37–46.

Chen, F.J., Wu, G., and Ge, F. 2004. Impacts of elevated CO_2 on the population abundance and reproductive activity of aphid *Sitobion avenae* Fabricius feeding on spring wheat. *JEN* **128**: 723–730.

Docherty, M., Wade, F.A., Hurst, D.K., Whittaker, J.B., and Lea, P.J. 1997. Responses of tree sap-feeding herbivores to elevated CO_2. *Global Change Biology* **3**: 51–59.

Gate, I.M., McNeill, S., and Ashmore, M.R. 1995. Effects of air pollution on the searching behaviour of an insect parasitoid. *Water, Air and Soil Pollution* **85**: 1425–1430.

Holopainen, J.K. 2002. Aphid response to elevated ozone and CO_2. *Entomologia Experimentalis et Applicata* **104**: 137–142.

Hughes, L. and Bazzaz, F.A. 2001. Effects of elevated CO_2 on five plant-aphid interactions. *Entomologia Experimentalis et Applicata* **99**: 87–96.

Klaiber, J., Najar-Rodriguez, A.J., Piskorski, R., and Dorn, S. 2013. Plant acclimation to elevated CO_2 affects important plant functional traits, and concomitantly reduces plant colonization rates by an herbivorous insect. *Planta* **237**: 29–42.

Ma, C.S., Hau, B., and Poehling, M.-M. 2004. The effect of heat stress on the survival of the rose grain aphid, *Metopolophium dirhodum* (Hemiptera: Aphididae). *European Journal of Entomology* **101**: 327–331.

Mondor, E.B., Tremblay, M.N., Awmack, C.S., and Lindroth, R.L. 2004. Divergent pheromone-mediated insect behavior under global atmospheric change. *Global Change Biology* **10**: 1820–1824.

Newman, J.A. 2003. Climate change and cereal aphids: the relative effects of increasing CO_2 and temperature on aphid population dynamics. *Global Change Biology* **10**: 5–15.

Newman, J.A., Gibson, D.J., Hickam, E., Lorenz, M., Adams, E., Bybee, L., and Thompson, R. 1999. Elevated carbon dioxide results in smaller populations of the bird cherry-oat aphid *Rhopalosiphum padi*. *Ecological Entomology* **24**: 486–489.

Newman, J.A., Gibson, D.J., Parsons, A.J., and Thornley, J.H.M. 2003. How predictable are aphid population responses to elevated CO_2? *Journal of Animal Ecology* **72**: 556–566.

Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., and Karnosky, D.F. 2002. Altered performance of forest pests under atmospheres enriched by CO_2 and O_3. *Nature* **420**: 403–407.

Stacey, D. and Fellowes, M. 2002. Influence of elevated CO_2 on interspecific interactions at higher trophic levels. *Global Change Biology* **8**: 668–678.

Stilling, P., Rossi, A.M., and Hungate, B., *et al*. 1999. Decreased leaf-miner abundance in elevated CO_2: reduced leaf quality and increased parasitoid attack. *Ecological Applications* **9**: 240–244.

Webster, J.A. 1990. Yellow sugarcane aphid (Homoptera: Aphididae): detection and mechanisms of resistance among Ethiopian sorghum lines. *Journal of Economic Entomology* **83**: 1053–1057.

Whittaker, J.B. 1999. Impacts and responses at population level of herbivorous insects to elevated CO_2. *European Journal of Entomology* **96**: 149–156.

Zhang, J., Liu, J., and Wang, G., *et al*. 2001. Effect of elevated atmospheric CO_2 concentration on *Rhopalsiphum padi* population under different soil water levels. *Yingyong Shengtai Xuebao* **12**: 253–256.

5.5.2 Moths

Among the insects most responsible for herbivore pressure on plants is moths. This section reviews research on how moths are likely to fare in a warmer world with higher levels of CO_2 in the air.

Kerslake *et al*. (1998) collected five-year-old heather plants from a Scottish moor and grew them in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm for 20 months, with and without soil nitrogen fertilization. Twice during the study, larvae of *Operophtera brumata*, a voracious winter moth whose outbreaks have caused extensive damage to heather moorland in recent years, were allowed to feed on current-year shoots for up to one month. The survivorship of larvae placed on CO_2-enriched foliage was not significantly different from that of larvae placed on foliage produced in ambient air, regardless of nitrogen treatment. In addition, feeding on CO_2-enriched foliage did not affect larval growth rate, development, or final pupal weight. Consequently, Kerslake *et al*. conclude their study "provides no evidence that increasing atmospheric CO_2 concentrations will affect the potential for outbreak of *Operophtera brumata* on this host."

Hattenschwiler and Schafellner (1999) grew seven-year-old spruce trees at atmospheric CO_2 concentrations of 280, 420, and 560 ppm in various nitrogen deposition treatments for three years, after which they performed needle quality assessments and allowed nun moth (*Lymantria monacha*) larvae to feed on current-year needles for 12 days. This moth is an especially voracious defoliator that resides in most parts of Europe and East Asia between 40 and 60° N latitude, and it is commonly regarded as the "coniferous counterpart" of its close relative the gypsy moth, which feeds primarily on deciduous trees.

The two scientists observed elevated CO_2 significantly enhanced needle starch, tannin, and phenolic concentrations, while significantly decreasing needle water and nitrogen contents. Thus, atmospheric CO_2 enrichment reduced overall needle quality from the perspective of this foliage-consuming moth, as nitrogen content is the primary factor associated with leaf quality. Increasing nitrogen deposition, on the other hand, tended to enhance needle quality, for it lowered starch, tannin, and phenolic concentrations while boosting needle nitrogen content. The positive influence of nitrogen deposition on needle quality was not large enough to completely offset the quality reduction caused by elevated CO_2.

Larvae placed on CO_2-enriched foliage consumed less needle biomass than larvae placed on low-CO_2-grown foliage, regardless of nitrogen treatment, and the larvae feeding on CO_2-enriched foliage exhibited reduced relative growth rates and attained an average biomass only two-thirds of that attained by larvae consuming foliage produced at 280 ppm CO_2. Hattenschwiler and Schafellner conclude, "altered needle quality in response to elevated CO_2 will impair the growth and development of *Lymantria monacha* larvae," which should lead to reductions in the degree of spruce tree destruction caused by this voracious defoliator.

Stiling *et al*. (2002) studied the effects of an approximate doubling of the air's CO_2 concentration on a number of characteristics of several insect herbivores feeding on plants native to a scrub-oak forest ecosystem at the Kennedy Space Center, Florida (USA) in eight ambient and eight CO_2-enriched open-top chambers. They found the "relative levels of damage by the two most common herbivore guilds, leaf-mining moths and leaf-chewers (primarily larval lepidopterans and grasshoppers), were significantly lower in elevated CO_2 than in ambient CO_2," and "the response to elevated CO_2 was the same across all plant species." Also, "more host-plant induced mortality was found for all miners on all plants in elevated CO_2 than in ambient CO_2.” These effects were so powerful that in addition to the relative densities of insect herbivores being reduced in the CO_2-enriched chambers, and “even though there were more leaves of most plant species in the elevated CO_2 chambers,” the total densities of leaf miners in the high-CO_2 chambers were also lower for all plant species. It would appear that in a higher CO_2 world of the future, Earth’s natural ecosystems may be able to better withstand the onslaughts of various insect pests, including moths, that have plagued them in the past. Stiling *et al.* note, is “reductions in herbivore loads in elevated CO_2 could boost plant growth beyond what might be expected based on pure plant responses to elevated CO_2.”

In a follow-up study to that of Stilling *et al.*, conducted at the same facilities, Rossi *et al.* (2004), focused on the abundance of a guild of lepidopteran leafminers that attack the leaves of myrtle oak, as well as various leaf chewers. They periodically examined 100 marked leaves in each of 16 open-top chambers for nine months, after which “differences in mean percent of leaves with leafminers and chewed leaves on trees from ambient and elevated chambers were assessed using paired *t*-tests.” This protocol revealed “both the abundance of the guild of leafmining lepidopterans and damage caused by leaf chewing insects attacking myrtle oak were depressed in elevated CO_2.” Leafminer abundance was 44% lower ($P = 0.096$) in the CO_2-enriched chambers compared to the ambient-air chambers, and the amount of leaves suffering chewing damage was 37% lower ($P = 0.072$) in the CO_2-enriched air.

Williams *et al.* (2003) bagged first instar gypsy moth larvae on branches of red maple saplings entering their fourth year of growth within open-top chambers maintained at four sets of CO_2/temperature conditions: (1) ambient temperature, ambient CO_2, (2) ambient temperature, elevated CO_2 (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO_2, and (4) elevated temperature, elevated CO_2. For these conditions they measured several parameters to test their hypothesis that a CO_2-enriched atmosphere would lead to reductions in foliar nitrogen concentrations and increases in defensive phenolics that would in turn lead to increases in insect mortality.

The results indicated “larvae feeding on CO_2-enriched foliage ate a comparably poorer food source than those feeding on ambient CO_2-grown plants, irrespective of temperature.” Nevertheless, they determined “CO_2-induced reductions in foliage quality were unrelated to insect mortality, development rate and pupal weight.” They concluded, “phytochemical changes resulted in no negative effects on gypsy moth performance,” but neither did they help them.

Noting increases in the atmosphere’s CO_2 concentration typically lead to greater decreases in the concentrations of nitrogen in the foliage of C_3 as opposed to C_4 grasses, Barbehenn *et al.* (2004) note “it has been predicted that insect herbivores will increase their feeding damage on C_3 plants to a greater extent than on C_4 plants (Lincoln *et al.*, 1984, 1986; Lambers, 1993).” To test this hypothesis, they grew *Lolium multiflorum* (Italian ryegrass, a common C_3 pasture grass) and *Bouteloua curtipendula* (sideoats gramma, a native C_4 rangeland grass) in chambers maintained at either the ambient atmospheric CO_2 concentration of 370 ppm or the doubled CO_2 concentration of 740 ppm for two months, after which newly molted sixth-instar larvae of *Pseudaletia unipuncta* (a grass-specialist noctuid) and *Spodoptera frugiperda* (a generalist noctuid) were allowed to feed on the two grasses.

As expected, Barbehenn *et al.* found foliage protein concentration decreased by 20% in the C_3 grass but by only 1% in the C_4 grass when they were grown in CO_2-enriched air. They write, “to the extent that protein is the most limiting of the macronutrients examined, these changes represent a decline in the nutritional quality of the C_3 grass.” However, and “contrary to our expectations,” they add, “neither caterpillar species significantly increased its consumption rate to compensate for the lower concentration of protein in [the] C_3 grass.” They note “this result does not support the hypothesis that C_3 plants will be subject to greater rates of herbivory relative to C_4 plants in future [high-CO_2] atmospheric conditions (Lincoln *et al.*, 1984).” In addition, and “despite significant changes in the nutritional quality of *L. multiflorum* under elevated CO_2,” they note “no effect on the relative growth rate of either caterpillar species on either grass species resulted,” and there were “no significant differences in insect performance between CO_2 levels.” They suggest “post-ingestive mechanisms could provide a sufficient means of compensation for the lower nutritional quality of C_3 plants grown under elevated CO_2.”

Barbehenn *et al.* suggest “there will not be a single pattern that characterizes all grass feeders” with respect to their feeding preferences and developmental responses in a world where certain C_3 plants may experience foliar protein concentrations lower than those they exhibit today, nor will the changes that may occur necessarily be detrimental to herbivore development or the health and vigor of their host plants. Nevertheless, subsequent studies continue to suggest moth species likely will be negatively impacted by the ongoing rise in the air's CO_2 content.

A case in point is the study of Chen *et al*. (2005), who grew well-watered and fertilized cotton plants of two varieties (one expressing *Bacillus thuringiensis* toxin genes and one a non-transgenic cultivar from the same recurrent parent) in pots placed within open-top chambers maintained at either 376 or 754 ppm CO_2 in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October. Immature bolls were periodically collected and analyzed for various chemical characteristics, and others were stored under refrigerated conditions for later feeding to larvae of the cotton bollworm. They found the elevated CO_2 treatment increased immature boll concentrations of condensed tannins by approximately 22% and 26% in transgenic and non-transgenetic cotton, respectively, and it slightly decreased the body biomass of the cotton bollworm and reduced moth fecundity. The Bt treatment was even more effective in this regard, and in the combined Bt-high-CO_2 treatment the negative cotton bollworm responses were expressed most strongly.

Bidart-Bouzat *et al*. (2005) grew three genotypes of mouse-ear cress (*Arabidopsis thaliana*) from seed in pots within controlled-environment chambers maintained at either ambient CO_2 (360 ppm) or elevated CO_2 (720 ppm). On each of half of the plants (the herbivory treatment) in each of these CO_2 treatments, they placed two second-instar larvae of the diamondback moth (*Plutella xylostella*) at bolting time and removed them at pupation, which resulted in an average of 20% of each plant's total leaf area in the herbivory treatment being removed. Then, each pupa was placed in a gelatin capsule until adult emergence and ultimate death, after which insect gender was determined and the pupa's weight recorded.

At the end of this herbivory trial, the leaves of the control and larvae-infested plants were analyzed for concentrations of individual glucosinolates—a group of plant-derived chemicals that can act as herbivore deterrents (Mauricio and Rausher, 1997)—and total glucosinolate production was determined by summation of the individual glucosinolate assays. Influences of elevated CO_2 on moth performance and its association with plant defense-related traits also were evaluated.

Overall, the researchers found herbivory by larvae of the diamondback moth did not induce any increase in the production of glucosinolates in the mouse-ear cress in the ambient CO_2 treatment. However, the three scientists report, "herbivory-induced increases in glucosinolate contents, ranging from 28% to 62% above basal levels, were found under elevated CO_2 in two out of the three genotypes studied." In addition, "elevated CO_2 decreased the overall performance of diamondback moths." And because "induced defenses can increase plant fitness by reducing subsequent herbivore attacks (Agrawal, 1999; Kessler and Baldwin, 2004)," Bidart-Bouzat *et al*. suggest "the pronounced increase in glucosinolate levels under CO_2 enrichment may pose a threat not only for insect generalists that are likely to be more influenced by rapid changes in the concentration of these chemicals, but also for other insect specialists more susceptible than diamondback moths to high glucosinolate levels (Stowe, 1998; Kliebenstein *et al*., 2002)."

In a study of a major crop species, Wu *et al*. (2006) grew spring wheat (*Triticum aestivum* L.) from seed to maturity in pots placed in open-top chambers maintained at either 370 or 750 ppm CO_2 in Sanhe County, Hebei Province, China, after which they reared three generations of cotton bollworms (*Helicoverpa armigera* Hubner) on the milky grains of the wheat while monitoring a number of bollworm developmental characteristics. They report, "significantly lower pupal weights were observed in the first, second and third generations," and "the fecundity of *H. armigera* decreased by 10% in the first generation, 13% in the second generation and 21% in the third generation," resulting in a "potential population decrease in cotton bollworm by 9% in the second generation and 24% in the third generation." In addition, they observe, "population consumption was significantly reduced by 14% in the second generation and 24% in the third generation," and the efficiency of conversion of ingested food was reduced "by 18% in the first generation, 23% in the second generation and 30% in the third generation." They conclude, the "net damage of cotton bollworm on wheat will be less under elevated atmospheric CO_2," while "at the same time, gross wheat production is expected to increase by 63% under elevated CO_2."

Wu *et al*. (2007) write, "significant decreases in the protein, total amino acid, water and nitrogen content by 15.8%, 17.7%, 9.1% and 20.6% and increases in free fatty acid by 16.1% were observed in cotton bolls grown under elevated CO_2." When fed with these cotton bolls, the larval survival rate of *H. armigera* "decreased by 7.35% in the first generation, 9.52% in the second generation and 11.48% in the third generation under elevated CO_2 compared with ambient CO_2." In addition, "the fecundity of *H. armigera* decreased by 7.74% in the first generation, 14.23% in the second generation and 16.85% in the third generation." They conclude, "fecundity capacity is likely to be reduced even further in the next generation."

The synergistic effects of these several phenomena, note Wu *et al.*, "resulted in a potential population decrease in cotton bollworm by 18.1% in the second generation and 52.2% in the third generation under elevated CO_2," with the result that "the potential population consumption of cotton bollworm decreased by 18.0% in the second generation and 55.6% in the third generation ... under elevated CO_2 compared with ambient CO_2." They conclude, "the potential population dynamics and potential population consumption of cotton bollworm will alleviate the harm to [cotton] plants in the future rising-CO_2 atmosphere."

Esper *et al.* (2007) reconstructed an annually resolved history of population cycles of a foliage-feeding Lepidopteran commonly known as the larch budmoth (*Zeiraphera diniana* Gn.)—or LBM for short—in the European Alps in the southern part of Switzerland. As is typical of many such insect pests, they note, "during peak activity, populations may reach very high densities over large areas," resulting in "episodes of massive defoliation and/or tree mortality" that could be of great ecological and economic significance.

The team of Swiss and U.S. researchers first developed a history of LBM outbreaks over the 1,173-year period AD 832–2004, which they describe as "the longest continuous time period over which any population cycle has ever been documented." They did so using radiodensitometric techniques to characterize the tree-ring density profiles of 180 larch (*Larix deciduas* Mill.) samples, where "LBM outbreaks were identified based upon characteristic maximum latewood density (MXD) patterns in wood samples, and verified using more traditional techniques of comparison with tree-ring chronologies from non-host species," i.e., fir and spruce. Then they developed a matching temperature history for the area by combining "a tree-ring width-based reconstruction from AD 951 to 2002 integrating 1527 pine and larch samples (Buntgen *et al.*, 2005) and a MXD-based reconstruction from AD 755 to 2004 based upon the same 180 larch samples used in the current study for LBM signal detection (Buntgen *et al.*, 2006)."

From AD 832 to 1981, there were 123 LBM outbreaks with a mean reoccurrence time of 9.3 years, and "there was never a gap that lasted longer than two decades." From 1981 to the end of their study in 2004, however, there were no LBM outbreaks, and since there had never before (within their record) been such a long outbreak hiatus, they conclude, "the absence of mass outbreaks since the 1980s is truly exceptional."

To what do Esper *et al.* attribute this unprecedented recent development? Noting "conditions during the late twentieth century represent the warmest period of the past millennium"—as per their temperature reconstruction for the region of the Swiss Alps in which they worked—they point to "the role of extraordinary climatic conditions as the cause of outbreak failure," and they discuss what they refer to as the "probable hypothesis" of Baltensweiler (1993), who described a scenario by which local warmth may lead to reduced LBM populations.

Warmth may indeed explain the lack of LBM outbreaks, but given the results of other studies examined in this section, it should be noted atmospheric CO_2 concentrations since 1980 also have been unprecedented over the 1,173-year period of Esper *et al.*'s study. The suppression of LBM outbreaks over the past quarter-century may have been the result of some synergistic consequence of the two factors (temperature and CO_2) acting in unison, and a third possibility may involve only the increase in the air's CO_2 content.

Esper *et al.* say their findings highlight the "vulnerability of an otherwise stable ecological system in a warming environment," in what would appear to be an attempt to attach an undesirable connotation to the observed outcome. This wording seems strange indeed, for it is clear the "recent disruption of a major disturbance regime," as Esper *et al.* refer to the suppression of LBM outbreaks elsewhere in their paper, would be considered by most people to be a positive outcome, indeed something to be welcomed.

Buntgen *et al.* (2009) analyzed raw measurements of 3,151 tree-ring width (TRW) series and 150 maximum latewood density (MXD) series from 70 larch host sites and 73 spruce non-host sites spread across the European Alps and Tatra Mountains that extended back in time approximately 300 years. Focusing on the European Alps—"because periodic growth depressions caused by LBM outbreaks were not found in the TRW and MXD chronologies from the Tatra Mountains"—Buntgen *et al.* discovered "a distinct periodicity at 8–9 years from sites at elevations between 1750 and 1900 meters above sea level." In the middle of the twentieth century, for example, they documented synchronized outbreak pulses at approximately 1936, 1945, 1954, 1963, 1972, and 1981. These outbreaks, the scientists write, "occurred independently of rising temperatures," all the way from the beginning-of-the-end of "the Little Ice Age until recent warmth." They report this long stretch of persistent and synchronized Alpine-wide defoliation—which Esper *et al*. (2007) had followed back to AD 832—finally "ceased during recent decades," when "unprecedented warming in all seasons characterized the post–1980 period."

Knepp *et al*. (2007) studied two species of oak tree—*Quercus alba* L. (white oak) and *Quercus velutina* Lam. (black oak)—and their susceptibility to *Antheraea polyphemus*, a leaf-chewing generalist lepidopteran herbivore that represents the most abundant feeding guild in the hardwood trees that grow beneath the canopy of the unmanaged loblolly pine plantation that hosts the Forest Atmosphere Carbon Transfer and Storage (FACTS–1) research site in the Piedmont region of North Carolina (USA), where the leaf-chewer can consume 2–15% of the forest's net primary production in any given year. The researchers examined host plant preference and larval performance of *A. polyphemus* when fed foliage of the two tree species that had been grown in either ambient or CO_2-enriched air (to 200 ppm above ambient) in this long-running FACE experiment. They determined "growth under elevated CO_2 reduced the food quality of oak leaves for caterpillars," and "consuming leaves of either oak species grown under elevated CO_2 slowed the rate of development of *A. polyphemus* larvae." In addition, they found feeding on foliage of *Q. velutina* that had been grown under elevated CO_2 led to reduced consumption by the larvae and greater mortality. They conclude, "reduced consumption, slower growth rates, and increased mortality of insect larvae may explain [the] lower total leaf damage observed previously in plots of this forest exposed to elevated CO_2," as documented by Hamilton *et al*. (2004) and Knepp *et al*. (2005).

Kampichler *et al*. (2008) also worked with oak trees. Noting, however, "systems studied so far have not included mature trees," they attempted to remedy this situation by determining "the abundance of dominant leaf-galls (spangle-galls induced by the cynipid wasps *Neuroterus quercusbaccarum* and *N. numismalis*) and leaf-mines (caused by the larvae of the moth *Tischeria ekebladella*) on freely colonized large oaks in a mixed forest in Switzerland, which received CO_2 enrichment [540 ppm vs. 375 ppm during daylight hours] from 2001 to 2004" via "the Swiss Canopy Crane (SCC) and a new CO_2 enrichment technique (web-FACE)" in a forest that they say "is 80–120 years old with a canopy height of 32–38 m, consisting of seven deciduous and four coniferous species."

The German, Mexican, and Swiss researchers discovered that although elevated CO_2 reduced various leaf parameters (water content, proteins, non-structural carbohydrates, tannins, etc.) at the SCC site, "on the long term, their load with cynipid spangle-galls and leaf-mines of *T. ekebladella* was not distinguishable from that in oaks exposed to ambient CO_2 after 4 years of treatment." Consequently, although speculation has run rampant over the years about the long-term effects of atmospheric CO_2 enrichment on plant foliage and its subsequent effects on animals of various trophic levels, Kampichler *et al*. conclude in the situation they investigated, "CO_2 enrichment had no lasting effect in all three [animal] taxa, despite the substantial and consistent change in leaf chemistry of oak due to growth in elevated CO_2."

The results of the studies reviewed above indicate the ongoing rise in the air's CO_2 content will not cause greater damage to Earth's vegetation by the larvae of the many moths that inhabit the planet. If anything, it could reduce the damage they cause.

References

Agrawal, A.A. 1999. Induced-responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecology* **80**: 1713–1723.

Baltensweiler, W. 1993. Why the larch bud moth cycle collapsed in the subalpine larch-cembran pine forests in the year 1990 for the first time since 1850. *Oecologia* **94**: 62–66.

Barbehenn, R.V., Karowe, D.N., and Spickard, A. 2004. Effects of elevated atmospheric CO_2 on the nutritional ecology of C_3 and C_4 grass-feeding caterpillars. *Oecologia* **140**: 86–95.

Bidart-Bouzat, M.G., Mithen, R., and Berenbaum, M.R. 2005. Elevated CO_2 influences herbivory-induced defense responses of *Arabidopsis thaliana*. *Oecologia* **145**: 415–424.

Buntgen, U., Esper, J., Frank, D.C., Nicolussi, K., and Schmidhalter, M. 2005. A 1052-year tree-ring proxy for alpine summer temperatures. *Climate Dynamics* **25**: 141–153.

Buntgen, U., Frank, D., Liebhold, A., Johnson, D., Carrer, M., Urbinati, C., Grabner, M., Nicolussi, K., Levanic, T., and Esper, J. 2009. Three centuries of insect outbreaks across the European Alps. *New Phytologist* **182**: 929–941.

Buntgen, U., Frank, D.C., Nievergelt, D., and Esper, J. 2006. Alpine summer temperature variations, AD 755–2004. *Journal of Climate* **19**: 5606–5623.

Chen, F., Wu, G., Ge, F., Parajulee, M.N., and Shrestha, R.B. 2005. Effects of elevated CO_2 and transgenic Bt cotton on plant chemistry, performance, and feeding of an insect herbivore, the cotton bollworm. *Entomologia Experimentalis et Applicata* **115**: 341–350.

Esper, J., Buntgen, U., Frank, D.C., Nievergelt, D., and Liebhold, A. 2007. 1200 years of regular outbreaks in alpine insects. *Proceedings of the Royal Society B* **274**: 671–679.

Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J.S., Aldea, M., and DeLucia, E.H. 2004. Insect herbivory in an intact forest understory under experimental CO_2 enrichment. *Oecologia* **138**: 566–573.

Hattenschwiler, S. and Schafellner, C. 1999. Opposing effects of elevated CO_2 and N deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia* **118**: 210–217.

Kampichler, C., Teschner, M., Klein, S., and Korner, C. 2008. Effects of 4 years of CO_2 enrichment on the abundance of leaf-galls and leaf-mines in mature oaks. *Acta Oecologica* **34**: 139–146.

Kerslake, J.E., Woodin, S.J., and Hartley, S.E. 1998. Effects of carbon dioxide and nitrogen enrichment on a plant-insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytologist* **140**: 43–53.

Kessler, A. and Baldwin, I.T. 2004. Herbivore-induced plant vaccination. Part I. The orchestration of plant defenses in nature and their fitness consequences in the wild tobacco, *Nicotiana attenuata*. *Plant Journal* **38**: 639–649.

Kliebenstein, D., Pedersen, D., Barker, B., and Mitchell-Olds, T. 2002. Comparative analysis of quantitative trait loci controlling glucosinolates, myrosinase and insect resistance in *Arabidopsis thaliana*. *Genetics* **161**: 325–332.

Knepp, R.G., Hamilton, J.G., Mohan, J.E., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2005. Elevated CO_2 reduces leaf damage by insect herbivores in a forest community. *New Phytologist* **167**: 207–218.

Knepp, R.G., Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2007. Foliage of oaks grown under elevated CO_2 reduces performance of *Antheraea polyphemus* (Lepidoptera: Saturniidae). *Environmental Entomology* **36**: 609–617.

Lambers, H. 1993. Rising CO_2, secondary plant metabolism, plant-herbivore interactions and litter decomposition. Theoretical considerations. *Vegetatio* **104/105**: 263–271.

Lincoln, D.E., Couvet, D., and Sionit, N. 1986. Responses of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia* **69**: 556–560.

Lincoln, D.E., Sionit, N., and Strain, B.R. 1984. Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. *Environmental Entomology* **13**: 1527–1530.

Mauricio, R. and Rausher, M.D. 1997. Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. *Evolution* **51**: 1435–1444.

Rossi, A.M., Stiling, P., Moon, D.C., Cattell, M.V., and Drake, B.G. 2004. Induced defensive response of myrtle oak to foliar insect herbivory in ambient and elevated CO_2. *Journal of Chemical Ecology* **30**: 1143–1152.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2002. Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* DOI 10.1007/s00442-002-1075-5.

Stowe, K.A. 1998. Realized defense of artificially selected lines of *Brassica rapa*: effects of quantitative genetic variation in foliar glucosinolate concentration. *Environmental Entomology* **27**: 1166–1174.

Williams, R.S., Lincoln, D.E., and Norby, R.J. 2003. Development of gypsy moth larvae feeding on red maple saplings at elevated CO_2 and temperature. *Oecologia* **137**: 114–122.

Wu, G., Chen, F.-J., and Ge, F. 2006. Response of multiple generations of cotton bollworm *Helicoverpa armigera* Hubner, feeding on spring wheat, to elevated CO_2. *Journal of Applied Entomology* **130**: 2–9.

Wu, G., Chen, F.-J., Sun, Y.-c., and Ge, F. 2007. Response of successive three generations of cotton bollworm, *Helicoverpa armigera* (Hubner), fed on cotton bolls under elevated CO_2. *Journal of Environmental Sciences* **19**: 1318–1325.

5.5.3 Other Herbivores

Besides aphids and moths, other herbivores consume vast amounts of foliage, roots, seeds, and other forms of vegetation. Because experiments involving temperatures and CO_2 content of the air often are conducted on specific types of plants, it is useful to sort the research results by the types of plants being studied. This section looks at research on herbaceous plants, woody plants, and finally other plants.

5.5.3.1 Herbaceous Plants

Insect pests have greatly vexed Earth's herbaceous plants in the past and likely will continue to do so in the future. It is possible, however, that the ongoing rise in the atmosphere's CO_2 content may impact this phenomenon, for better or for worse. Several studies have addressed this subject as it applies to herbaceous plant species, and these studies indicate such plants will be able to continue to cope with the periodic assaults of leaf-damaging herbivores as the air's CO_2 content continues to increase.

Kerslake *et al*. (1998) grew five-year-old heather (*Calluna vulgaris*) plants collected from a Scottish moor in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm. Twice during the study, larvae of the destructive winter moth *Operophtera brumata*, outbreaks of which periodically cause extensive damage to heather moorland, were allowed to feed upon current-year shoots. Feeding on the high-CO_2-grown foliage did not affect larval growth rates, development, or final pupal weights, nor was moth survivorship significantly altered. The authors conclude their study "provides no evidence that increasing atmospheric CO_2 concentrations will affect the potential for outbreak of *Operophtera brumata* on this host."

Newman *et al*. (1999) inoculated tall fescue (*Festuca arundinacea*) plants growing in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm with bird cherry-oat aphids (*Rhopalosiphum padi*). After nine weeks, the plants growing in the CO_2-enriched air had experienced a 37% increase in productivity and were covered with far fewer aphids than the plants growing in ambient air.

Goverde *et al*. (1999) collected four genotypes of *Lotus corniculatus* near Paris and grew them in controlled environment chambers kept at atmospheric CO_2 concentrations of 350 and 700 ppm. Larvae of the Common Blue Butterfly (*Polyommatus icarus*) that were allowed to feed on the foliage produced in the CO_2-enriched air ate more, grew larger, and experienced shorter development times than larvae feeding on the foliage produced in the ambient-air treatment, suggesting this butterfly species likely will become increasingly robust and plentiful as the air's CO_2 content continues to rise.

Brooks and Whittaker (1999) removed grassland monoliths containing eggs of the xylem-feeding spittlebug *Neophilaenus lineatus* from the UK's Great Dun Fell in Cumbria and placed them in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm for two years. Survival of the spittlebug's nymphal states was reduced by 24% in both of the generations produced in their experiment, suggesting this particular insect likely will cause less tissue damage to the plants of this species-poor grassland in a CO_2-enriched world of the future.

Joutei *et al*. (2000) grew bean (*Phaseolus vulgaris*) plants in controlled environments kept at atmospheric CO_2 concentrations of 350 and 700 ppm, to which they introduced the destructive agricultural mite *Tetranychus urticae*. Female mites produced 34% and 49% less offspring in the CO_2-enriched chambers in their first and second generations, respectively. This CO_2-induced reduction in the reproductive success of this invasive insect, which negatively affects more than 150 crop species worldwide, bodes well for mankind's ability to grow the food needed to feed the planet's growing population in the years ahead.

Peters *et al*. (2000) fed foliage derived from FACE plots of calcareous grasslands of Switzerland (maintained at 350 and 650 ppm CO_2) to terrestrial slugs, finding they exhibited no preference toward the CO_2 treatment from which the foliage was derived. Also, in a study that targeted no specific insect pest, Castells *et al*. (2002) found a doubling of the air's CO_2 content enhanced the total phenolic concentrations of two Mediterranean perennial grasses (*Dactylis glomerata* and *Bromus erectus*) by 15% and 87%, respectively; these compounds tend to enhance plant defensive and resistance mechanisms to attacks by both herbivores and pathogens (see Section 2.19).

Plants re-emit a substantial portion of their assimilated CO_2 back to the atmosphere as volatile organic compounds (VOCs). These substances affect both the chemical and physical properties of the air, where they generate large quantities of organic aerosols that can impact the planet's climate by forming cloud condensation nuclei that may lead to enhanced cooling during the day by reflecting a greater portion of the incoming solar radiation back to space. In addition, many VOCs protect numerous plants from a host of insect pests.

To see how these phenomena may be affected by the ongoing rise in the atmosphere's CO_2 concentration and by localized areas and time periods of high ozone (O_3) pollution, Himanen *et al*. (2009) exposed groups of both normal (non-transgenic) oilseed rape (*Brassica napus* ssp. *oleifera* L.) plants and transgenic plants, containing an introduced gene that produces *Bacillus thuringiensis* (Bt) crystal endotoxin (Cry) proteins that limit herbivorous insect attacks, to air of 360 and 720 ppm CO_2, as well as O_3-free air and air of 100 ppb O_3. These experiments were conducted in controlled-environment chambers where the plants were grown from seed for 17–18 days in 0.66-liter pots filled with a 2:1:1 mixture of fertilized compost, *Sphagnum* peat, and sand. The non-transgenic plants grown in CO_2-enriched air produced 27% more shoot biomass than those grown in ambient air, and the transgenic plants produced 25% more. In the O_3-enriched air, the non-transgenic plants produced 29% less shoot biomass than those grown in O_3-free air, and the transgenic plants produced 34% less. In addition, on a per-dry-weight basis, Himanen *et al*. say the "doubled CO_2 significantly increased terpenoid emissions from intact oilseed rape plants compared with those released from the corresponding plants grown in control CO_2," and they report there were no O_3-induced increases in VOC emissions. Thus, in addition to the fact that "production of *Bacillus thuringiensis* crystal endotoxin proteins in a crop plant limits specific herbivorous insect attack without the need for chemical treatments," the seven scientists conclude "elevated CO_2 conditions could modify herbivore-induced defenses [VOC emissions] at the vegetative stage, and enhance indirect defense in the future."

Although many studies have explored the direct effects of atmospheric CO_2 enrichment on plant growth and development, Klaiber *et al*. (2013) note the effects of elevated CO_2 on the behavioral responses of insect pests associated with major food crops have not been thoroughly investigated: "the potential effects of plant acclimation to CO_2 on host plant colonization by specialized herbivorous insects, which is a key step in the process of plant attack leading to potential yield losses, are largely unknown."

Klaiber *et al*. "used a model system comprised of Brussels sprout (*Brassica oleraceae* var. *gemmifera*) and a specialized herbivorous insect, the cabbage aphid (*Brevicoryne brassicae*) to test for the effects of various periods of exposure to an elevated (2 x ambient) CO_2 concentration on key plant functional traits and on host plant location behavior by the insect, assessed as plant colonization rates."

Plant height, leaf number, leaf area, fresh weight, and dry weight all increased in the elevated CO_2 treatments with respect to values obtained under ambient conditions, regardless of the length of CO_2 exposure. Leaf stomatal conductance also benefited at the higher CO_2 level, being reduced by nearly 50% by the end of the 10-week experiment. With respect to plant/herbivore interactions, the four Swiss scientists say "doubling the ambient CO_2 concentration had a marked effect on plant colonization by winged aphids particularly when plants were exposed to CO_2 for longer periods." After an exposure of only two weeks, for example, there was no difference in colonization rate, whereas after six and 10 weeks "elevated CO_2 led to a respective 15 and 26% reduction of colonization rates" by the cabbage aphid. The authors also note plant volatile emissions, which have been linked to attracting insects, were reduced significantly at the higher CO_2 concentration. Klaiber *et al*. conclude, "in agroecosystems, reduced crop plant colonization by an herbivorous pest insect under elevated CO_2 might be advantageous."

The majority of evidence to date suggests rising atmospheric CO_2 concentrations may reduce the frequency and severity of pest outbreaks detrimental to agriculture, without seriously impacting herbivorous organisms found in natural ecosystems that are normally viewed in a more favorable light.

References

Brooks, G.L. and Whittaker, J.B. 1999. Responses of three generations of a xylem-feeding insect, *Neophilaenus lineatus* (Homoptera), to elevated CO_2. *Global Change Biology* **5**: 395–401.

Castells, E., Roumet, C., Peñuelas, J., and Roy, J. 2002. Intraspecific variability of phenolic concentrations and their responses to elevated CO_2 in two mediterranean perennial grasses. *Environmental and Experimental Botany* **47**: 205–216.

Goverde, M., Bazin, A., Shykoff, J.A., and Erhardt, A. 1999. Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO_2 and plant genotype. *Functional Ecology* **13**: 801–810.

Himanen, S.J., Nerg, A.-M., Nissinen, A., Pinto, D.M., Stewart Jr., C.N., Poppy, G.M., and Holopainen, J.K. 2009. Effects of elevated carbon dioxide and ozone on volatile terpenoid emissions and multitrophic communication of transgenic insecticidal oilseed rape (*Brassica napus*). *New Phytologist* **181**: 174–186.

Joutei, A.B., Roy, J., Van Impe, G., and Lebrun, P. 2000. Effect of elevated CO_2 on the demography of a leaf-sucking mite feeding on bean. *Oecologia* **123**: 75–81.

Kerslake, J.E., Woodin, S.J., and Hartley, S.E. 1998. Effects of carbon dioxide and nitrogen enrichment on a plant-insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytologist* **140**: 43–53.

Klaiber, J., Najar-Rodriguez, A.J., Piskorski, R., and Dorn,

S. 2013. Plant acclimation to elevated CO_2 affects important plant functional traits, and concomitantly reduces plant colonization rates by an herbivorous insect. *Planta* **237**: 29–42.

Newman, J.A., Gibson, D.J., Hickam, E., Lorenz, M., Adams, E., Bybee, L., and Thompson, R. 1999. Elevated carbon dioxide results in smaller populations of the bird cherry-oat aphid *Rhopalosiphum padi*. *Ecological Entomology* **24**: 486–489.

Peters, H.A., Baur, B., Bazzaz, F., and Korner, C. 2000. Consumption rates and food preferences of slugs in a calcareous grassland under current and future CO_2 conditions. *Oecologia* **125**: 72–81.

5.5.3.2 Woody Plants

Insect pests have vexed Earth's trees in the past and likely will continue to do so in the future. The ongoing rise in the atmosphere's CO_2 content may affect this phenomenon, for better or for worse. The sections that follow review the results of several studies that have addressed this subject as it applies to woody plant species. These studies suggest Earth's woody plants will fare much better in a CO_2-enriched future with respect to the periodic assaults of leaf-damaging herbivores.

5.5.3.2.1 Cotton

Bt toxins produced by *Bacillus thuringiensis* supplied to plants via foliar application have been used as a means of combating crop pests for more than 50 years. The effectiveness of this pest management technique depends primarily on the amount of Bt-produced toxins ingested by susceptible insects. Consequently, Coviella and Trumble (2000) wondered whether atmospheric CO_2 enrichment might enhance the effectiveness of the technique by inducing susceptible insects to eat more treated foliage and thus be more effectively eradicated. If soil nitrogen levels are low, foliar nitrogen concentrations in CO_2-enriched air are often reduced from what they are at the current atmospheric CO_2 concentration, and, it is supposed, insects thus must eat more foliage to get the amount of nitrogen they require for proper growth and development. In eating more foliage, the insects would ingest more Bt-produced toxins, and they would be more severely affected by them.

To test this hypothesis, Coviella and Trumble grew cotton plants in 20 three-liter pots in each of six Teflon-film chambers in a temperature-controlled greenhouse; three of the chambers were maintained at an atmospheric CO_2 concentration of 370 ppm, and three were maintained at 900 ppm CO_2. In addition, half of the plants in each chamber received high levels of nitrogen (N) fertilization, while half received low levels (30 as opposed to 130 mg N/kg soil/week). After 45 days, leaves were removed from the plants and dipped in a solution containing *Bacillus thuringiensis*, after which known amounts of treated leaf material were fed to *Spodoptera exigua* larvae and their responses measured and analyzed.

These protocols revealed plants grown in the elevated CO_2 chambers did indeed have significantly lower foliar nitrogen concentrations than plants grown in the ambient CO_2 chambers under the low N fertilization regime, but this was not the case under the high N regime. Also, older larvae fed with foliage grown in elevated CO_2 with low N fertilization consumed significantly more plant material than those fed with foliage grown in ambient CO_2, but again no differences were observed in the high N treatment. In addition, and "consistent with the effect of higher Bt toxin intake due to enhanced consumption," the researchers found "insects fed on low N plants had significantly higher mortality in elevated CO_2," but again, no such effect was evident in the high N treatment. Coviella and Trumble conclude, "increasing atmospheric CO_2 is making the foliar applications more efficacious," especially in the case of soils low in nitrogen.

In addition to applying Bt toxins to plants by spraying, the ability of plants to produce them internally has been achieved by means of genetic engineering. However, there is concern foreign genes from agricultural plants may be transferred into wild relatives of transgenic crop lines and thereby upset the "balance of nature." In one of the first studies to address this concern, Coviella *et al*. (2000) grew cotton plants in the same manner as Coviella and Trumble—in 12 Teflon-film chambers in a temperature-controlled greenhouse, where six of the chambers were maintained at an atmospheric CO_2 concentration of 370 ppm and six were maintained at 900 ppm. Half the plants in each chamber were of a transgenic line containing the Bt gene for the production of the Cry1Ac toxin that is mildly toxic to *Spodoptera exigua*, and the other half were of a near isogenic line without the Bt gene. In addition, half the plants in each chamber received high levels of nitrogen (N) fertilization, while half received low levels (30 as opposed to 130 mg N/kg soil/week). Between 40 and 45 days after emergence, leaves were removed from the plants and fed to the *S. exigua* larvae, after which a number of larval responses were measured and analyzed, along with various leaf properties.

The researchers found the low-N plants in the elevated CO_2 treatment had lower foliar N concentrations than the low-N plants in the ambient CO_2 treatment; the transgenic plants from the low-N, high CO_2 treatment produced lower levels of Bt toxin than did the transgenic plants from the low-N, ambient CO_2 treatment. The high level of N fertilization only partially compensated for this latter high-CO_2 effect. In the ambient CO_2 treatment there was also a significant increase in days to pupation for insects fed transgenic plants, but this difference was not evident in elevated CO_2. In addition, pupal weight in ambient CO_2 was significantly higher in nontransgenic plants, and, again this difference was not observed in elevated CO_2.

Coviella *et al.* say their results "support the hypothesis that the lower N content per unit of plant tissue caused by the elevated CO_2 will result in lower toxin production by transgenic plants when nitrogen supply to the plants is a limiting factor." They also note "elevated CO_2 appears to eliminate differences between transgenic and nontransgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight." These results, in turn, suggest that in the case of inadvertent Bt gene transference to wild relatives of transgenic crop lines, elevated levels of atmospheric CO_2 will tend to negate certain of the negative effects the wayward genes might otherwise inflict on the natural world.

Coviella *et al.*'s results suggest transgenic plants designed to produce Bt-type toxins may become less effective in carrying out the objective of their design as the air's CO_2 content continues to rise. Coupling this observation with the fact that the foliar application of *Bacillus thuringiensis* to crops should become even more effective in a higher-CO_2 world of the future, as per the findings of Coviella and Trumble, it could be argued the implantation of toxin-producing genes in plants is not the way to proceed in the face of the ongoing rise in the air's CO_2 content, which reduces the effectiveness of the genetic implantation technique at the same time it increases the effectiveness of foliar application. It is important to see what other researchers have learned about the subject.

Chen *et al.* (2005b) grew well-watered and fertilized cotton plants of two varieties (GK–12, expressing Cry1A (c) genes from *Bacillus thuringiensis*, and Simian–3, a non-transgenic cultivar from the same recurrent parent) in pots in open-top chambers maintained at either 376 or 754 ppm CO_2 in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October. Throughout this period, several immature bolls were collected and analyzed for chemical characteristics. Others were stored under refrigerated conditions for later feeding to larvae of the cotton bollworm, when various parameters related to bollworm growth and development were monitored. The scientists found the elevated CO_2 treatment increased immature boll concentrations of condensed tannins by approximately 22% and 26% in transgenic and non-transgenetic cotton, respectively. In addition, Chen *et al.* report elevated CO_2 slightly decreased the body biomass of the cotton bollworm and reduced moth fecundity. The Bt treatment was even more effective in this regard, and in the combined Bt-high-CO_2 treatment the negative cotton bollworm responses were expressed most strongly.

In a parallel study, Chen *et al.* (2005a) grew transgenic *Bacillus thuringiensis* cotton (GK–12) plants from seed for a period of 30 days in well-watered and fertilized sand/vermiculite mixtures in pots located in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 370, 700, and 1,050 ppm. Three generations of cotton aphids (*Aphis gossypii*) were subsequently allowed to feed on some of the plants, and a subset of the aphid-infected plants was supplied with predatory ladybugs. Chen *et al.* report "plant height, biomass, leaf area, and carbon:nitrogen ratios were significantly higher in plants exposed to elevated CO_2 levels," and "more dry matter and fat content and less soluble protein were found in *A. gossypii* in elevated CO_2." They report "cotton aphid fecundity significantly increased ... through successive generations reared on plants grown under elevated CO_2." They also report "significantly higher mean relative growth rates were observed in lady beetle larvae under elevated CO_2," and "the larval and pupal durations of the lady beetle were significantly shorter and [their] consumption rates increased when fed *A. gossypii* from elevated CO_2 treatments." Hence, they conclude, their study "provides the first empirical evidence that changes in prey quality mediated by elevated CO_2 can alter the prey preference of their natural enemies." They found this phenomenon could "enhance the biological control of aphids by lady beetle" while enhancing control by means of negative Bt-induced effects on the aphids.

Wu *et al.* (2011) state, "secondary metabolites present in plants provide protection against invaders because of their antimicrobial activity (Kamra *et al*., 2006)," and "elevated CO_2 leads to plants allocating more carbohydrate resources to their secondary metabolism (Agrell *et al*., 2004; Casteel *et al*., 2008)," which may thus induce them to "generate higher concentrations of defensive compounds that are toxic [to] herbivorous insects (Coviella and Trumble, 1999)." Preeminent in this group of compounds are condensed tannins, naturally occurring secondary carbon compounds produced in the leaves of virtually all families of plants that comprise up to 50% of the dry weight of their leaves. Another such compound of note is gossypol, a natural toxin present in the cotton plant that helps to protect it from insect pests such as the cotton bollworm.

Wu *et al*. studied the allocation of the carbohydrate resources of two cotton (*Gossypium hirsutum* L.) cultivars—transgenic Bt cotton (cv. GK–12) and non-transgenic Bt cotton (cv. Simian–3)—to condensed tannins and gossypol both before and after injury inflicted on the plants by the cotton bollworm (*Helicoverpa armigera* Hubner) over periods of one, three, and 12 hours in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 370 or 750 ppm.

Before any bollworm injury to the plants, the extra CO_2 led to increases of 12 and 14% in the condensed tannin concentrations in the foliage of the Bt-transgenic and non-transgenic cotton plants, respectively; increases of 10 and 10% in the gossypol concentrations of the transgenic and non-transgenic plants, respectively; and a 4% decrease in Bt toxin in the transgenic plants. After bollworm injury for periods of one, three, and 12 hours, the non-transgenic plants experienced condensed tannin increases of 14, 9, and 9%, respectively, and transgenic plants experienced increases of 16, 9, and 9%, respectively. Corresponding results for gossypol were increases of 7, 10, and 6% for the non-transgenic cultivar and 7, 7, and 6% for the transgenic cultivar. The transgenic plants also exhibited Bt toxin decreases of 3, 3, and 5%, respectively.

In discussing the implications of their findings, the four Chinese scientists state prior studies have demonstrated increases in condensed tannins and gossypol typically occur "in response to an increasing CO_2 atmosphere, especially in combination with injury caused by herbivorous insects (Druy *et al*., 1998; Roth and Lindroth, 1994)," and they suggest these increases "may compensate for the Bt toxin loss in the transgenic Bt cotton," which appears to be an outcome of their study as well. Thus we may expect cotton to become ever less susceptible to damage by the cotton bollworm as the air's CO_2 content continues to rise.

References

Agrell, J., Anderson, P., Oleszek, W., Stochmal, A., and Agrell, C. 2004. Combined effects of elevated CO_2 and herbivore damage on alfalfa and cotton. *Journal of Chemical Ecology* **30**: 2309–2324.

Casteel, C.L., O'Neill, B.F., Zavala, J.A., Bilgin, D.D., Berenbaum, M.R., and DeLucia, E.H. 2008. Transcriptional profiling reveals elevated CO_2 and elevated O_3 alter resistance of soybean (*Glycine max*) to Japanese beetles (*Popillia japonica*). *Plant, Cell and Environment* **31**: 419–434.

Chen, F., Ge, F., and Parajulee, M.N. 2005a. Impact of elevated CO_2 on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Leis axyridis*. *Environmental Entomology* **34**: 37–46.

Chen, F., Wu, G., Ge, F., Parajulee, M.N., and Shrestha, R.B. 2005b. Effects of elevated CO_2 and transgenic Bt cotton on plant chemistry, performance, and feeding of an insect herbivore, the cotton bollworm. *Entomologia Experimentalis et Applicata* **115**: 341–350.

Coviella, C.E., Morgan, D.J.W., and Trumble, J.T. 2000. Interactions of elevated CO_2 and nitrogen fertilization: Effects on production of *Bacillus thuringiensis* toxins in transgenic plants. *Environmental Entomology* **29**: 781–787.

Coviella, C.E. and Trumble, J.T. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology* **13**: 700–712.

Coviella, C.E. and Trumble, J.T. 2000. Effect of elevated atmospheric carbon dioxide on the use of foliar application of *Bacillus thuringiensis*. *BioControl* **45**: 325–336.

Drury, S.J., Good, J.E.G., Perrins, C.M., Buse, A., and Kaye, T. 1998. The effects of increasing CO_2 and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology* **4**: 55–61.

Kamra, D.N., Agrawal, N., and Chaudhary, L.C. 2006. Inhibition of ruminal methanogenesis by tropical plants containing secondary compounds. *International Congress Series* **1293**: 156–163.

Roth, S.K. and Lindroth, R.L. 1994. Effects of CO_2-mediated changes in paper birch and white pine chemistry on gypsy moth performance. *Oecologia* **98**: 133–138.

Wu, G., Chen, F.J., Ge, F., and Xiao, N.-W. 2011. Impacts of elevated CO_2 on expression of plant defensive compounds in Bt-transgenic cotton in response to infestation by cotton bollworm. *Agricultural and Forest Entomology* **13**: 77–82.

5.5.3.2.2 Maple

Williams *et al.* (2003) studied *Acer rubrum* saplings beginning their fourth year of growth in open-top chambers maintained at four atmospheric CO_2/ temperature conditions: (1) ambient temperature, ambient CO_2, (2) ambient temperature, elevated CO_2 (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO_2, and (4) elevated temperature, elevated CO_2. They bagged first instar gypsy moth larvae on various branches of the trees and observed their behavior.

They found "larvae feeding on CO_2-enriched foliage ate a comparably poorer food source than those feeding on ambient CO_2-grown plants, irrespective of temperature," and there was a minor reduction in leaf water content due to CO_2 enrichment. They report the "CO_2-induced reductions in foliage quality (e.g. nitrogen and water) were unrelated to insect mortality, development rate and pupal weight," and these and any other phytochemical changes that may have occurred "resulted in no negative effects on gypsy moth performance." They also found "irrespective of CO_2 concentration, on average, male larvae pupated 7.5 days earlier and female larvae 8 days earlier at elevated temperature." Noting anything that prolongs the various development stages of insects potentially exposes them to greater predation and parasitism risk, they conclude the observed temperature-induced hastening of the insects' development likely would expose them to less predation and parasitism risk, which would confer an advantage on this particular herbivore in this particular situation.

Hamilton *et al.* (2004) note many single-species investigations have suggested increases in atmospheric CO_2 will increase herbivory (Bezemer and Jones, 1998; Cannon, 1998; Coviella and Trumble, 1999; Hunter, 2001; Lincoln *et al.*, 1993; Whittaker, 1999). However, because there are so many feedbacks and complex interactions among the numerous components of real-world ecosystems, they warn against putting too much faith in these predictions until relevant real-world ecosystem-level experiments have been completed.

In one such study they conducted at the Duke Forest FACE facility near Chapel Hill, North Carolina (USA), Hamilton *et al.* "measured the amount of leaf tissue damaged by insects and other herbivorous arthropods during two growing seasons in a deciduous forest understory continuously exposed to ambient (360 ppm) and elevated (560 ppm) CO_2 conditions." This forest is dominated by loblolly pine trees that account for fully 92% of the ecosystem's total woody biomass. In addition, it contains 48 species of other woody plants (trees, shrubs, and vines) that have naturally established themselves in the forest's understory. Hamilton *et al.* quantify the loss of foliage due to herbivory experienced by three deciduous tree species, one of which was *Acer rubrum*.

The results indicate "elevated CO_2 led to a trend toward reduced herbivory in [the] deciduous understory in a situation that included the full complement of naturally occurring plant and insect species." In 1999, for example, "elevated CO_2 reduced overall herbivory by more than 40%," and in 2000 they observed "the same pattern and magnitude of reduction."

With respect to changes in foliage properties that might have been expected to lead to increases in herbivory, Hamilton *et al.* report they "found no evidence for significant changes in leaf nitrogen, C/N ratio, sugar, starch or total leaf phenolics in either year of [the] study," noting these findings agree with those of "another study performed at the Duke Forest FACE site that also found no effect of elevated CO_2 on the chemical composition of leaves of understory trees (Finzi and Schlesinger, 2002)."

Hamilton *et al.* thus conclude their landmark paper by emphasizing that "despite the large number of studies that predict increased herbivory, particularly from leaf chewers, under elevated CO_2, our study found a trend toward reduced herbivory two years in a row." In addition, they note their real-world results "agree with the only other large-scale field experiment that quantified herbivory for a community exposed to elevated CO_2 (Stilling *et al.*, 2003)."

Consequently, and contrary to the predictions of increased destruction of natural ecosystems by insects and other herbivorous arthropods in a CO_2-enriched world of the future, just the opposite appears to be the more likely outcome: greater plant productivity plus less foliage consumption by herbivores, "whether expressed on an absolute or a percent basis," as Hamilton *et al.* found in their study.

Knepp *et al.* (2005) quantified leaf damage by chewing insects on saplings of seven species (including *Acer rubrum*) in 2001, 2002, and 2003; five additional species (including *Acer barbatum*) were included in 2001 and 2003. They found "across the seven species that were measured in each of the three years, elevated CO_2 caused a reduction in the percentage of leaf area removed by chewing insects," such that "the percentage of leaf tissue damaged by insect herbivores was 3.8% per leaf under ambient

CO_2 and 3.3% per leaf under elevated CO_2." The greatest effects were observed in 2001, when "across 12 species the average damage per leaf under ambient CO_2 was 3.1% compared with 1.7% for plants under elevated CO_2," "indicative of a 46% decrease in the total area and total mass of leaf tissue damaged by chewing insects in the elevated CO_2 plots."

Knepp *et al.* write, "given the consistent reduction in herbivory under high CO_2 across species in 2001, it appears some universal feature of chemistry or structure that affected leaf suitability was altered by the treatment." Another possibility they discuss is "forest herbivory may decrease under elevated CO_2 because of a decline in the abundance of chewing insects," citing Stilling *et al.* (2002) to this effect and noting "slower rates of development under elevated CO_2 prolongs the time that insect herbivores are susceptible to natural enemies, which may be abundant in open-top chambers and FACE experiments but absent from greenhouse experiments." In addition, they suggest "decreased foliar quality and increased per capita consumption under elevated CO_2 may increase exposure to toxins and insect mortality," also noting "CO_2-induced changes in host plant quality directly decrease insect fecundity," citing Coviella and Trumble (1999) and Awmack and Leather (2002).

Knepp *et al.* conclude, "in contrast to the view that herbivore damage will increase under elevated CO_2 as a result of compensatory feeding on lower quality foliage, our results and those of Stiling *et al.* (2002) and Hamilton *et al.* (2004) in open experimental systems suggest that damage to trees may decrease."

But what if herbivore-induced damage increases, for whatever reason in some situations, in a future CO_2-enriched world?

The likely answer is provided by Kruger *et al.* (1998), who grew well-watered and fertilized one-year-old *Acer saccharum* saplings in glasshouses maintained at atmospheric CO_2 concentrations of either 356 or 645 ppm for 70 days, to determine the effects of elevated CO_2 on photosynthesis and growth. On the 49th day of differential CO_2 exposure, 50% of the saplings' leaf area was removed from half of the trees in order to study the impact of concomitant simulated herbivory. They found the 70-day CO_2 enrichment treatment increased the total dry weight of the non-defoliated seedlings by about 10%. When the trees were stressed by simulated herbivory, the CO_2-enriched maples produced 28% more dry weight over the final phase of the study than the maples in the ambient-air treatment.

Kruger *et al.* thus conclude, in a high-CO_2 world of the future "sugar maple might be more capable of tolerating severe defoliation events which in the past have been implicated in widespread maple declines."

References

Awmack, C.S. and Leather, S.R. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* **47**: 817–844.

Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. *Oikos* **82**: 212–222.

Cannon, R.J. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* **4**: 785–796.

Coviella, C.E. and Trumble, J.T. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology* **13**: 700–712.

Finzi, A.C. and Schlesinger, W.H. 2002. Species control variation in litter decomposition in a pine forest exposed to elevated CO_2. *Global Change Biology* **8**: 1217–1229.

Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J., Aldea, M., and DeLucia, E.H. 2004. Insect herbivory in an intact forest understory under experimental CO_2 enrichment. *Oecologia* **138**: 10.1007/s00442-003-1463-5.

Hunter, M.D. 2001. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agricultural and Forest Entomology* **3**: 153–159.

Knepp, R.G., Hamilton, J.G., Mohan, J.E., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2005. Elevated CO_2 reduces leaf damage by insect herbivores in a forest community. *New Phytologist* **167**: 207–218.

Kruger, E.L., Volin, J.C., and Lindroth, R.L. 1998. Influences of atmospheric CO_2 enrichment on the responses of sugar maple and trembling aspen to defoliation. *New Phytologist* **140**: 85–94.

Lincoln, D.E., Fajer, E.D., and Johnson, R.H. 1993. Plant-insect herbivore interactions in elevated CO_2 environments. *Trends in Ecology and Evolution* **8**: 64–68.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2003. Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* **134**: 82–87.

Whittaker, J.B. 1999. Impacts and responses at population level of herbivorous insects to elevated CO_2. *European Journal of Entomology* **96**: 149–156.

Williams, R.S., Lincoln, D.E., and Norby, R.J. 2003. Development of gypsy moth larvae feeding on red maple

saplings at elevated CO_2 and temperature. *Oecologia* **137**: 114–122.

5.5.3.2.3 Oak

Dury *et al.* (1998) grew four-year-old *Quercus robur* seedlings in pots in greenhouses maintained at ambient and twice-ambient atmospheric CO_2 concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year to study the interactive effects of elevated CO_2 and temperature on leaf nutritional quality. They found the elevated air temperature treatment significantly reduced leaf palatability, and leaf toughness increased as a consequence of temperature-induced increases in condensed tannin concentrations. In addition, the higher temperatures significantly reduced leaf nitrogen content, and elevated CO_2 caused a temporary increase in leaf phenolic concentrations and a decrease in leaf nitrogen content.

In one of the first attempts to move outside the laboratory and greenhouse and study the effects of atmospheric CO_2 enrichment on trophic food webs in a natural ecosystem, Stiling *et al.* (1999) enclosed portions of a native scrub-oak community in Florida (USA) within 3.6-m-diameter open-top chambers and fumigated them with air having CO_2 concentrations of either 350 or 700 ppm for approximately one year, to see whether elevated CO_2 would impact leaf miner densities, feeding rates, and mortality in this nutrient-poor ecosystem.

They found total leaf miner densities were 38% less on the foliage of trees growing in CO_2-enriched air than on the foliage of trees growing in ambient air. In addition, atmospheric CO_2 enrichment consistently reduced the absolute numbers of the study's six leaf miner species. However, the elevated CO_2 treatment increased the leaf area consumed by the less abundant herbivore miners by approximately 40% relative to the areas mined by the more abundant herbivores present on the foliage exposed to ambient air. In spite of this increase in feeding, the leaf miners in the CO_2-enriched chambers experienced significantly greater mortality than those in the ambient-air chambers. Although CO_2-induced reductions in leaf nitrogen content played a minor role in this phenomenon, the greatest factor contributing to increased herbivore mortality was a four-fold increase in parasitization by various wasps, which could more readily detect the more-exposed leaf miners on the CO_2-enriched foliage.

If extended to agricultural ecosystems, these findings suggest crops may experience less damage from such herbivores in a high-CO_2 world of the future, thus increasing potential harvest and economic gains. In addition, with reduced numbers of leaf miners in CO_2-enriched air, farmers could reduce their dependency on chemical pesticides to control them, thus reducing the negative impacts of these agricultural chemicals on the environment.

In another study conducted on five scrub-oak forest species at the same experimental facility, Stiling *et al.* (2002b) investigated the effects of an approximate doubling of the air's CO_2 concentration on a number of characteristics of several insect herbivores. As before, they found the "relative levels of damage by the two most common herbivore guilds, leaf-mining moths and leaf-chewers (primarily larval lepidopterans and grasshoppers), were significantly lower in elevated CO_2 than in ambient CO_2, for all five plant species," and they found "the response to elevated CO_2 was the same across all plant species." In addition, "more host-plant induced mortality was found for all miners on all plants in elevated CO_2 than in ambient CO_2." These effects were so powerful that in addition to the relative densities of insect herbivores being reduced in the CO_2-enriched chambers, and "even though there were more leaves of most plant species in the elevated CO_2 chambers," the total densities of leaf miners in the high-CO_2 chambers were lower for all plant species. In a high-CO_2 world of the future, many plants may be able to better withstand the onslaughts of various insect pests that have plagued them in the past. Another intriguing implication of this finding, as Stiling *et al.* note, is "reductions in herbivore loads in elevated CO_2 could boost plant growth beyond what might be expected based on pure plant responses to elevated CO_2."

Rossi *et al.* (2004) studied the same ecosystem, which is dominated by two species of scrub oak (*Quercus geminata* and *Q. myrtifolia*) that account for more than 90% of the ecosystem's biomass, focusing on the abundance of a guild of lepidopteran leaf-miners that attack the leaves of *Q. myrtifolia*, as well as various leaf chewers. They followed 100 marked leaves in each of 16 open-top chambers (half of them exposed to ambient air and half exposed to air containing an extra 350 ppm of CO_2) for nine months. "Differences in mean percent of leaves with leafminers and chewed leaves on trees from ambient and elevated chambers were assessed using paired *t*-tests."

The researchers report, "both the abundance of the guild of leafmining lepidopterans and damage caused by leaf chewing insects attacking myrtle oak were depressed in elevated CO_2." They found leafminer abundance was 44% lower ($P = 0.096$) in the CO_2-enriched chambers compared to the ambient-air chambers, and the abundance of leaves suffering chewing damage was 37% lower ($P = 0.072$) in the CO_2-enriched air.

Concentrating on the same ecosystem, where atmospheric enrichment with an extra 350 ppm of CO_2 was begun in May 1996, Hall *et al.* (2005b) studied the four species that dominate the community and are present in every experimental chamber: the three oaks (*Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*) plus the nitrogen-fixing legume *Galactia elliottii*. At three-month intervals from May 2001 to May 2003, undamaged leaves were removed from each of these species in all chambers and analyzed for various chemical constituents, and 200 randomly selected leaves of each species in each chamber were scored for the presence of six types of herbivore damage.

The researchers found no significant differences between the CO_2-enriched and ambient-treatment leaves of any single species in terms of condensed tannins, hydrolyzable tannins, total phenolics, or lignin. However, in all four species together there were always greater concentrations of all four leaf constituents in the CO_2-enriched leaves, with across-species mean increases of 6.8% for condensed tannins, 6.1% for hydrolyzable tannins, 5.1% for total phenolics, and 4.3% for lignin. In addition, there were large and often significant CO_2-induced decreases in all leaf damage categories among all species: chewing (-48%, $P < 0.001$), mines (-37%, $P = 0.001$), eye spot gall (-45%, $P < 0.001$), leaf tier (-52%, $P = 0.012$), leaf mite (-23%, $P = 0.477$), and leaf gall (-16%, $P = 0.480$). Hall *et al.* conclude the changes they observed in leaf chemical constituents and herbivore damage "suggest that damage to plants may decline as atmospheric CO_2 levels continue to rise."

Hall *et al.* (2005a) studied the effects of an extra 350 ppm of CO_2 on litter quality, herbivore activity, and their interactions. Over the three years of this experiment (2000, 2001, 2002), they determined "changes in litter chemistry from year to year were far larger than effects of CO_2 or insect damage, suggesting that these may have only minor effects on litter decomposition." The one exception to this finding was "condensed tannin concentrations[, which] increased under elevated CO_2 regardless of species, herbivore damage, or growing season," rising by 11% in 2000, 18% in 2001, and 41% in 2002 as a result of atmospheric CO_2 enrichment, as best we can determine from their bar graphs. The five researchers also report, "lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO_2 plants (Fajer *et al.*, 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al.*, 1999)," noting further that at their field site, "which hosts the longest continuous study of the effects of elevated CO_2 on insects, herbivore populations decline[d] markedly under elevated CO_2 (Stiling *et al.*, 1999, 2002a, 2003; Hall *et al.*, 2005)."

Focusing their attention on two species of oak tree—*Quercus alba* L. (white oak) and *Quercus velutina* Lam. (black oak)—Knepp *et al.* (2007) examined host plant preference and larval performance of *A. polyphemus* when fed foliage of the two tree species that had been grown in either ambient or CO_2-enriched air (to 200 ppm above ambient) in a long-running FACE experiment at the Forest Atmosphere Carbon Transfer and Storage (FACTS–1) research site in the Piedmont region of North Carolina (USA). They found "growth under elevated CO_2 reduced the food quality of oak leaves for caterpillars," and "consuming leaves of either oak species grown under elevated CO_2 slowed the rate of development of *A. polyphemus* larvae." In addition, they report feeding on foliage of *Q. velutina* grown under elevated CO_2 led to reduced consumption by the larvae and greater mortality. The researchers opine, "reduced consumption, slower growth rates, and increased mortality of insect larvae may explain [the] lower total leaf damage observed previously in plots of this forest exposed to elevated CO_2," as documented by Hamilton *et al.* (2004) and Knepp *et al.* (2005).

Stiling *et al.* (2010) note in a CO_2-enriched atmosphere, "plant quality for herbivores is reduced because of decreases in plant nitrogen concentrations and increases in secondary metabolites (Poorter *et al.*, 1997; Curtis and Wang, 1998; Peñuelas and Estiarte, 1998)," but "Stiling *et al.* (2009) recently showed that, over long time periods under continuously elevated CO_2, the increases in plant biomass under elevated CO_2 over compensate for reductions in foliage quality by providing a greater quantity of biomass for herbivores." Seeking to determine whether this might also be true for insectivores and detritivores, Stiling *et al.* employed pitfall trapping over the last three of 11 years of continuous CO_2 enrichment (to 350 ppm above ambient) in eight of 16 open-top chambers that enclosed portions of a scrub-oak ecosystem in Florida (USA) composed of a mix of three oak tree species (*Quercus myrtifolia, Q. geminate,* and *Q. chapmanii*) that accounted for approximately 90% of the total aboveground ecosystem biomass, and they employed sticky traps over another six months of the study.

The three researchers report 110,618 insects and other arthropods from 25 orders were recovered from the pitfall traps, and 39,305 insects and other arthropods from 14 orders were found on the sticky traps. These data, they write, "revealed increases of insect herbivore species such as Thysanoptera (thrips), Hemiptera, and Lepidoptera, but no effects on insectivores such as spiders, parasitic wasps, and ants, or on detritivores such as Diptera (flies), Psocoptera (book lice), Blattodea (cockroaches), Collembola (spring tails), Orthoptera (crickets) and Coleoptera (beetles)."

Stiling *et al*. conclude the "increase in the number of herbivores, including raspers, suckers, and chewers, under elevated CO_2" was "likely caused by an increase in plant biomass under elevated CO_2," which for the scrub-oak ecosystem they studied amounted to 67% (Seiler *et al*., 2009). But they additionally conclude, "increases in plant biomass and herbivore abundance brought about by elevated CO_2 do not influence insect abundance at other trophic levels such as insectivores, parasitoids and predators, or decomposers." They note their results are similar to those of two other studies (Sanders *et al*., 2004; Hillstrom and Lindroth, 2008) that also "failed to detect effects of elevated CO_2 on most guilds." Thus, the "bottom-up effect brought about by higher plant biomass as a result of many years of elevated CO_2" in this experiment appears to enhance abundance of herbivores only.

The evidence cited above suggests herbivore damage to oak trees by various insect pests will decline as the air's CO_2 concentration continues to climb.

References

Curtis, P.S. and Wang, X. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. *Oecologia* **113**: 299–313.

Dury, S.J., Good, J.E.G., Perrins, C.M., Buse, A., and Kaye, T. 1998. The effects of increasing CO_2 and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology* **4**: 55–61.

Fajer, E.D., Bowers, M.D., and Bazzaz, F.A. 1991. The effects of enriched CO_2 atmospheres on the buckeye butterfly, *Junonia coenia*. *Ecology* **72**: 751–754.

Hall, M.C., Stiling, P., Hungate, B.A., Drake, B.G., and Hunter, M.D. 2005a. Effects of elevated CO_2 and herbivore damage on litter quality in a scrub oak ecosystem. *Journal of Chemical Ecology* **31**: 2343–2356.

Hall, M.C., Stiling, P., Moon, D.C., Drake, B.G., and Hunter, M.D. 2005b. Effects of elevated CO_2 on foliar quality and herbivore damage in a scrub oak ecosystem. *Journal of Chemical Ecology* **31**: 267–285.

Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J.S., Aldea, M., and DeLucia, E.H. 2004. Insect herbivory in an intact forest understory under experimental CO_2 enrichment. *Oecologia* **138**: 566–573.

Hillstrom, M.L. and Lindroth, R.L. 2008. Elevated atmospheric carbon dioxide and ozone alter forest insect abundance and community composition. *Insect Conservation and Diversity* **1**: 233–241.

Knepp, R.G., Hamilton, J.G., Mohan, J.E., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2005. Elevated CO_2 reduces leaf damage by insect herbivores in a forest community. *New Phytologist* **167**: 207–218.

Knepp, R.G., Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2007. Foliage of oaks grown under elevated CO_2 reduces performance of *Antheraea polyphemus* (Lepidoptera: Saturniidae). *Environmental Entomology* **36**: 609–617.

Lindroth, R.L. 1996. CO_2-mediated changes in tree chemistry and tree-Lepidoptera interactions. In: Koch, G.W. and Mooney, H.A. (Eds.) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, California, USA, pp. 105–120.

Peñuelas, J. and Estiarte, M. 1998. Can elevated CO_2 affect secondary metabolism and ecosystem function? *Trends in Ecology and Evolution* **13**: 20–24.

Poorter, H., van Berkel, Y., Baxter, B., Den Hertog, J., Dijkstra, P., Gifford, R.M., Griffin, K.L., Roumet, C., Roy, J., and Wong, S.C. 1997. The effect of elevated CO_2 on the chemical composition and construction costs of leaves. *Plant, Cell and Environment* **10**: 472–482.

Rossi, A.M., Stiling, P., Moon, D.C., Cattell, M.V., and Drake, B.G. 2004. Induced defensive response of myrtle oak to foliar insect herbivory in ambient and elevated CO_2. *Journal of Chemical Ecology* **30**: 1143–1152.

Sanders, N.J., Belote, R.T., and Weltzen, J.F. 2004. Multitrophic effects of elevated atmospheric CO_2 on understory plant and arthropod communities. *Environmental Entomology* **33**: 1609–1616.

Seiler, T.J., Rasse, D.P., Li, J., Dijkstra, P., Anderson, H.P., Johnson, D.P., Powell, T.L., Hungate, B.A., Hinkle, C.R., and Drake, B.G. 2009. Disturbance, rainfall and contrasting species responses mediated aboveground biomass response to 11 years of CO_2 enrichment in a Florida scrub-oak ecosystem. *Global Change Biology* **15**: 356–367.

Stiling, P., Cattell, M., Moon, D.C., Rossi, A., Hungate, B.A., Hymus, G., and Drake, B.G. 2002a. Elevated atmospheric CO_2 lowers herbivore abundance, but increases leaf abscission rates. *Global Change Biology* **8**: 658–667.

Stiling, P., Forkner, R., and Drake, B. 2010. Long-term exposure to elevated CO_2 in a Florida scrub-oak forest increases herbivore densities but has no effect on other arthropod guilds. *Insect Conservation and Diversity* **3**: 152–156.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2002b. Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* **134**: 82–87.

Stiling, P., Moon, D.C., Rossi, A.M., Hungate, B., and Drake, B. 2009. Seeing the forest for the trees: long term exposure to elevated CO_2 increases some herbivore densities. *Global Change Biology* **15**: 1895–1902.

Stiling, P., Rossi, A.M., Hungate, B., Dijkstra, P., Hinkle, C.R., Knot III, W.M., and Drake, B. 1999. Decreased leaf-miner abundance in elevated CO_2: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* **9**: 240–244.

5.5.3.3 Other Plants

Gleadow *et al*. (1998) grew eucalyptus seedlings in glasshouses maintained at 400 and 800 ppm CO_2 for a period of six months, observing biomass increases of 98% and 134% in high and low nitrogen treatments, respectively. They also studied a sugar-based compound called prunasin, which produces cyanide in response to tissue damage caused by foraging herbivores. Although elevated CO_2 caused no significant change in leaf prunasin content, the proportion of nitrogen allocated to prunasin increased by approximately 20% in the CO_2-enriched saplings, suggestive of a potential for increased prunasin production had the saplings been under attack by herbivores.

In a study involving mechanical defoliation, Lovelock *et al*. (1999) grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed within open-top chambers maintained at atmospheric CO_2 concentrations of 390 and 860 ppm. At the 14-day point of the experiment, half of the seedlings in each treatment had about 40% of their total leaf area removed. None of the defoliated trees of either CO_2 treatment fully recovered from this manipulation, but at the end of the experiment the total plant biomass of the defoliated trees in the CO_2-enriched treatment was 15% greater than that of the defoliated trees in the ambient-CO_2 treatment, attesting to the benefits of atmospheric CO_2 enrichment in helping trees deal with herbivory.

Docherty *et al*. (1997) grew beech and sycamore saplings in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm, and groups of three sap-feeding aphid species and two sap-feeding leafhopper species were allowed to feed on them. Overall, elevated CO_2 had few significant effects on the performance of the insects, although there was a non-significant tendency for elevated CO_2 to reduce the individual weights and populations of the aphids.

Hattenschwiler and Schafellner (1999) grew seven-year-old spruce (*Picea abies*) trees at atmospheric CO_2 concentrations of 280, 420, and 560 ppm and various nitrogen deposition treatments for three years, allowing nun moth larvae to feed on current-year needles for 12 days. Larvae placed on the CO_2-enriched foliage consumed less needle biomass than larvae placed on the ambiently grown foliage, regardless of nitrogen treatment. This effect was so pronounced that the larvae feeding on needles produced by the CO_2-enriched trees attained an average final biomass only two-thirds of that attained by the larvae that fed on needles produced at 280 ppm CO_2. Since the nun moth is a deadly defoliator that resides in most parts of Europe and East Asia between 40 and 60°N latitude and is commonly regarded as the coniferous counterpart of its close relative the gypsy moth, which feeds primarily on deciduous trees, the results of this study suggest the ongoing rise in the air's CO_2 content likely will lead to significant reductions in damage to spruce and other coniferous trees by this voracious insect pest.

Holton *et al*. (2003) reared parasitized and non-parasitized forest tent caterpillars (*Malacosoma disstria*) on two quaking aspen (*Populus tremuloides*) genotypes (216, which is O_3-tolerant, and 259, which is O_3-sensitive) alone and in combination at the Aspen FACE site in northern Wisconsin (USA), in plots exposed to ambient air, ambient air + 200 ppm extra CO_2, ambient air + 50% extra ozone, and ambient air + 200 ppm extra CO_2 and 50% extra O_3 during the daylight hours of one full growing season. They found "elevated CO_2 had little effect on both primary and secondary metabolites of aspen." Thus it was not surprising to learn "elevated CO_2 had few biologically significant effects on forest tent caterpillar performance." Elevated O_3, on the other hand, altered foliar composition much more than did elevated CO_2, and, as they discovered, it improved tent caterpillar performance under ambient CO_2 conditions, but not in CO_2-enriched air. In addition, elevated O_3 decreased the larval survivorship of the parasite of the caterpillar. Without an increase in the air's CO_2 content commensurate with that projected for O_3 over the coming half-century, therefore, quaking aspen—the most widely distributed tree in North America—would be in for a world of hurt.

Mattson *et al.* (2004) note "although there have been many studies on the effects of elevated CO_2 on the interaction between plants and their insect herbivores (see Bezemer and Jones, 1998; Hunter, 2001), comparable studies on mammalian herbivores are lacking altogether, even though mammals play important roles in dynamics of many ecosystems (McNaughton and Sabuni, 1988; Pastor and Naiman, 1992)." Mattson *et al.* grew one-year-old seedlings of silver birch (*Betula pendula*) in closed-top chambers for one summer and autumn in pots containing an unfertilized commercial peat maintained at three soil nitrogen (N) levels (low = 0 kg N ha^{-1}, medium = 150 kg N ha^{-1}, high = 500 kg N ha^{-1}) and two temperature (T) levels (ambient and ambient + 3°C) in air of either 362 or 700 ppm CO_2 concentration. Feeding trials with caged Eurasian hares (*Lepus timidus*) were then carried out, and a number of chemical analyses were made of the tops of the seedlings and the basal parts of their stems.

In a second experiment, Mattson *et al.* grew paper birch (*Betula papyrifera*) from seed for two 140-day growing seasons in well-watered and fertilized pots placed within FACE rings maintained at atmospheric CO_2 concentrations of either 362 or 562 ppm, after which (in an unplanned aspect of the study) North American eastern cottontail rabbits (*Sylvilagus floridanus*) fed *ad libitum*, consuming bark tissue down to and scoring the wood, on the basal third of the seedlings, and these tissues were tested for the presence of various herbivore-deterring chemical constituents.

"As expected," they write, the results indicate "elevated CO_2 substantially increased the above-ground woody biomass growth of both paper birch (63%) and silver birch (21%)." In addition, noting "numerous studies have shown that elevated atmospheric CO_2 often, but not always, elicits increases in carbon partitioning to carbon-based secondary plant compounds," which often act as deterrents to herbivory, they say their findings "confirm this general pattern in silver and paper birch." Finally, they report high CO_2 reduced hare feeding on silver birch shoots by as much as 48% and reduced rabbit feeding on paper birch stems by about 51%, whereas neither temperature nor severe early-season defoliation (another experimental treatment) affected the trees' resistance against these mammalian herbivores.

Calling the anti-herbivory effect of elevated CO_2 "remarkably strong" and noting rabbits "overwhelmingly preferred ambient CO_2 plants," Mattson *et al.* say their data "clearly suggest that the defensive biochemistry of paper birch twigs as well as the main stem were [positively] altered as the result of elevated CO_2." As the air's CO_2 content continues to rise, at least these two species of birch trees apparently will have a significantly easier time of getting established and growing to maturity.

Sanders *et al.* (2004) studied effects of atmospheric CO_2 enrichment on the plant and arthropod communities of the understory of a closed-canopy sweetgum plantation (which reduces the light available to the understory between 70 and 95% during the growing season) in a FACE study where the air's CO_2 content was increased by approximately 48%. The authors report under such conditions there were large adjustments in the relative productivities of the five dominant species that account for more than 90% of the biomass and annual production of the understory vegetation. Overall, however, the total understory productivities of the two CO_2 treatments were not significantly different from each other. Also, Sanders *et al.* report, "C:N ratios for four of the five dominant plant taxa did not differ between ambient and elevated CO_2," and "there were no overall treatment or species x treatment effects" with respect to this parameter.

The three scientists further report they "found no effect of elevated CO_2 on herbivory," and "even for the one species that showed an effect of CO_2 on C:N ratio, herbivores did not compensate by foraging more." In addition, total arthropod abundance did not differ between ambient and elevated CO_2 plots, nor did the abundances of detritivores, omnivores, or parasitoids. They conclude, "changes in plant community composition did not translate into differences in arthropod communities." Sanders *et al.* state "idiosyncratic, species-specific responses to elevated CO_2 may buffer one another: the abundances of some species increase while others decrease," and, therefore, "to understand the potential effects of global [environmental] change on the complexity of multitrophic interactions that structure most communities, field experiments on entire communities are necessary."

Noting the "detrimental effects of ozone on plants are well known," and "carbon dioxide [CO_2]

generally affects trees in opposite ways to ozone [O_3]," Valkama *et al*. (2007) conducted a literature review they describe as "the first quantitative analysis of the interactive effects of elevated O_3 and elevated CO_2 on tree chemistry and herbivore performance," based on the results of "63 studies conducted on 22 tree species and 10 insect herbivore species and published between 1990 and 2005."

With respect to ways elevated O_3 may benefit insect herbivores that tend to damage trees, Valkama *et al*. determined "elevated O_3 significantly shortened development time of insect herbivores [when they are exposed and vulnerable to attack by various enemies] and increased their pupal mass in the overall dataset." In addition, the "relative growth rate of chewers was significantly increased by 3.5% under elevated O_3." However, "these effects were counteracted by elevated CO_2," such that "elevated O_3 in combination with CO_2 had no effect on herbivore performance," with the exception that when elevated CO_2 was added to the O_3-enriched air, it not only counteracted the O_3-induced increase in pupal biomass, but reduced it by 7% below what it was in ambient air. This analysis of the vast majority of pertinent experimental data obtained prior to 2006 suggests the ongoing rise in the air's CO_2 content likely plays an extremely important role in negating, and in some cases even more than negating, the damage otherwise capable of being done to Earth's forests by voracious insect pests.

In a study involving only changes in temperature, Andrew and Hughes (2007) "investigated how the relationship of herbivorous insects and their host plants may change under a warmer climate" by "transplanting a host plant species to locations subject to mean annual temperatures 1.2°C higher than at the species' current warmest boundary and 5.5°C higher than at its coolest edge." They "compared the structure and composition of the herbivorous insect community that colonized the transplants (i) to that of the host plant species within its natural range and (ii) to a congeneric plant species that grew naturally at the transplant latitude." In addition, they "investigated whether the herbivore community and rates of herbivory were affected by the latitudinal origin of the transplants."

According to the two Australian researchers, their study indicated "rates of herbivory did not significantly differ between the transplants and plants at sites within the natural range," and "there were no significant differences in herbivore species richness or overall rates of herbivory on the transplants originating from different latitudes." They state in the abstract of their paper, "if this result holds for other plant-herbivore systems, we might expect that under a warmer climate, broad patterns in insect community structure and rates of herbivory may remain similar to that at present, even though species composition may change substantially." Or as stated in their concluding paragraph, "if these results can be generalized to other plant hosts, we might predict that as climate zones shift poleward and mobile organisms like flying insects respond by migrating to stay within their current climatic envelope, plants will be colonized by new herbivore species within similar guilds to those currently supported," and "changes in the composition, but not necessarily the structure, of these new communities may, therefore, result."

Huttunen *et al*. (2007) grew silver birch (*Betula pendula* Roth) seedlings in pots filled with peat at three levels of nitrogen (N) fertility—no N, moderate N (130 kg N ha^{-1}), and high N (270 kg N ha^{-1})—within climate-controlled closed-top chambers from mid-June to October 2002 at the Mekrijarvi Research Station of the University of Joensuu, Finland. The chambers were maintained at atmospheric CO_2 concentrations of either 360 or 720 ppm and at either ambient air temperatures or elevated air temperatures 2°C above ambient from June to August and 4°C above ambient for the remainder of the growing season, while mimicking larval and adult leaf-feeding patterns exhibited during real-world defoliation by manually damaging the leaves of the seedlings by tearing off the apical halves of either 25% or 50% of all leaves greater than 1 cm in length on 1 July (mid-season) and again on 29 July (late-season). They then determined total plant shoot and root biomass once the plants went dormant in October.

As best as can be determined from the authors' bar graphs of their results, and averaged over all three defoliation treatments, the elevated CO_2 treatment increased the biomass of the seedlings in the moderate and high N fertility treatments much more than in the no N fertility treatment (29 and 30%, respectively, vs. 13%). The same was true of the combined elevated CO_2 and elevated temperature treatment, where the corresponding treatment-induced biomass increases were 34 and 36% vs. 20%. These results indicate the heightened temperatures tended to augment the beneficial effects of the elevated CO_2 treatment, with the greatest amplification being manifest in the no N fertility treatment (54% vs. 17 and 20% in the moderate and high N treatments, respectively). Averaged over all three N fertility treatments, the elevated CO_2 increased the plant biomass of the undefoliated seedlings by approximately 25%, that of the 25%-defoliated seedlings by

24%, and that of the 50%-defoliated seedlings by 22%. The elevated CO_2 and elevated temperature treatment increased the plant biomass of the same three categories of seedlings by approximately 31%, 30%, and 29%, respectively. The six Finnish scientists conclude "climatic change"—which they specifically define to mean elevated atmospheric temperature and CO_2—"will have a positive impact on the compensatory ability of defoliated silver birch seedlings."

One year later in a similar analysis, Huttunen *et al.* (2008) studied the leaf palatability of first-year silver birch (*Betula pendula*) seedlings to adult blue alder leaf beetles (*Agelastica alni*), periodically measuring a host of seedling parameters related to plant chemical and morphological defense properties. The seedlings were grown in climate-controlled closed-top chambers maintained at ambient and twice-ambient atmospheric CO_2 concentrations and at ambient and ambient plus 2°C air temperatures. The authors also examined the additional effects of three levels of added soil nitrogen (none, moderate, and high) plus two levels of manual defoliation (25% and 50%) on leaf palatability.

The researchers' findings were varied and complex, indicative of complicated interactions with the potential to cascade through several trophic levels and change the dynamics of forest ecosystems. "In the worst scenario," as they describe what could happen, "the consequences may include widespread damage to trees." However, they report, their study indicated the blue alder leaf beetle's "total leaf consumption was higher under the ambient climatic conditions than under elevated temperature, elevated CO_2, or the combination of elevated temperature and CO_2."

Hamilton *et al.* (2012) write, "the response of complex plant and animal communities to global change is highly variable (Tylianakis *et al.*, 2008)," but they note "recent studies have documented that loss of foliage to arthropod herbivores decreases under elevated CO_2 in woody communities (Hamilton *et al.*, 2004; Knepp *et al.*, 2005; Stiling and Cornelissen, 2007)." They also note the fitness and in some cases population size of herbivorous insects may decline in communities exposed to elevated CO_2 (Hillstrom and Lindroth, 2008; Hillstrom *et al.*, 2010)," although the "effects of elevated CO_2 on naturally occurring arthropod assemblages have not yet been widely characterized."

Working at the Duke Forest FACE facility in the Piedmont region of North Carolina (USA)—where three 30-meter-diameter plots of an expansive stand of loblolly pine had their atmospheric CO_2 concentrations boosted by approximately 200 ppm, and where three other such plots were maintained at the normal ambient CO_2 concentration—Hamilton *et al.* counted arthropods found in each of the six plots every two weeks throughout June and July 2005, in order to assign them to different feeding guilds. In addition, "stable isotope data for spiders collected in ambient and elevated CO_2 plots were analyzed to determine the extent to which herbivorous prey species moved into and out of the elevated CO_2 plots."

The seven U.S. scientists say their isotopic data "gave no indication that the treatment plots represented a 'boundary' to the movement of insects." In addition, there was no detectable effect of elevated CO_2 on the total number of individual arthropods in the two sets of treatment plots. However, "there was an increase in the numbers of individuals collected in primarily predaceous orders (Araneae and Hymenoptera; from 60% to more than 150%) under elevated CO_2 and a decrease in the numbers in primarily herbivorous orders (Lepidoptera and Coleoptera; from -30 to -45%)." Hamilton *et al.* conclude, "decreases in herbivorous arthropods and increases in predaceous arthropods may contribute to reduced herbivory under elevated CO_2 in forest systems."

Novick *et al.* (2012) write "warmer climates induced by elevated atmospheric CO_2 are expected to increase damaging bark beetle activity in pine forests," yet they say, "the effect of elevated CO_2 on resin production—the tree's primary defense against beetle attack—remains largely unknown." They note "resin physically ejects or entombs attacking beetles and, when volatile components of resin have evaporated, seals wounds in the bark," as revealed by the studies of Ruel *et al.* (1998) and Wilkens *et al.* (1998). Novick *et al.* assessed the effect of elevated CO_2 on resin production of dominant-and-unfertilized 27-year-old loblolly pine (*Pinus taeda* L.) trees growing under both ambient and elevated (ambient + 200 ppm) atmospheric CO_2 concentrations in the Duke Forest of North Carolina (USA) over the period March to October 2009.

The four researchers report the elevated CO_2 treatment increased resin flow by 140% in dominant trees growing in unfertilized subplots. This CO_2-induced resin flow enhancement "persisted throughout the growing season." Novick *et al.* conclude, "forests with low- to mid-range fertility"—which, in their words, "currently represent the majority of southern pine forests (Fox *et al.*, 2007)"—"may become increasingly protected from bark beetle attacks in an elevated CO_2 climate." They note, "previous studies have shown that even more modest increases in resin flow (i.e., enhancements less than or equal to 100%) significantly increase the survival probability of pine trees experiencing bark beetle attack," as demonstrated by Reeve *et al*. (1995) and Strom *et al*. (2002).

Working at the aspen free-air CO_2 enrichment (Aspen FACE) site in north-central Wisconsin (USA), Nabity *et al*. (2012) investigated how herbivore damage types (leaf-chewing, gall-forming, and leaf-folding) alter component processes of photosynthesis under both ambient and elevated (ambient + 200 ppm) atmospheric CO_2 concentrations in aspen (*Populus tremuloides*, genotype 216) trees, as well as how leaf-chewing insects impact photosynthesis in birch (*Betula papyrifera*) trees. They found "growth under elevated CO_2 reduced the distance that herbivore-induced reductions in photosynthesis propagated away from the point of damage in aspen and birch." Nabity *et al.* conclude their findings suggest "at least for these species," elevated CO_2 "may reduce the impact of herbivory on photosynthesis," a very positive development.

The balance of evidence suggests Earth's non-woody plants are adequately prepared to deal with the challenges of herbivorous insects as the air's CO_2 content continues to rise.

References

Andrew, N.R. and Hughes, L. 2007. Potential host colonization by insect herbivores in a warmer climate: a transplant experiment. *Global Change Biology* **13**: 1539–1549.

Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. *Oikos* **82**: 212–222.

Docherty, M., Wade, F.A., Hurst, D.K., Whittaker, J.B., and Lea, P.J. 1997. Responses of tree sap-feeding herbivores to elevated CO_2. *Global Change Biology* **3**: 51–59.

Fox, T.R., Jokela, E.J., and Allen, H.L. 2007. The development of pine plantation silviculture in the southern United States. *Journal of Forestry* **105**: 337–347.

Gleadow, R.M., Foley, W.J., and Woodrow, I.E. 1998. Enhanced CO_2 alters the relationship between photosynthesis and defense in cyanogenic *Eucalyptus cladocalyx* F. Muell. *Plant, Cell and Environment* **21**: 12–22.

Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J.S., Aldea, M., and DeLucia, E.H. 2004. Insect herbivory in an intact forest understory under experimental CO_2 enrichment. *Oecologia* **138**: 566–573.

Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Sparks, J.P., Elich, L., Eisenstein, A., and DeLucia, E.H. 2012. Elevated atmospheric CO_2 alters the arthropod community in a forest understory. *Acta Oecologica* **43**: 80–85.

Hattenschwiler, S. and Schafellner, C. 1999. Opposing effects of elevated CO_2 and N deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia* **118**: 210–217.

Hillstrom, M.L. and Lindroth, R.L. 2008. Elevated atmospheric carbon dioxide and ozone alter forest insect abundance and community composition. *Insect Conservation and Diversity* **1**: 233–241.

Hillstrom, M.L., Vigue, L.M., Coyle, D.R., Raffa, K.F., and Lindroth, R.L. 2010. Performance of the invasive weevil *Polydrusus sericeus* is influenced by atmospheric CO_2 and host species. *Agricultural and Forest Entomology* **12**: 285–292.

Holton, M.K., Lindroth, R.L., and Nordheim, E.V. 2003. Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO_2, O_3, and plant genotype. *Oecologia* **137**: 233–244.

Hunter, M.D. 2001. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agricultural and Forest Entomology* **3**: 153–159.

Huttunen, L., Niemela, P., Julkunen-Titto, R., Heiska, S., Tegelberg, R., Rousi, M., and Kellomaki, S. 2008. Does defoliation induce chemical and morphological defenses in the leaves of silver birch seedlings under changing climate? *Chemoecology* **18**: 85–98.

Huttunen, L., Niemela, P., Peltola, H., Heiska, S., Rousi, M., and Kellomaki, S. 2007. Is a defoliated silver birch seedling able to overcompensate the growth under changing climate? *Environmental and Experimental Botany* **60**: 227–238.

Knepp, R.G., Hamilton, J.G., Mohan, J.E., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2005. Elevated CO_2 reduces leaf damage by insect herbivores in a forest community. *New Phytologist* **167**: 207–218.

Lovelock, C.E., Posada, J., and Winter, K. 1999. Effects of elevated CO_2 and defoliation on compensatory growth and photosynthesis of seedlings in a tropical tree, *Copaifera aromatica*. *Biotropica* **31**: 279–287.

Mattson, W.J., Kuokkanen, K., Niemela, P., Julkunen-Tiitto, R., Kellomaki, S., and Tahvanainen, J. 2004. Elevated CO_2 alters birch resistance to Lagomorpha herbivores. *Global Change Biology* **10**: 1402–1413.

McNaughton, S.J. and Sabuni G.A. 1988. Large African mammals as regulators of vegetation structure. In: Werger, M.J.A., Van der Aart, P.J.M., During, H.J., and Verhoeven, J.T.A. (Eds.) *Plant Form and Vegetation Structure*. SPB Academic Publishing, The Hague, The Netherlands, pp. 339–354.

Nabity, P.D., Hillstrom, M.L., Lindroth, R.L., and DeLucia, E.H. 2012. Elevated CO_2 interacts with herbivory to alter chlorophyll fluorescence and leaf temperature in *Betula papyrifera* and *Populus tremuloides*. *Oecologia* **169**: 905–913.

Novick, K.A., Katul, G.G., McCarthy, H.R., and Oren, R. 2012. Increased resin flow in mature pine trees growing under elevated CO_2 and moderate soil fertility. *Tree Physiology* **32**: 752–763.

Pastor, J. and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forest. *American Naturalist* **139**: 690–705.

Reeve, J.D., Ayres, M.P., Lorio Jr., P.L. Cappuccino, N., and Price, P.W. 1995. Host suitability, predation, and bark beetle population dynamics. In: Cappuccino, N. and Price, P.W. (Eds.) *Population Dynamics: New Approaches and Synthesis*. Academic Press, San Diego, California, USA, pp. 339–357.

Ruel, J.J., Ayres, M.P., and Lorio, P.L. 1998. Loblolly pine responds to mechanical wounding with increased resin flow. *Canadian Journal of Forest Research* **28**: 596–602.

Sanders, N.J., Belote, R.T., and Weltzin, J.F. 2004. Multitriphic effects of elevated atmospheric CO_2 on understory plant and arthropod communities. *Environmental Entomology* **33**: 1609–1616.

Stiling, P. and Cornelissen, T. 2007. How does elevated carbon dioxide (CO_2) affect plant-herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology* **13**: 1–20.

Strom, B.L., Goyer, R.A., Ingram Jr., L.L., Boyd, G.D.L., and Lott, L.H. 2002. Oleoresin characteristics of progeny of loblolly pines that escaped attack by the southern pine beetle. *Forest Ecology and Management* **157**: 169–178.

Tylianakis, J.M., Didham, R.K., Bascompte, J., and Wardle, D.A. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* **11**: 1351–1363.

Valkama, E., Koricheva, J., and Oksanen, E. 2007. Effects of elevated O_3, alone and in combination with elevated CO_2, on tree leaf chemistry and insect herbivore performance: a meta-analysis. *Global Change Biology* **13**: 184–201.

Wilkens, R.T., Ayres, M.P., Lorio Jr., P.L., and Hodges, J.D. 1998. Environmental effects on pine tree carbon budgets and resistance to bark beetles. In: Mickler, R.A. and Fox, S. (Eds.) *The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment.* Springer, New York, New York, USA, pp. 591–616.

5.5.4 Butterflies

- Global warming is creating opportunities for butterflies to expand their populations and ranges, just the opposite of alarmist projections of range contractions and butterfly species demise in response to a CO_2-induced warming of Earth.

IPCC claims butterflies are at risk of extinction due to global warming. This section reviews research studying how butterflies respond to rising air temperatures and CO_2 concentrations and comes to a very different conclusion.

5.5.4.1 Response to Temperature

Research on the impact on butterflies of temperature changes has found impacts on populations and ranges and also has revealed how butterflies adapt, evolve, and in other ways respond to changes in temperature. The following sections summarize that research.

5.5.4.1.1 Population Dynamics

In response to model-based projections in which global warming enhances the prospect for animal species demise, several researchers have conducted studies on butterflies to test the viability of this hypothesis. Fleishman *et al*. (2001), for example, used comprehensive data on butterfly distributions from six mountain ranges in the U.S. Great Basin to study how butterfly populations of that region may respond to IPCC-projected climate change. Their work revealed “few if any species of montane butterflies are likely to be extirpated from the entire Great Basin (i.e., lost from the region as a whole).” The three researchers note “during the Middle Holocene, approximately 8000–5000 years ago, temperatures in the Great Basin were several degrees warmer than today.” They conclude, “we might expect that most of the montane species—including butterflies—that currently inhabit the Great Basin would be able to tolerate the magnitude of climatic warming forecast over the next several centuries.”

Other scientists have focused on the response of butterflies to warming during the twentieth century, warming IPCC claims is unprecedented in the past one to two thousand years.

Davies *et al*. (2006) studied the silver-spotted skipper butterfly (*Hesperia comma*), noting during the twentieth century it “became increasingly rare in

Britain [as] a result of the widespread reduction of sparse, short-turfed calcareous grassland containing the species' sole larval host plant, sheep's fescue grass," while describing the "refuge" colonies of 1982 as but a "remnant" of what once had been. To examine whether global warming might drive the already-decimated species to extinction, the four researchers analyzed population density data and estimates of the percent of bare ground and the percent of sheep's fescue available to the butterflies, based on surveys conducted in Surrey in the chalk hills of the North Downs, south of London, in 1982 (Thomas *et al*., 1986), 1991 (Thomas and Jones, 1993), 2000 (Thomas *et al*., 2001; Davies *et al*., 2005), and 2001 (R.J. Wilson, unpublished data). They also assessed egg-laying rates in different microhabitats, the effects of ambient and oviposition site temperatures on egg-laying, and the effects of sward composition on egg location. This multifaceted work revealed, "in 1982, 45 habitat patches were occupied by *H. comma*," but "in the subsequent 18-year period, the species expanded and, by 2000, a further 29 patches were colonized within the habitat network." In addition, they found "the mean egg-laying rate of *H. comma* females increased with rising ambient temperatures" and "a wider range of conditions have become available for egg-laying."

Davies *et al*. write, "climate warming has been an important driving force in the recovery of *H. comma* in Britain [as] the rise in ambient temperature experienced by the butterfly will have aided the metapopulation re-expansion in a number of ways." First, they note, "greater temperatures should increase the potential fecundity of *H. comma* females," and "if this results in larger populations, for which there is some evidence (e.g. 32 of the 45 habitat patches occupied in the Surrey network experienced site-level increases in population density between 1982 and 2000), they will be less prone to extinction," with "larger numbers of dispersing migrant individuals being available to colonize unoccupied habitat patches and establish new populations." Second, "the wider range of thermal and physical microhabitats used for egg-laying increased the potential resource density within each grassland habitat fragment," and "this may increase local population sizes." Third, "colonization rates are likely to be greater as a result of the broadening of the species realized niche, [because] as a larger proportion of the calcareous grassland within the species' distribution becomes thermally suitable, the relative size and connectivity of habitat patches within the landscape increases." Fourth, "higher temperatures may directly increase flight (dispersal) capacity, and the greater fecundity of immigrants may improve the likelihood of successful population establishment." Davies *et al.* conclude, "the warmer summers predicted as a consequence of climate warming are likely to be beneficial to *H. comma* within Britain," and "warmer winter temperatures could also allow survival in a wider range of microhabitats."

Dennis and Sparks (2007) analyzed data on the general abundance of Lepidoptera in Britain over the period 1864–1952, based on information assembled by Beirne (1955) via his examination of "several thousand papers in entomological journals describing annual abundances of moths and butterflies." The two researchers report "abundances of British Lepidoptera were significantly positively correlated with Central England temperatures in the current year for each month from May to September and November," and "increased overall abundance in Lepidoptera coincided significantly with increased numbers of migrants," having derived the latter data from Williams (1965). In addition, they report Pollard (1988) subsequently found much the same thing for 31 butterfly species over the period 1976–1986, and Roy *et al*. (2001) extended the latter investigation to 1997 and found "strong associations between weather and population fluctuations and trends in 28 of 31 species which confirmed Pollard's (1988) findings." These observations indicate the warming-driven increase in Lepidopteran species and numbers in Britain has been an ongoing phenomenon since the end of the Little Ice Age.

Checa *et al*. (2009) studied the composition and structure of butterfly communities of the "rotting-carrion guild" of the Nymphalidae family over a period of 13 months (April 2002–April 2003) in areas surrounding the Yasuni Scientific Research Station in the Ecuadorian Amazon inside the Yasuni National Park. They obtained their data using traps baited with rotten shrimp that had been fermenting for 11–20 days. Checa *et al*. captured 9,236 individual Nymphalidae butterflies representing 208 species, including two species that had not previously been found in Ecuador, and two "new" species that had not previously been found anywhere. They discovered "a constant replacement of species throughout the year," and "these communities had the highest species richness and abundance during the months with high temperatures." They note the mean temperature of their study area "only varies over one degree during the whole year."

The four researchers comment on "temperature's central role in the biology and life history of butterflies," noting "several key processes for butterfly survival depend on regulation of internal temperature," including mimetism and fast flight (Chai and Srygley, 1990), and fecundity and longevity, which they say have been found to be "higher at higher temperatures (Karlsson and Wiklund, 2005)." Hence, they conclude, "the tight relationship between temperature and butterfly population levels," or abundance, as well as butterfly species richness, likely will be "of major importance" for tropical butterflies in surviving potential future global warming.

References

Beirne, B.P. 1955. Natural fluctuations in abundance of British Lepidoptera. *Entomologist's Gazette* **6**: 21–52.

Chai, P. and Srygley, B. 1990. Predation and the flight, morphology and temperature of neotropical rain-forest butterflies. *The American Naturalist* **135**: 748–765.

Checa, M.F., Barragan, A., Rodriguez, J., and Christman, M. 2009. Temporal abundance patterns of butterfly communities (Lepidoptera: Nymphalidae) in the Ecuadorian Amazonia and their relationship with climate. *Annales de la Société Entomologique de France (NS)* **45**: 470–486.

Davies, Z.G., Wilson, R.J., Brereton, T.M., and Thomas, C.D. 2005. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation* **124**: 189–198.

Davies, Z.G., Wilson, R.J., Coles, S., and Thomas, C.D. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* **75**: 247–256.

Dennis, R.L.H. and Sparks, T.H. 2007. Climate signals are reflected in an 89 year series of British Lepidoptera records. *European Journal of Entomology* **104**: 763–767.

Fleishman, E., Austin, G.T., and Murphy, D.D. 2001. Biogeography of Great Basin butterflies: revisiting patterns, paradigms, and climate change scenarios. *Biological Journal of the Linnean Society* **74**: 501–515.

Karlsson, B. and Wiklund, C. 2005. Butterfly life history and temperature adaptations: Dry open habitats select for increased fecundity and longevity. *The Journal of Animal Ecology* **74**: 99–104.

Pollard, E. 1988. Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology* **25**: 819–828.

Roy, D.B., Rothery, P., Moss, D., Pollard, E., and Thomas, J.A. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology* **70**: 201–217.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., and Conradt, L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–581.

Thomas, C.D. and Jones, T.M. 1993. Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology* **62**: 472–481.

Thomas, J.A., Thomas, C.D., Simcox, D.J., and Clarke, R.T. 1986. Ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology* **23**: 365–380.

Williams, C.B. 1965. *Insect Migration*. London, UK: Collins.

5.5.4.1 2 Range Expansion

IPCC claims the increase in temperature predicted to result from the ongoing rise in the air's CO_2 content will be of such magnitude and speed that many species of plants and animals will not be able to migrate poleward in latitude or upward in elevation rapidly enough to avoid extinction, as they are forced to seek cooler living conditions. However, there are many reasons for rejecting this contention, one of the most powerful being increases in the air's CO_2 content generally enable plants to endure warmer weather, so there is little or no need for them to shift the heat-limiting warm-temperature boundaries of their ranges as temperatures rise (See Sections 3.13, 4.2.3, and 4.4, this volume). At the cold-limiting cool-temperature boundaries of their ranges, on the other hand, warming provides opportunities for plants to push poleward and upward, which results in expansions of their ranges and reductions in their risk of extinction.

This section reviews several studies examining butterfly range habitat, revealing butterflies may be mimicking the respective shifts and stability of the cold- and heat-limited boundaries of the ranges of the plants on which they depend for food.

Parmesan *et al*. (1999) examined the distributional changes of non-migratory butterfly species whose northern boundaries were in northern Europe and whose southern boundaries were in southern Europe or northern Africa, over the prior century of global warming. They found the northern range boundaries shifted northward for 65% of the 52 species examined, remained stable for 34%, and shifted southward for 2%. As to the southern boundaries, of the 40 species examined there, 22% shifted their southern range boundary northward, for 72% it remained stable, and for 5% it shifted southward. Because "nearly all northward shifts involved extensions at the northern boundary with the southern boundary remaining stable," as the 13 researchers explain, "most species effectively expanded the size of their range when shifting northwards."

Thomas *et al*. (2001) documented an unusually rapid expansion of the ranges of two butterfly species (the silver-spotted skipper and the brown argus) along with two cricket species (the long-winged cone-head and Roesel's bush cricket). They observed the warming-induced "increased habitat breadth and dispersal tendencies have resulted in about 3- to 15-fold increases in expansion rates." In commenting on these findings, Pimm (2001) remark the geographical ranges of these insects were "expanding faster than expected" and the synergies involved in the many intricacies of the range expansion processes were "unexpected."

Crozier (2004) notes "*Atalopedes campestris*, the sachem skipper butterfly, expanded its range from northern California into western Oregon in 1967, and into southwestern Washington in 1990," where she reports temperatures rose by 2–4°C over the prior half-century. In an attempt to assess the importance of this regional warming for the persistence of *A. campestris* in the recently colonized areas, Crozier "compared population dynamics at two locations (the butterfly's current range edge and just inside the range) that differ by 2–3°C." Then, to determine the role of over-winter larval survivorship, she "transplanted larvae over winter to both sites."

According to Crozier, "combined results from population and larval transplant analyses indicate that winter temperatures directly affect the persistence of *A. campestris* at its northern range edge, and that winter warming was a prerequisite for this butterfly's range expansion." Noting "populations are more likely to go extinct in colder climates," Crozier writes, "the good news about rapid climate change [of the warming type] is that new areas may be available for the introduction of endangered species." The species she studied responded to regional warming by extending its northern range boundary, thereby expanding its range.

Menendez *et al*. (2006) provided what they call "the first assessment, at a geographical scale, of how species richness has changed in response to climate change," concentrating on British butterflies. They tested "whether average species richness of resident British butterfly species has increased in recent decades, whether these changes are as great as would be expected given the amount of warming that has taken place, and whether the composition of butterfly communities is changing towards a dominance by generalist species." They determined "average species richness of the British butterfly fauna at 20 x 20 km grid resolution has increased since 1970–82, during a period when climate warming would lead us to expect increases." They also found, as expected, "southerly habitat generalists increased more than specialists," which require a specific type of habitat that is sometimes difficult for them to find, especially in the modern world where habitat destruction is commonplace. In addition, they determined observed species richness increases lagged behind those expected on the basis of climate change.

These results "confirm," according to the nine U.K. researchers, "that the average species richness of British butterflies has increased since 1970–82." Some of the range shifts responsible for the increase in species richness take more time to occur than those of other species, and the researchers state their results imply "it may be decades or centuries before the species richness and composition of biological communities adjusts to the current climate."

In another analysis from Britain, Gonzalez-Megias *et al*. (2008) investigated species turnover in 51 butterfly assemblages by examining regional extinction and colonization events that occurred between the two periods 1976–1982 and 1995–2002. The five researchers found regional colonizations exceeded extinctions: "over twice as many sites gained species as lost species," so "the average species richness of communities has increased." They also found species abundances following colonization likewise increased, because of "climate-related increases in the [land's] carrying capacity."

Comparing their results with a broader range of animal studies, Gonzalez-Megias *et al*. found "analyses of distribution changes for a wide range of other groups of animals in Britain suggest that southern representatives of most taxa are moving northwards at a rate similar to—and in some cases faster than—butterflies (Hickling *et al*., 2006)," and they report, "as with butterflies, most of these taxonomic groups have fewer northern than southern representatives, so climate-driven colonisations are likely to exceed extinctions." They suggest "most of these taxa will also be experiencing slight community-level increases in species richness."

White and Kerr (2006) "report butterfly species' range shifts across Canada between 1900 and 1990 and develop spatially explicit tests of the degree to which observed shifts result from climate or human population density," describing the latter factor as "a reasonable proxy for land use change." In this category they included such elements as "habitat loss, pesticide use, and habitat fragmentation," all of which anthropogenic-driven factors have been tied to declines of various butterfly species. In addition, they state to their knowledge, "this is the broadest scale, longest term dataset yet assembled to quantify global change impacts on patterns of species richness." They found butterfly species richness "generally increased over the study period, a result of range expansion among the study species." They further found this increase "from the early to late part of the 20th century was positively correlated with temperature change," which had to have been the cause of the increase, for they also found species richness was "negatively correlated with human population density change."

Westwood and Blair (2010) measured the responses of 19 common butterfly species of the boreal forests of Manitoba (Canada) to temperature changes experienced there during 1971–2004, focusing on each species' date of first appearance, week of peak abundance, and length of flight period. Autumn temperatures were found to have warmed significantly, and the two Canadian researchers observed "13 of 19 species showed a significant increase in flight period extending longer into the autumn," when "flight period extensions increased by 31.5 ± 13.9 days over the study period." They also note "two species, *Junonia coenia* and *Euphydryas phaeton*, increased their northerly ranges by ~150 and 70 km, respectively."

Westwood and Blair state "warmer autumns and winters may be providing opportunities for range extensions of more southerly butterfly species held at bay by past climatic conditions." They cite other investigators who have obtained similar results, stating "northward expansions in butterfly species range correlating with northward shifts in isotherms have been documented in both Europe and North America (Karl *et al*., 1996; Parmesan, 1996; Parmesan *et al*., 1999; Hill *et al*., 1999; Hickling *et al*., 2006)," and "in Canada, the Gorgone checkerspot (*Chlosyne gorgone*, Hubner) and the Delaware skipper (*Anatryone logan*, W.H. Edwards) have recently expanded their northern ranges significantly (Kerr, 2001)."

Forister *et al*. (2010) analyzed 35 years of butterfly presence-absence data collected by a single observer at 10 sites approximately every two weeks along an elevation gradient stretching from sea level to an altitude of 2,775 meters in the Sierra Nevada Mountains of Northern California (USA). During the data-collection period both maximum and minimum temperatures rose, low-altitude habitat was negatively affected by encroaching land development, and there was no systematic variation in precipitation. The eight researchers found species richness over this period "declined at half of the sites, with the most severe reductions at the lowest elevations," where "habitat destruction [was] greatest." At intermediate elevations, they report, there were "clear upward shifts in the elevational ranges of species, consistent with the influence of global warming." And at the highest site, they found species richness increased, and "in addition to an increase in richness, abundance has also generally increased at the highest-elevation site."

Noting the Arctic is predicted to be especially susceptible to potential threats from climate change, citing Overpeck *et al*. (1996), Franzen and Ockinger (2012) studied temporal changes in the insect species richness and community composition of wild bees, butterflies, and moths over a period of 64 years at five sites in northern Sweden's Padjelanta National Park (one of the largest National Parks in Europe, located just north of the Arctic Circle, between 66°45' and 67°35'N, and 15°06' and 18°36'E). The insect data were collected during surveys conducted over the period 2006–2008 and were compared with similar data collected in 1998 and 1944, while corresponding climate data were obtained from a weather station located at 66.89°N, 18.02°E.

The two researchers determined there had been a significant increase in the daily mean temperature during the vegetation season (May–September) between 1944 and 2008, when the temperature rose at a rate of 0.015°C per year, yielding an increase of almost 1°C over the 64-year study period. With respect to insect responses, they found the total number of bumble bee, butterfly, and moth species increased from 52 in 1944 to 64 in 2008; for wild bees, which increased only from 15 to 16 species, the increase was not statistically significant. For butterflies and moths, the combined species number increase (from 37 to 48) was statistically significant. Franzen and Ockinger state, "high alpine insect species are apparently still performing relatively well," noting "both southern species, such as *Erebia ligea* and *Polyommatus icarus*, and high alpine species, such as *Boloria chariclea* and *Lasionycta staudingeri*, seem to have colonized the area," and "ranges and species richness are even increasing in our study region, due to retreating glaciers and plant colonizations." In light of these real-world observations, they say "it is possible that warming will simply improve the performance and abundance of species in cold areas, as their mobility increases and new habitats become available," citing Ashton *et al*. (2009), Bale and Hayward (2010), and Kullman (2010).

According to Oliver *et al*. (2012), "climate warming threatens the survival of species at their warm, trailing-edge range boundaries but also provides opportunities for the ecological release of populations at the cool, leading edges of their distributions," so "as the climate warms," they continue, "leading-edge populations are expected to utilize an increased range of habitat types, leading to larger population sizes and range expansion." Oliver *et al*. tested "the hypothesis that the habitat associations of British butterflies have expanded over three decades of climate warming." They characterized "the habitat breadth of 27 southerly distributed species from 77 monitoring transects between 1977 and 2007 by considering changes in densities of butterflies across 11 habitat types."

In response to the overall climate warming that occurred between 1977 and 2007, but "contrary to expectation," as the five UK researchers report, 20 of the 27 species of butterflies they studied "showed long-term contractions in their habitat associations, despite some short-term expansions in habitat breadth in warmer-than-usual years," when the butterflies they studied spread out from their primary habitat to occupy other sites. They say these findings suggest some non-climatic driver must be responsible for most of the habitat contractions of British butterflies over the past three decades, for they note, "butterfly population declines in the past century have been primarily driven by habitat destruction and degradation, particularly in relation to agricultural intensification and abandonment," citing Asher *et al*. (2001) and Warren *et al*. (2001). They lament the likelihood these other anthropogenic-induced constraints "appear to be out-weighing the positive effects of a warming climate on habitat breadth." In the final sentence of their paper, they suggest, "only if other non-climatic drivers can be reduced or reversed will species be able to fully exploit any emerging opportunities provided by climate warming."

It appears the real world of nature is behaving just the opposite of alarmist projections of range contractions and butterfly species demise in response to a CO_2-induced warming of Earth.

References

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G., and Jeffcoate, S. 2001. *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford, United Kingdom.

Ashton, S., Gutierrez, D., and Wilson, R.J. 2009. Effects of temperature and elevation on habitat use by a rare mountain butterfly: implications for species responses to climate change. *Ecological Entomology* **34**: 437–446.

Bale, J.S. and Hayward, S.A.L. 2010. Insect overwintering in a changing climate. *Journal of Experimental Biology* **213**: 980–994.

Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* **85**: 231–241.

Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P., and Shapiro, A.M. 2010. Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences USA* **107**: 2088–2092.

Franzen, M. and Ockinger, E. 2012. Climate-driven changes in pollinator assemblages during the last 60 years in an Arctic mountain region in Northern Scandinavia. *Journal of Insect Conservation* **16**: 227–238.

Gonzalez-Megias, A., Menendez, R., Roy, D., Brereton, T., and Thomas, C.D. 2008. Changes in the composition of British butterfly assemblages over two decades. *Global Change Biology* **14**: 1464–1474.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., and Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**: 450–455.

Hill, J.K., Thomas, C.D., and Huntley, B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London, Series B* **266**: 1197–1206.

Karl, T.R., Knight, R.W., Easterling, D.R., and Quayle, R.G. 1996. Indices of climate change for the United States. *Bulletin of the American Meteorological Society* **77**: 279–292.

Kerr, J.K. 2001. Butterfly species richness patterns in Canada: energy, heterogeneity, and the potential consequences of climate change. *Conservation Ecology* **5**: 10.

Kullman, L. 2010. Alpine flora dynamics: a critical review of responses to climate change in the Swedish Scandes since the early 1950s. *Nordic Journal of Botany* **28**: 398–408.

Menendez, R., Gonzalez-Megias, A., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B., and Thomas, C.D. 2006. Species richness changes lag behind climate change. *Proceedings of the Royal Society B* **273**: 1465–1470.

Oliver, T.H., Thomas, C.D., Hill, J.K., Brereton, T., and Roy, D.B. 2012. Habitat associations of thermophilous butterflies are reduced despite climatic warming. *Global Change Biology* **18**: 2720–2729.

Overpeck, J., Rind, D., Lacis, A., and Healy, R. 1996. Possible role of dust-induced regional warming in abrupt climate change during the last glacial period. *Nature* **384**: 447–449.

Parmesan, C. 1996. Climate and species' range. *Nature* **382**: 765–766.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., and Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583.

Pimm, S.L. 2001. Entrepreneurial insects. *Nature* **411**: 531–532.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., and Conradt, L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–581.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., and Thomas, C.D. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**: 65–69.

Westwood, A.B. and Blair, D. 2010. Effect of regional climate warming on the phenology of butterflies in boreal forests in Manitoba, Canada. *Environmental Entomology* **39**: 1122–1133.

White, P. and Kerr, J.T. 2006. Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. *Ecography* **29**: 908–918.

5.5.4.1.3 Adaptation, Evolution, and Phenotypic Responses

Few studies have investigated adaptive or evolutionary responses of butterflies to increased temperature. But those that have done so suggest butterflies are well-equipped to manage any of the temperature changes projected by IPCC for the future.

Hughes *et al.* (2007) examined evolutionary changes in adult flight morphology in six populations of the speckled wood butterfly—*Pararge aegeria*—along a transect from its distribution core to its warming-induced northward-expanding range margin. The results were compared with the output of an individual-based spatially explicit model developed "to investigate impacts of habitat availability on the evolution of dispersal in expanding populations." The empirical data the researchers gathered in Britain "were in agreement with model output" and "showed increased dispersal ability with increasing distance from the distribution core." This included favorable changes in thorax shape, abdomen mass, and wing aspect ratio for both males and females, as well as thorax mass and wing loading for females. The researchers state, "increased dispersal ability was evident in populations from areas colonized >30 years previously."

Hughes *et al.* suggest "evolutionary increases in dispersal ability in expanding populations may help species track future climate changes and counteract impacts of habitat fragmentation by promoting colonization." However, they report, in the specific situation they investigated, "at the highest levels of habitat loss, increased dispersal was less evident during expansion and reduced dispersal was observed at equilibrium, indicating that for many species, continued habitat fragmentation is likely to outweigh any benefits from dispersal."

Another means by which butterflies can cope with higher temperatures is through the production of heat-shock proteins (HSPs). According to Karl *et al.* (2008), HSPs "are thought to play an important ecological and evolutionary role in thermal adaptation," where "the up-regulation of stress-inducible HSPs may help organisms to cope with stress thus enhancing survival (Sorensen *et al.*, 2003; Dahlhoff, 2004; Dahlhoff and Rank, 2007)." Working with *Lycaena tityrus,* a widespread temperate-zone butterfly that ranges from western Europe to central Asia, Karl *et al.* tested this hypothesis by comparing expression patterns of stress-inducible HSPs across replicated populations originating from different altitudes and across different ambient temperatures. Their observations revealed "a significant interaction between altitude and rearing temperature [that] indicates that low-altitude animals showed a strongly increased HSP70 expression at the higher compared with at the lower rearing temperature." This is exactly where one would expect to see such a response in light of its obvious utility in warmer conditions.

Karl *et al.* observe "HSP70 expression increased substantially at the higher rearing temperature in low-altitude butterflies ... [which] might represent an adaptation to occasionally occurring heat spells," suggesting this response should serve these organisms well if the dramatic warming predicted by IPCC should come to pass.

Pateman *et al*. (2012) note there are many situations in nature where one species has a close-to-exclusive relationship with another species, such as a predator-prey relationship in the animal kingdom, an animal-plant symbiotic relationship such as that between corals and the zooxanthellae they host, or the relationship between a butterfly and the plant species that acts as a host for the larval stage of the butterfly. Such interactions, according to Pateman *et al*., are most commonly regarded as additional constraints, "because they may limit species to a narrower set of physical conditions (and, hence, narrower geographic ranges) than their fundamental climatic niches might otherwise allow." Thus if the world warms to a substantial degree, there may be a mismatch between the climatic needs of the two species, resulting in one or both of them suffering from the change in climate.

Pateman *et al*. studied the brown argus butterfly (*Aricia agestis*), which "has spread northward in Great Britain by ~79 km in 20 years, which is 2.3 times faster than the average expansion rate documented for species globally (Chen *et al*., 2011)," endeavoring to discover what accelerated the butterfly's dramatic rate of range expansion. They analyzed the effect of climate on brown argus butterfly populations associated with different larval host plants, based on count data developed by volunteers who monitored more than 200 fixed transects in Britain, as described by Pollard and Yates (1993). Results revealed warmer summers typically result in higher brown argus larval population densities on both rockrose and Geraniaceae plants, but under cooler conditions the rockrose host plant was more favorable than Geraniaceae plants. Over the past two decades, as the frequency of warm summers increased, the five UK researchers found the brown argus butterfly adapted by expanding its larval presence onto Geraniaceae plants they had largely avoided under cooler conditions. That led to a significant expansion in the size of their range, as they had an additional plant species on which to lay their eggs and have their larvae develop successfully.

The five researchers state in the concluding sentence of the abstract of their paper, "interactions among species are often seen as constraints on species' responses to climate change, but we show that temperature-dependent changes to interspecific interactions can also facilitate change." Or as they state in the concluding sentence of the body of their paper, "we suggest that altered interactions among species do not necessarily constrain distribution changes but can facilitate expansions," thereby providing another real-world example of a previously unappreciated means by which an animal species can benefit from global warming and expand its range of territorial occupancy. And contrary to the view that generalist species will more rapidly exploit new regions made available by climate change, field assays of butterflies in recently colonized areas are composed of more specialized species, such as the UK brown argus butterfly, because of their aggressive colonization of their widely dispersed host plant (Bridle *et al*., 2014).

References

Bridle, J.R., Buckley, J., Bodsworth, E.J., and Thomas, C.D. 2014. Evolution on the move: specialization on widespread resources associated with rapid range expansion in response to climate change. *Proceedings of the Royal Society B* **281**: 20131800, doi:10.1098/rspb.2013.1800.

Chen, I.C., Hill, J.K., Ohlemülle, R., Roy, D.B., and Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**: 1024–1026.

Dahlhoff, E.P. 2004. Biochemical indicators of stress and metabolism: applications for marine ecological studies. *Annual Review of Physiology* **66**: 183–207.

Dahlhoff, E.P. and Rank, N.E. 2007. The role of stress proteins in responses of a montane willow leaf beetle to environmental temperature variation. *Journal of Biosciences* **32**: 477–488.

Hughes, C.L., Dytham, C., and Hill, J.K. 2007. Modelling and analyzing evolution of dispersal in populations at expanding range boundaries. *Ecological Entomology* **32**: 437–445.

Karl, I., Sorensen, J.G., Loeschcke, V., and Fischer, K. 2008. HSP70 expression in the Copper butterfly *Lycaena tityrus* across altitudes and temperatures. *Journal of Evolutionary Biology* **22**: 172–178.

Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R., and Thomas, C.D. 2012. Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science* **336**: 1028–1030.

Pollard, E. and Yates, T.J. 1993. *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London, United Kingdom.

Sorensen, J.G., Kristensen, T.N., and Loeschcke, V. 2003. The evolutionary and ecological role of heat shock proteins. *Ecology Letters* **6**: 1025–1037.

5.5.4.2 Response to Elevated CO_2

Few studies have been conducted on the response of butterflies to increased levels of atmospheric CO_2,but those that have been done suggest rising CO_2 will confer a net benefit on their growth and survival.

Early work on the subject was provided by Groverde *et al.* (1999). Birdfoot Deer Vetch (*Lotus corniculatus*) is a cyanogenic plant that produces foliar cyanoglycosides to deter against herbivory by insects. The Common Blue Butterfly (*Polyommatus icarus*), however, regularly feeds on this plant—it possesses an enzyme that detoxifies these cyanide-containing defensive compounds. To study the effects of elevated CO_2 and genotype on the leaf quality of Birdfoot Deer Vetch and the larval development of the Common Blue Butterfly, Groverde *et al.* grew four genotypes of *Lotus corniculatus*, differing in cyanoglycoside and tannin concentrations, in controlled environmental chambers receiving atmospheric CO_2 concentrations of either 350 or 700 ppm.

Elevated CO_2 significantly increased leaf tannin and starch contents in a genotypically dependent and independent manner, respectively, while decreasing leaf cyanoglycoside contents, regardless of genotype. Atmospheric CO_2 enrichment did not significantly affect leaf water, sugar, protein, or nitrogen content. Thus, these CO_2-induced changes in leaf chemistry (higher starch and tannin and lower cyanoglycoside concentrations) increased its palatability, as indicated by greater leaf dry weight consumption of CO_2-enriched leaves by butterfly larvae. In addition, increased leaf consumption of CO_2-enriched leaves led to greater larval biomass and shorter larval developmental times, indicating atmospheric CO_2 enrichment affected leaf quality to positively influence larvae of the Common Blue Butterfly. Moreover, larval mortality was lower when feeding on CO_2-enriched, rather than ambiently grown, leaves. Thus, as the CO_2 content of the air rises, it is likely Birdfoot Deer Vetch plants will increase their photosynthetic rates and differentially invest their additional carbon gains in storage, structural, and defensive compounds. Atmospheric CO_2 enrichment likely will increase leaf starch and tannin contents and decrease cyanoglycoside contents, without affecting sugar, protein, water, and nitrogen contents. Collectively, these chemical changes would improve the palatability of Birdfoot Deer Vetch leaves to the Common Blue Butterfly larvae.

In a follow-up study four years later, Groverde *et al.* (2004), abandoned the controlled environment chamber design of Groverde *et al.* (1999) and grew Birdfoot Deer Vetch plants from seed for three months in tubes recessed into the ground under natural conditions in a nutrient-poor calcareous grassland where an extra 232 ppm of CO_2 was supplied to them via a screen-aided CO_2 control (SACC) system (Leadley *et al.*, 1997; 1999) and insect larvae were allowed to feed on the plants (half of which received extra phosphorus fertilizer) for the final month of the experiment.

The 63% increase in atmospheric CO_2 concentration enhanced the total dry weight of plants growing on the unfertilized soil by 21.5% and that of the plants growing on the phosphorus-enriched soil by 36.3%. The elevated CO_2 treatment had no effect on pupal and adult insect mass. Goverde *et al.* report there were "genotype-specific responses in the development time of *P. icarus* to elevated CO_2 conditions," with larvae originating from different mothers developing better under either elevated CO_2 or ambient CO_2, and for still others the CO_2 concentration had no effect on development. Condensed tannins in the foliage of plants growing on the nutrient-poor calcareous soil were increased by 23.7% in the CO_2-enriched air.

The results of this study and its predecessor suggest the ongoing rise in the air's CO_2 content likely will be positive for *L. corniculatus* plants, while ranging from positive to nil for the insect herbivore *P. icarus* that feeds on them. In addition, the authors suggest rising levels of CO_2 might be "a selective factor, affecting both plant and herbivore populations and their interaction," and, therefore, "genotype-specific responses must be considered because this will affect the outcome of elevated CO_2 for plant-herbivore interactions." It is currently unclear what the range of those potential outcomes might be. Finally, since the presence of condensed tannins in foliage eaten by ruminants tends to decrease their emissions of methane, it might be expected the CO_2-induced increases in the concentrations of these substances in the leaves of *L. corniculatus* may help reduce the atmospheric concentration of this powerful greenhouse gas in a CO_2-enriched world of the future.

Groverde *et al.* (2002) raised larvae of the satyrid butterfly (*Coenonympha pamphilus*) in seminatural, undisturbed calcareous grassland plots exposed to atmospheric CO_2 concentrations of 370 and 600 ppm for five growing seasons. Elevated atmospheric CO_2 concentration was shown to increase foliar concentrations of total nonstructural carbohydrates and condensed tannins in the grassland plants. In what is often considered a negative impact, however, it decreased foliar nitrogen concentrations. Nevertheless, this phenomenon had no discernible negative impact on butterfly growth and performance characteristics. Larval developmental time, for example, was not affected by elevated CO_2, nor was adult dry mass. The elevated CO_2 increased lipid concentrations in adult male butterflies by nearly 14%, and marginally increased the number of eggs in female butterflies.

As atmospheric CO_2 concentrations increase, larvae of the satyrid butterfly likely will not be negatively affected by feeding on grassland plants that may exhibit reduced foliar nitrogen concentrations. Increases in the air's CO_2 concentration may increase the fitness of this butterfly species. Adult males exposed to elevated CO_2, for example, exhibited greater body concentrations of lipids, compounds used as energy resources in these and other butterflies. In addition, elevated CO_2 increased egg numbers in females, which also suggests an increase in fitness. Thus, this species—and perhaps others—likely will respond positively to future increases in the air's CO_2 concentration.

References

Goverde, M., Bazin, A., Shykoff, J.A., and Erhardt, A. 1999. Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO_2 and plant genotype. *Functional Ecology* **13**: 801–810.

Goverde, M., Erhardt, A., and Niklaus, P.A. 2002. In situ development of a satyrid butterfly on calcareous grassland exposed to elevated carbon dioxide. *Ecology* **83**: 1399–1411.

Goverde, M., Erhardt, A., and Stocklin, J. 2004. Genotype-specific response of a lycaenid herbivore to elevated carbon dioxide and phosphorus availability in calcareous grassland. *Oecologia* **139**: 383–391.

Leadley, P.W., Niklaus, P., Stocker, R., and Korner, C. 1997. Screen-aided CO_2 control (SACC): a middle-ground between FACE and open-top chamber. *Acta Oecologia* **18**: 207–219.

Leadley, P.W., Niklaus, P.A., Stocker, R., and Korner, C. 1999. A field study of the effects of elevated CO_2 on plant biomass and community structure in a calcareous grassland. *Oecologia* **118**: 39–49.

5.5.5 Other Insects

5.5.5.1 Response to Temperature

It is important to determine what effect global warming might have on the delicate balance between various plants and the insects that feed on them. Several researchers have done just that for several insect species. This section examines what has been reported for other types of insects not previously discussed in this chapter.

In some cases, researchers have found higher temperatures do indeed inhibit insect growth and survival. For some insect species, humankind might consider this a good thing.

Zhang *et al.* (2009), for example, note "the Oriental migratory locust (*Locusta migratoria manilensis*) has been one of the most damaging agricultural pests throughout Chinese history." Based on the decadal locust abundance data of Ma (1958) for the AD 950s–1950s, the decadal Yangtze Delta flood and drought frequency data of Jiang *et al.* (2005) for the AD 1000s–1950s, and the decadal mean temperature records of Yang *et al.* (2002) for the AD 950s–1950s, Zhang *et al.* employed wavelet analysis "to shed new light on the causal relationships between locust abundance, floods, droughts and temperature in ancient China."

The international team of Chinese, French, German, and Norwegian researchers say coolings of 160- to 170-year intervals dominated climatic variability in China over the past millennium, and these cooling periods promoted locust plagues by enhancing temperature-associated drought/flood events. The six scientists say their results suggest "global warming might not only imply reduced locust plague[s], but also reduced risk of droughts and floods for entire China." They note these findings "challenge the popular view that global warming necessarily accelerates natural and biological disasters such as drought/flood events and outbreaks of pest insects," the view long championed by the assessment reports of the Intergovernmental Panel on Climate Change. In direct contrast to that view, Zhang *et al.* say their results are an example of "benign effects of global warming on the regional risk of natural disasters."

Reineke and Hauck (2012) note "the grape leafhopper *Empoasca vitis* is regarded as a major insect pest in many European grapevine growing areas, with an increasing importance realized in recent years, maybe as a result of climatic change."

Reineke and Hauck studied in the laboratory the development of larval instars of two leafhopper species, *E. vitis* and *E. rosae,* on grapevine leaves under different temperature regimes. The two German researchers report the shortest larval developmental time they observed occurred at night temperatures of 13–15°C and day temperatures of 23–25°C, which they say "was in agreement with predicted optimal temperatures for both species." In addition, "at the temperature regime of 20°C night and 30°C day temperature, either no egg hatch was observed or early development of first-instar larvae was not successful for both species." Reineke and Hauck conclude, "these results suggest that warm (18°C) nights and moderately warm (28°C) days are representing the upper thermal threshold for development of both *E. vitis* and *E. rosae* embryonic stages on grapevine leaves, questioning current assumptions of an increasing importance of *E. vitis* as a grapevine pest under future climate change."

Bertelsmeier *et al.* (2013) write, "climate change and invasive species are two of the most serious threats of biodiversity," noting "a general concern is that these threats interact, and that a globally warming climate could favor invasive species," with the result that "many native species are displaced, leading to local extinctions of fauna and flora." They note "several studies suggest that climate change could exacerbate the threat posed by invasive species, especially poikilotherms [animals having a body temperature that varies with the temperature of their surroundings], by removing thermal barriers and allowing them to establish at higher latitudes."

The three French researchers focused their attention on ants, because "ants are among the worst invasive species (Rabitsch 2011; Holway *et al.* 2002; Lach and Hooper-Bui 2010)," and "they are small, numerous and colonial" and can therefore "rapidly colonize a new habitat." They studied the big-headed ant, *Pheidole megacephala*, considered one of the world's 100 worst invasive species. They used ecological niche models to estimate the species' potential suitable habitat in 2020, 2050, and 2080 with an ensemble forecast obtained from five modeling techniques, including three global circulation models and two CO_2 emission scenarios, by means of which they generated world maps with suitable climatic conditions and assessed changes, both qualitatively and quantitatively.

"Surprisingly," Bertelsmeier *et al.* write, their results suggest "the invasion of big-headed ants is not only unlikely to benefit from climate change, but may even suffer from it," as their projections showed "a global decrease in the invasive potential of big-headed ants as early as 2020 and becoming even stronger by 2080, reaching a global loss of 19.4% of area with favorable climate." They note this finding is just the opposite of classical views of global climate change, wherein the ranges of many invading species are believed to increase in response to warming, especially those that are currently limited by climate. *P. megacephala* "will experience very little shifts in potential habitat," the French scientists conclude, as their niche envelope, presenting favorable climatic conditions, "will mostly shrink."

The analysis of Bertelsmeier *et al.* suggests, as they clearly state, "the worst invasive species of today may not be the worst invasive species of tomorrow," if Earth begins to warm again. After the planet's nearly two-decade climate-change hiatus, it's anyone's guess as to when that might happen.

Other insect species have benefited from a little global warming, as illustrated by recent temperature-induced expansions of their ranges.

Hickling *et al.* (2005), for example, analyzed changes in the northern and southern range boundaries of 37 non-migratory British Odonata (dragonfly and damselfly) species—four of which have northern ranges, 24 of which have southern ranges, and nine of which are ubiquitous—between the two ten-year periods 1960–1970 and 1985–1995. Their work revealed all but two of the 37 species increased their ranges between the two ten-year periods. They report their "findings that species are shifting northwards faster at their northern range margin than at their southern range margin, are consistent with the results of Parmesan *et al.* (1999)," adding, "this could suggest that species at their southern range margins are less constrained by climate than by other factors."

Poniatowski and Fartmann (2011) state the majority of central European orthopterans (an order of insects that includes grasshoppers, crickets, and locusts) "are flightless and have low dispersal ability," citing Reinhardt *et al.* (2005). However, they note, "since the 1980s—the beginning of the strong global temperature increase—some short-winged (brachypterous) species have been able to expand their ranges rapidly," as reported by Thomas *et al.* (2001), Simmons and Thomas (2004), Gardiner (2009), and Wissmann *et al.* (2009). In those cases, the scientists write, "long-winged (macropterous) individuals of the predominantly short-winged (flightless) species are assumed to have been responsible for the range shifts," citing the findings and conclusions of Simmons and Thomas (2004), Gardiner (2009), and Hochkirch and Damerau (2009).

Poniatowski and Fartmann studied the migration behavior of *Metrioptera roeselii*, a medium-sized bush-cricket, 13–26 mm in total length, which is currently expanding its range northwards in large parts of Europe (Kleukers *et al*., 2004; Gardiner, 2009; Wissmann *et al*., 2009).” This species is wing-dimorphic, but they note “the short-winged (brachypterous) morph dominates.”

Based on their analyses of the relationships between bush-cricket densities and several meso-climate/weather parameters, the two German researchers found cricket abundances were positively correlated with warm and dry weather conditions during the hatching times of the nymphs, leading them to conclude, “the development of long-winged individuals is determined by density stress (crowding), as has been shown for locusts (Uvarov, 1966).” They further note, “similar results have also been reported for other bush-crickets,” citing Ando and Hartley (1982), Sanger (1984), and Higaki and Ando (2003). Poniatowski and Fartmann conclude, “the rapid northward range expansion of *M. roeselii* is indirectly driven by climate change,” explaining, “favorable (warm/dry) weather conditions lead to high densities at high latitudes (cf. Bale *et al*., 2002) and in turn result in many macropters,” the “potential dispersers” that get the species where it needs to go in order to survive in a world of evolving warmth.

Instead of experiencing range expansions in response to rising temperatures, other insect species have invoked adapted mechanisms allowing them to maintain their populations and habitat area.

Sparks *et al*. (2010) note “honeybees are an essential component of modern agriculture,” and “large acreages of pollinator-dependent crops, such as apples, almonds, blueberries and cranberries, require managed pollinators, mainly the honeybee, to ensure maximized production.” They report several modern studies suggest synchronization of pollinator activity and flowering may be changed by rapid global warming, leading to deficient pollination when it is most needed and resulting in reduced crop productivity. Noting little work has focused on this imagined problem, the six Polish scientists decided to investigate the dates of honeybees’ first cleansing flights, which occur in the early spring of each year after overwintering and “are undertaken by worker bees excreting faeces accumulated in their recta while restricted in the hive for the winter during cold weather.”

Sparks *et al*. analyzed annual records of the first observed cleansing flights of honeybees from 80–130 hives for each of the 25 years of the 1985–2009 period in the vicinity of Poznan, Poland. They found a significant relationship between the date of the first cleansing flight and the January to March mean temperature, as well as the previous June to September mean temperature. In the two-variable model of this phenomenon they developed, “the regression coefficients suggested a 1°C increase in previous June to September mean temperature was associated with a 9.11 ± 2.36 day advance, and a 1°C increase in January to March temperature was associated with a 3.41 ± 1.00 day advance, in first cleansing flight date.”

Thus they discovered “first cleansing flight dates in [their] study advanced by over 1 month during the 25 years that observations were kept,” and this advancement was “similar to changes reported in first appearance dates of other insects (e.g. Roy and Sparks, 2000; Sparks *et al*., 2005; Harrington *et al*., 2007), including other hymenopterans like wasps (Tryjanowski *et al*., 2010).” This demonstrates, as has been observed by still others, “cleansing behavior is related to late winter/spring temperature (e.g. Kronenberg and Heller, 1982; Seeley, 1985),” and provides more evidence of honeybees “continued synchrony with the plant species that rely heavily on this major pollinator,” as the plants’ flowering dates fluctuate with the ups and downs of spring temperatures and their longer-term trends.

Bartomeus *et al*. (2011) preface their analysis by noting “the phenology of many ecological processes is modulated by temperature, making them potentially sensitive to climate change,” and because of this fact, “mutualistic interactions may be especially vulnerable because of the potential for phenological mismatching if the species involved do not respond similarly to changes in temperature.” Bartomeus *et al*. explored this situation with real-world data by presenting “an analysis of climate-associated shifts in the phenology of wild bees, the most important pollinators worldwide, and [comparing] these shifts to published studies of bee-pollinated plants over the same time period.” They “used long-term data to compare phenological shifts for 10 bee species to shifts in 106 native plant species that are visited by these same bee species,” which typically “have annual cycles that include an obligatory larval or adult diapause before spring emergence.” The plant data for this comparison were provided by Primack *et al*. (2004) and Miller-Rushing *et al*. (2006) for Massachusetts (AD 1885–2003), by Bradley *et al*. (1999) for Wisconsin (1936–1999), by Cook *et al*. (2008) for New York (1931–2008), and by Abu-Asab *et al*. (2001) for Washington, DC (1970–1999, a time interval bracketing the period of greatest temperature increase), and the bee data were developed by Bartomeus *et al*.

The results indicate "over the past 130 years, the phenology of 10 bee species from northeastern North America has advanced by a mean of 10.4 ± 1.3 days," and "most of this advance has taken place since 1970, paralleling global temperature increases." The scientists note "when the best available data are used to estimate analogous rates of advance for plants, these rates are not distinguishable from those of the bees." Bartomeus *et al*. conclude, among the generalist bee species they studied, "bee emergence is keeping pace with shifts in host-plant flowering." This finding suggests historical global warming—which IPCC contends has been unprecedented over the past millennium or two—has not detrimentally interfered with the longstanding mutually beneficial relationship between the emergence of adult wild bees and the flowering of the plants they visit.

Balanya *et al*. (2006) determined the magnitude and direction of shifts over time [13 to 46 years, mean = 24.1 years] in chromosome inversion frequencies and in ambient temperature for 26 populations of the cosmopolitan fly species *Drosophila subobscura* on three continents, to determine whether "ambient temperatures have warmed at these sites and also whether genotypes characteristic of low latitudes have increased in frequency." The authors report warming occurred at 22 of the 26 sites they investigated, and "chromosome frequencies shifted toward a more low-latitude pattern in 21 of the 22 sites that warmed over the sample interval," indicating "inversion frequencies have changed in step with climate on three continents." As a result, "genotype frequencies and climate at a given site have become more equatorial over the sample intervals," with the observed shifts being "equivalent to moving the historical sample site ~1° of latitude closer to the equator."

The authors describe the genetic shift they uncovered as "exceptionally rapid," being "detectable even for samples separated by fewer than two decades." In addition, they say, "the ability of *D. subobscura* (Rodriguez-Trelles *et al*., 1998; Orengo and Prevosti, 1996; Sole *et al*., 2002)—and probably other species with short generation times (Bradshaw and Holzapfel, 2001; Umina *et al*., 2005; Levitan and Etges, 2005; Kinnison and Hendry, 2001)—to respond genetically and rapidly to imposed environmental shifts may partially buffer their persistence in a globally warming world (Bradshaw and Holzapfel, 2006)."

Zivanovic and Mestres (2011) collected *Drosophila subobscura* flies from a swampy area on the bank of the Danube river near the town of Apatin, approximately 200 km northwest of Belgrade, Serbia, and analyzed inversion polymorphisms in them, comparing their results (from 2008 and 2009) with results obtained from flies collected at the same site in June 1994, because, as they put it, "genes located within inversions are associated with a variety of traits including those involved in climate adaptation," citing Hoffmann and Rieseberg (2008). The scientists found a significant increase in the frequency of certain chromosomal arrangements characteristic of southern latitudes, which they describe as "warm adapted," and a significant decrease in the frequency of such arrangements characteristic of northern latitudes, which they describe as "cold adapted."

The two researchers say their observations suggest they have detected "the effect of selection on chromosomal polymorphism composition," and, therefore, "some form of natural selection appears to be acting as a reaction to the increase in temperature associated with [the] many heat waves that have markedly affected the Balkan Peninsula," especially over the past decade and a half. They also note their results "agree with those from southwestern and central European populations (Rodriguez-Trelles and Rodriguez, 1998; Sole *et al*., 2002; Balanya *et al*., 2004, 2006, 2009)." In addition, they note similar things have been observed in *D. melanogaster* in Australia, citing Anderson *et al*. (2005) and Umina *et al*. (2005), and in *D. robusta* in North America, citing Levitan and Etges (2005). They report, "the climate change of recent decades has led to heritable genetic changes in animal species as diverse as birds, squirrels and mosquitoes (Bradshaw and Holzapfel, 2006)," revealing many forms of animal life may be well equipped to evolve with sufficient rapidity to survive the challenges of rapid global warming.

Nyamukondiwa and Terblanche (2010) write, "acclimation, acclimatization or hardening responses all describe different forms of phenotypic plasticity (i.e. the ability of an organism to respond to environmental stimuli with a change in phenotype)," as described by West-Eberhard (2003) and Whitman (2009). In addition, they state, "phenotypic plasticity may alter the performance of an organism through compensatory modifications of physiological function and tolerance as a result of changes in environmental conditions," suggesting this multifaceted phenomenon likely will play a major role in determining future geographic distributions of insects in a warming world.

The two South African scientists explored the phenomenon as it operates in two species of fruit fly (*Ceratitis rosa* and *C. capitata*). Using a full-factorial design, as they describe it, they investigated one-week-long acclimation responses of each species' critical minimum and maximum temperature (CT_{min} and CT_{max}) to exposure to temperatures of 20, 25, and 30°C, as well as their interactions with short-term sub-lethal temperature exposures to the same conditions as arrived at via different rates of warming. They report, "generally, increasing the acclimation temperature significantly increased CT_{max}, whereas decreasing the acclimation temperature significantly lowered CT_{min}." In addition, "slower ramping rates significantly increase CT_{max} in both *C. rosa* and *C. capitata*." This suggests "more time during heating (i.e. a slower heating rate) provides the flies with an opportunity to develop some heat protection, and therefore suggests that *C. capitata*, and possibly also *C. rosa*, might have short-term phenotypic plasticity of high temperature tolerance." They describe this as being "similar to the rapid heat hardening or the heat shock responses in *Drosophila* (Loeschcke and Hoffmann, 2006; Johnson *et al*., 2009) and other insect species (Huang *et al*., 2007)."

Nyamukondiwa and Terblanche conclude fruit flies "are capable of adjusting their thermal tolerance within a single generation at both weekly and hourly time scales," noting "high temperature acclimation improves high temperature tolerance, in keeping with much of the literature on thermal acclimation (Whitman, 2009)." They also state "both *C. rosa* and *C. capitata* have the capacity to adjust their thermal tolerance over short timescales in the wild," further stating this phenomenon will "probably allow both species to track changes in ambient temperature and survive sudden extremes of temperature that might otherwise be potentially lethal," citing Chown and Nicolson (2004).

This phenomenon is not restricted to flies. The two researchers indicate, for example, in several insect species "survival of lethal temperatures or critical thermal limits to activity can be significantly improved by prior exposure to sub-lethal temperatures," citing Lee *et al*. (1987), Kelty and Lee (2001), Shreve *et al*. (2004), and Powell and Bale (2006). This phenomenon is a major mechanism used by insects to cope with temperature variation at both daily (Kelty and Lee, 2001; Kelty, 2007; Overgaard and Sorensen, 2008) and seasonal (Powell and Bale, 2006; Hoffmann *et al*., 2005; Terblanche *et al*., 2006) time scales.

Harada *et al*. (2011) write "in temperate areas, insects are adapted physiologically or behaviourally to either [1] tolerate seasonally fluctuating changes in temperature through diapause or to [2] avoid adverse conditions through migration," with the most predictable time cue for seasonal adaptation by insects being photoperiod (Tauber *et al*., 1986). Thus, "it is assumed that the critical photoperiod of insects is becoming gradually shortened as a result of global warming," and if populations are adapting to the consequent longer growing seasons and later onsets of winter, it would be expected that the number of yearly broods produced "should increase, that photoperiodic responses of diapause induction and wing-form determination will continue to diminish ... and that overwintering adults will cease to migrate between water courses and overwintering land sites far from water, and will begin overwintering nearer summer habitats."

In an effort to determine whether such adjustments have been occurring in the life cycle of nymphs of the water strider *Aquarius paludum* in the Kochi prefecture of Japan over the past two decades, Harada *et al*. measured a number of pertinent parameters that had been assessed by Harada and Numata (1993) two decades earlier, over the period 1989–1991. They found *A. paludum* nymphs were trivoltine (i.e., produced three broods yearly) in 1991, but more recently the generation number appears to have increased to four or more. They also found overwintering adults of both sexes had no mature flight muscles in October and November 2008, which "contrasts with previous observations," and "the 2008 population also shows a low flight propensity in response to shorter day lengths."

The Japanese scientists from Kochi University thus opine, "the absence of mature flight muscles in the autumn, and the lower flight propensity under shorter days, may comprise evidence of a cessation of dispersal between the freshwater summer habitats and overwintering sites on land far from the bodies of water." And they observe, "the increase in daily-minimum temperature during the winter in the Kochi-Nankoku area over the last 15 years may allow adults of *A. paludum* to overwinter without dispersal nearer to their summer habitat," which could lead to the proportion of adults overwintering close to the water bodies increasing from the current estimate of 60 to 70% to between 90 and 100% within ten years. Thus, they conclude, *A. paludum* populations in the Kochi-Nankoku region "are continuing to show adaptive change, apparently in relation to global warming."

Brakefield and de Jong (2011) note "a variety of processes can enable organisms, including insects, to respond successfully to climate change (Stenseth *et al*., 2002; Bradshaw and Holzapfel, 2006; Parmesan, 2006)," including "habitat tracking, phenotypic plasticity and genetic adaptation." Evidence for the first of these mechanisms, in their words, "is becoming commonplace," as is the case with many species of butterflies that are "clearly responding with northern extensions in their range limits (Parmesan and Yohe, 2003; Hickling *et al*., 2006)," as well as with moths and other insects that "are moving up altitudinal gradients (Chen *et al*., 2009)." On the other hand, they write, "the extent to which changes in phenotypic plasticity are (or will be) involved in the numerous reports of changes in phenology (Brakefield, 1987; Roy and Sparks, 2000; Amano *et al*., 2010) is not clear." And they remark, "there are as yet few reports of genetic changes within populations linked to climate change," although "the pitcher plant mosquito, *Wyeomyia smithii*, showed a genetic response to climate change, which involved changes in sensitivity to photoperiod (Bradshaw *et al*., 2006)," which "could be detected over a period as short as five years."

Hoping to contribute to the search for genetic responses to climate change, Brakefield and de Jong report on the most recent data describing changes in a cline in the frequency of melanism morphs of the two-spot ladybird beetle, *Adalia bipunctata* L., along a transect that extends inland from the seacoast in the Netherlands.

At the time of the beetle's first survey in 1980, the two researchers report, "the frequency of melanics increased over some 40 km from 10% near the coast to nearly 60% inland." Additional surveys in 1991 and 1995 "demonstrated some progressive change in cline shape," and new samples from 1998 and 2004 confirmed these dynamics, so "over a period of about fifty generations of the beetle, the cline had decayed rapidly to yield rather uniform frequencies of melanic morphs at around 20% along the whole transect by 2004." They remark, "climate data and evidence for thermal melanism in this species support our contention that these dynamics reflect a dramatic example of a rapid genetic response within populations to climate change and local selection." Brakefield and de Jong conclude by stating their study "adds to potential examples of how some organisms are likely to be responding to climate change through direct genetic responses within populations."

It appears rising temperatures will be beneficial for some insect species, but perhaps not for others. Nevertheless, it does not appear there will be a widespread extinction of insect species, as most will adapt as they likely have done as temperatures have waxed and waned in the past.

References

Abu-Asab, M.S., Peterson, P.M., Shetler, S.G., and Orli, S.S. 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. *Biodiversity and Conservation* **10**: 597–612.

Amano, T., Smithers, R.J., Sparks, T.H., and Sutherland, W.J. 2010. A 250-year index of first flowering dates and its response to temperature changes. *Proceedings of the Royal Society of London B* **277**: 2451–2457.

Anderson, A.R., Hoffmann, A.A., McKechnie, S.W., Umina, P.A., and Weeks, A.R. 2005. The latitudinal cline in the *In(3R) Payne* inversion polymorphism has shifted in the last 20 years in Australian *Drosophila melanogaster* populations. *Molecular Ecology* **14**: 851–858.

Ando, Y. and Hartley, J.C. 1982. Occurrence and biology of a long-winged form of conocephalus discolor. *Entomologia Experimentalis Applicata* **32**: 238–241.

Balanya, J., Huey, R.B., Gilchrist, G.W., and Serra, L. 2009. The chromosomal polymorphism of *Drosophila subobscura*: A micro evolutionary weapon to monitor global change. *Heredity* **103**: 364–367.

Balanya, J., Oller, J.M., Huey, R.B., Gilchrist, G.W., and Serra, L. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science* **313**: 1773–1775.

Balanya, J., Sole, E., Oller, J.M., Sperlich, D., and Serra, L. 2004. Long-term changes in the chromosomal inversion polymorphism of *Drosophila subobscura*. II. European populations. *Journal of Zoological Systematics and Evolutionary Research* **42**: 191–201.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartleuy, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., and Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**: 1–16.

Bartomeus, I., Ascher, J.S., Wagner, D, Danforth, B.N., Colla, S., Kornbluth, S., and Winfree, R. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences, USA* **108**: 20,645–20,649.

Bertelsmeier, C., Luque, G.M., and Courchamp, F. 2013. Global warming may freeze the invasion of big-headed ants. *Biological Invasions* **15**: 1561–1572.

Bradley, N.L., Leopold, A.C., Ross, J., and Huffaker, W. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences, USA* **96**: 9701–9704.

Bradshaw, W.E. and Holzapfel, C.M. 2001. From the Cover: Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences USA* **98**: 14,509–14,511.

Bradshaw, W.E. and Holzapfel, C.M. 2006. Evolutionary response to rapid climate change. *Science* **312**: 1477–1478.

Bradshaw, W.E., Holzapfel, C.M., and Mathias, D. 2006. Circadian rhythmicity and photoperiodism in the pitcher-plant mosquito: Can the seasonal timer evolve independently of the circadian clock? *American Naturalist* **167**: 601–605.

Brakefield, P.M. 1987. Geographical variability in, and temperature effects on, the phenology of *Maniola jurtina* and *Pyronia tithonus* in England and Wales. *Ecological Entomology* **12**: 139–148.

Brakefield, P.M. and de Jong, P.W. 2011. A steep cline in ladybird melanism has decayed over 25 years: a genetic response to climate change? *Heredity* **107**: 574–578.

Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S., Hill, J.K., and Thomas, C.D. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences USA* **106**: 1479–1483.

Chown, S.L. and Nicolson, S.W. 2004. *Insect Physiological Ecology: Mechanisms and Patterns*. Oxford, UK: Oxford University Press.

Cook, B.I., Cook, E.R., Huth, P.C., Thompson, J.E., and Smiley, D. 2008. A cross-taxa phenological dataset from Mohonk Lake, NY and its relationship to climate. *International Journal of Climatology* **28**: 1369–1383.

Gardiner, T. 2009. Macropterism of Roesel's bushcricket *Metrioptera roeselii* in relation to climate change and landscape structure in Eastern England. *Journal of Orthoptera Research* **12**: 95–102.

Harada, T. and Numata, H. 1993. Two critical daylengths for the determination of wing forms and the induction of adult diapause in the water strider, *Aquarius paludum*. *Die Naturwissenschaften* **80**: 430–432.

Harada, T., Takenaka, S., Maihara, S., Ito, K., and Tamura, T. 2011. Changes in life-history traits of the water strider *Aquarious paludum* in accordance with global warming. *Physiological Entomology* **36**: 309–316.

Harrington, R., Clark, S.J., Welham, S.J., Verrier, P.J., Denholm, C.H., Hulle, M., Maurice, D., Rounsevell, M.D., and Cocu, N. 2007. Environmental change and the phenology of European aphids. *Global Change Biology* **13**: 1550–1564.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., and Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**: 1–6.

Hickling, R., Roy, D.B., Hill, J.K., and Thomas, C.D. 2005. A northward shift of range margins in British Odonata. *Global Change Biology* **11**: 502–506.

Higaki, M. and Ando, Y. 2003. Effects of crowding and photoperiod on wing morph and egg production in *Eobiana engelhardti subtropica* (Orthoptera: Tettigoniiade). *Applied Entomology and Zoology* **38**: 321–325.

Hochkirch, A. and Damerau, M. 2009. Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. *Biological Journal of the Linnean Society* **97**: 118–127.

Hoffmann, A.A. and Rieseberg, L.H. 2008. Revisiting the impact of inversions in evolution: From population genetic markers to drivers of adaptive shifts and speciation? *Annual Review of Ecology, Evolution, and Systematics* **39**: 21–42.

Hoffmann, A.A., Shirriffs, J., and Scott, M. 2005. Relative importance of plastic versus genetic factors in adaptive differentiation: geographic variation for stress resistance in *Drosophila melanogaster* from eastern Australia. *Functional Ecology* **19**: 222–227.

Holway, D., Lach, L., Suarez, A.V., Tsutsui, N.D., and Case, T.J. 2002. The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics* **33**: 181–233.

Huang, L.H., Chen, B., and Kang, L. 2007. Impacts of mild temperature hardening on thermo tolerance, fecundity and Hsp gene expression in *Liriomyza huidobrensis*. *Journal of Insect Physiology* **53**: 1199–1205.

Jiang, T., Zhang, Q., Blender, R., and Fraedrich, K. 2005. Yangtze delta floods and droughts of the last millennium: abrupt changes and long-term memory. *Theoretical and Applied Climatology* **82**: 131–141.

Johnson, T.K., Cockerell, F.E., Carrington, L.B., Rako, L., Hoffmann, A.A., and McKechnie, S.W. 2009. The capacity of *Drosophila* to heat harden associates with low rates of heat-shocked protein synthesis. *Journal of Thermal Biology* **34**: 327–331.

Kelty, J.D. 2007. Rapid cold-hardening of *Drosophila melanogaster* in a field setting. *Physiological Entomology* **32**: 343–350.

Kelty, J.D. and Lee Jr., R.E. 2001. Rapid cold-hardening of *Drosophila melanogaster* (Diptera: Drosophilidae) during ecologically based thermoperiodic cycles. *Journal of Experimental Biology* **204**: 1659–1666.

Kinnison, M.T. and Hendry, A.P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**: 145–164.

Kleukers, R.M.J.C., van Nieukerken, E.J., Ode, B., Willemse, L.P.M., and van Wingerden, W.K.R.E. 2004. De sprinkhanen en krekels van Nederland (Orthoptera). In: *Nederlandse Fauna 1, 2nd Edition,* National Natuurhistorisch Museum, KNNV Uitgeverij & EIS-Nederland, Leiden, The Netherlands.

Kronenberg, F. and Heller, C. 1982. Colonial thermoregulation in honey bees (*Apis mellifera*). *Journal of Comparative Physiology* **148**: 65–76.

Lach, L. and Hooper-Bui, L.M. 2010. Consequences of ant invasions. In: Lach, L., Parr, C.L., and Abbott, K.L. (Eds.) *Ant Ecology*. Oxford University Press, New York, New York, USA, pp. 261–286.

Lee, R.E., Chen, C.P., and Denlinger, D.L. 1987. A rapid cold-hardening process in insects. *Science* **238**: 1415–1417.

Levitan, M. and Etges, W.J. 2005. Climate change and recent genetic flux in populations of *Drosophila robusta*. *BMC Evolutionary Biology* **5**: 10.1186/1471-2148-5-4.

Loeschcke, V. and Hoffmann, A.A. 2006. Consequences of heat hardening on a field fitness component in *Drosophila* depend on environmental temperature. *American Naturalist* **169**: 175–183.

Ma, S. 1958. The population dynamics of the oriental migratory locust (*Locusta migratoria manilensis* Meyen) in China. *Acta Entomologica Sinica* **8**: 1–40.

Miller-Rushing, A.J., Primack, R.B., Primack, D., and Mukunda, S. 2006. Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany* **93**: 1667–1674.

Nyamukondiwa, C. and Terblanche, J.S. 2010. Within-generation variation of critical thermal limits in adult Mediterranean and Natal fruit flies *Ceratitis capitata* and *Ceratitis rosa*: thermal history affects short-term responses to temperature. *Physiological Entomology* **35**: 255–264.

Orengo, D.J. and Prevosti, A. 1996. Evolution. *International Journal of Organic Evolution* **50**: 1346.

Overgaard, J. and Sorensen, J.G. 2008. Rapid thermal adaptation during field temperature variations in *Drosophila melanogaster*. *Cryobiology* **56**: 159–162.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* **37**: 637–669.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., and Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

Poniatowski, D. and Fartmann, T. 2011. Weather-driven changes in population density determine wing dimorphism in a bush-cricket species. *Agriculture, Ecosystems and Environment* **145**: 5–9.

Powell, S.J. and Bale, J.S. 2006. Effect of long-term and rapid cold hardening on the cold torpor temperature of an aphid. *Physiological Entomology* **31**: 348–352.

Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J., and Del Tredici, P. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* **91**: 1260–1264.

Rabitsch, W. 2011. The hitchhiker's guide to alien ant invasions. *BioControl* **56**: 551–572.

Reineke, A. and Hauck, M. 2012. Larval development of *Empoasca vitis* and *Edwardsiana rosae* (Homoptera: Cicadellidae) at different temperatures on grapevine leaves. *Journal of Applied Entomology* **136**: 656–664.

Reinhardt, K., Kohler, G., Maas, S., and Detzel, P. 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. *Ecography* **28**: 593–602.

Rodriguez-Trelles, F. and Rodriguez, M.A. 1998. Rapid microevolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. *Evolutionary Ecology* **12**: 829–838.

Rodriguez-Trelles, F., Rodriguez, M.A., and Scheiner, S.M. 1998. Tracking the genetic effects of global warming: *Drosophila* and other model systems. *Conservation Ecology* **2**: 2.

Roy, D.B. and Sparks, T.H. 2000. Phenology of British butterflies and climate change. *Global Change Biology* **6**: 407–416.

Sanger, K. 1984. Die Populationsdichte als Ursache makropterer Okomorphosen von Tessellana vittata (Charp.) (Orthoptera, Tettigoniidae). *Zoologischer Anzeiger* **213**: 68–76.

Seeley, T.D. 1985. *Honeybee Ecology*. Princeton University Press, Princeton, New Jersey, USA.

Shreve, S.M., Kelty, J.D., and Lee, R.E. 2004. Preservation of reproductive behaviors during modest cooling: rapid cold-hardening fine-tunes organismal response. *Journal of Experimental Biology* **207**: 1797–1802.

Simmons, A.D. and Thomas, C.D. 2004. Changes in dispersal during species' range expansions. *American Naturalist* **164**: 378–395.

Sole, E., Balanya, J., Sperlich, D., and Serra, L. 2002. Long-term changes in the chromosomal inversion polymorphism of *Drosophila subobscura*. I. Mediterranean populations from southwestern Europe. *Evolution: International Journal of Organic Evolution* **56**: 830–835.

Sparks, T.H., Croxton, P.J., Collinson, N., and Taylor, P.W. 2005. Examples of phenological change, past and present, in UK farming. *Annals of Applied Biology* **146**: 531–537.

Sparks, T.H., Langowska, A., Glazaczow, A., Wilkaniec, Z., Bienkowska, M., and Tryjanowski, P. 2010. Advances in the timing of spring cleaning by the honeybee *Apis mellifera* in Poland. *Ecological Entomology* **35**: 788–791.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S., and Lima, M. 2002. Ecological effects of climate fluctuations. *Science* **297**: 1292–1296.

Tauber, M.J., Tauber, C.A., and Masaki, S. 1986. *Seasonal Adaptations of Insects*. Oxford University Press, New York, New York, USA.

Terblanche, J.S., Klok, C.J., Krafsur, E.S., and Chown, S.L. 2006. Phenotypic plasticity and geographic variations in thermal tolerance and water loss of tsetse *Glossina pallidipes* (Diptera: Glossinidae): implications for distribution modeling. *American Journal of Tropical Medicine and Hygiene* **74**: 786–794.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G. Musche, M., and Conradt, L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–581.

Tryjanowski, P., Pawlikowski, T., Pawlikowski, K., Banaszak-Cibicka, W., and Sparts, T.H. 2010. Does climate influence phenological trends in social wasps (Hymenoptera: Vespinae) in Poland? *European Journal of Entomology* **107**: 203–208.

Umina, P.A., Weeks, A.R., Kearney, M.R., McKechnie, S.W., and Hoffmann, A.A. 2005. A rapid shift in a classic clinical pattern in *Drosophila* reflecting climate change. *Science* **308**: 691–693

Uvarov, B.P. 1966. *Grasshoppers and Locusts: A Handbook of General Acridology, Volume 1*. Cambridge University Press, Cambridge, United Kingdom.

West-Eberhard, M.J. 2003. *Developmental Plasticity and Evolution*. New York, NY: Oxford University Press.

Whitman, D.W. 2009. Acclimation. In Whitman, D.W. and Ananthakrishnan, T.N. (Eds.) *Phenotypic Plasticity of Insects. Mechanisms and Consequences*. Enfield, NH: Science Publishers, pp. 675–739.

Wissmann, J., Schielzeth, H., and Fartmann, T. 2009. Landscape-scale expansion of Roesel's bush-cricket *Metrioptera roeselii* (Orthoptera: Tettigoniidae) at the north-western range limit in Central Europe. *Entomologia Generalis*. **31**: 317–326.

Yang, B., Brauning, A., Johnson, K.R., and Yafeng, S. 2002. Temperature variation in China during the last two millennia. *Geophysical Research Letters* **29**: 10.1029/2001GL014485.

Zhang, Z., Cazelles, B., Tian, H., Stige, L.C., Brauning, A., and Stenseth, N.C. 2009. Periodic temperature-associated drought/flood drives locust plagues in China. *Proceedings of the Royal Society B* **276**: 823–831.

Zivanovic, G. and Mestres, F. 2011. Changes in chromosomal polymorphism and global warming: The case of *Drosophila subobscura* from Apatin (Serbia). *Genetics and Molecular Biology* **34**: 489–495.

5.5.5.2 Response to Elevated CO_2

As the air's CO_2 content continues to rise, it is important to determine what effect this might have on the delicate balance between various plants and the insects that feed on them. This section reviews the results of studies that have reported on insects not previously discussed at any length, where it is seen the ongoing rise in the air's CO_2 content likely plays an important role in negating the damage being done to Earth's vegetation by voracious insect pests.

Docherty *et al*. (1997), in addition to studying aphids, studied two sap-feeding leafhopper species that were allowed to feed on saplings of beech and sycamore grown in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm. As far as they could determine, there were no significant effects of the extra CO_2 on either the feeding or performance characteristics of either leafhopper species.

In a literature review of more than 30 studies published two years later, Whittaker (1999) found chewing insects (leaf chewers and leaf miners) showed either no change or reductions in abundance in response to atmospheric CO_2 enrichment. They note, however, population reductions in this feeding guild often were accompanied by increased herbivory in response to CO_2-induced reductions in leaf nitrogen content.

Contemporaneously, Brooks and Whittaker (1999) removed grassland monoliths from the Great Dun Fell of Cumbria, UK—which contained eggs of a destructive xylem-feeding spittlebug (*Neophilaenus lineatus*)—and grew them in glasshouses maintained for two years at atmospheric CO_2 concentrations of 350 and 600 ppm. During the course of their experiment, two generations of the xylem-feeding insect were produced; in each case, elevated CO_2 reduced the survival of nymphal stages by an average of 24%. Brooks and Whittaker suggest this reduction in survival rate may have been caused by CO_2-induced reductions in stomatal conductance and transpirational water loss, which may have reduced xylem nutrient-water availability.

Stiling *et al.* (1999) report the results of what may have been the first attempt to study the effects of elevated CO_2 on trophic webs in a natural ecosystem; specifically, a nutrient-poor scrub-oak community in Florida (USA), where 16 open-top chambers of 3.6-m diameter were fumigated with air of either 350 or 700 ppm CO_2 for approximately one year. At the end of this period, total leaf miner densities were 38% less on the CO_2-enriched foliage than on the foliage of the ambiently grown plants. Moreover, atmospheric CO_2 enrichment consistently reduced the numbers of all six species of leaf miners studied. In a compensatory development, exposure to elevated CO_2 increased the amount of leaf area consumed by the less-abundant leaf miners by approximately 40%. Nevertheless, leaf miners in the CO_2-enriched chambers experienced significantly greater mortality than those in the control chambers. Although CO_2-induced reductions in leaf nitrogen content were determined to have played a minor role in the mortality increase, the greatest factor contributing to this phenomenon was a fourfold increase in parasitization by various wasps that could more readily detect the more-exposed leaf miners on the CO_2-enriched foliage.

Three years later, Stiling *et al.* (2002) reported even more dramatic effects of elevated CO_2 on leaf chewers. The relative levels of damage by these insects (primarily larval lepidopterans and grasshoppers) were significantly lower in the elevated CO_2 chambers than in the ambient CO_2 chambers for all five of the plant species that accounted for more than 98% of the total plant biomass of the ecosystem. In addition, the response to elevated CO_2 was the same across all plant species. Also, they report more host-plant-induced mortality was found for all miners on all plants in elevated CO_2 than in ambient CO_2. These effects were so powerful that in addition to the relative densities of insect herbivores being reduced in the CO_2-enriched chambers, and even though there were more leaves on most plant species in the elevated CO_2 chambers, the total densities of leaf miners in the high-CO_2 chambers were also lower for all plant species. Stiling *et al.* note, "reductions in herbivore loads in elevated CO_2 could boost plant growth beyond what might be expected based on pure plant responses to elevated CO_2," a beneficial effect.

In a natural ecosystem in Wisconsin (USA) comprised predominantly of trembling aspen (*Populus tremuloides* Michx.), Percy *et al.* (2002) studied the effects of increases in CO_2 alone (to 560 ppm during daylight hours), O_3 alone (to 46.4–55.5 ppb during daylight hours), and CO_2 and O_3 together on the forest tent caterpillar (*Malacosoma disstria*), a common leaf-chewing lepidopteran found in North American hardwood forests. By itself, elevated CO_2 reduced caterpillar performance by reducing female pupal mass, and elevated O_3 alone improved caterpillar performance by increasing female pupal mass. When both gases were applied together, the elevated CO_2 completely counteracted the enhancement of female pupal mass caused by elevated O_3. Hence, either alone or in combination with undesirable increases in the air's O_3 concentration, elevated CO_2 tended to reduce the performance of the forest tent caterpillar. This finding is particularly satisfying because, in the words of Percy *et al.*, "historically, the forest tent caterpillar has defoliated more deciduous forest than any other insect in North America" and because "outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress."

Also working at the Aspen FACE site in northern Wisconsin, USA, Kopper and Lindroth (2003) studied the effects of elevated CO_2 (560 ppm) and elevated O_3 (1.5 x ambient) on trembling aspen (*Populus tremuloides* Michaux) trees, while the aspen blotch leafminer (*Phyllonorycter tremuloidiella* Braun) was allowed to naturally colonize the trees. Although there were some minor alterations in foliar chemistry in the CO_2- and O_3-enriched treatments, they produced "little to no change in larval performance," although both elevated CO_2 and O_3 "reduced colonization rates by nearly half."

Holton *et al.* (2003) reared both parasitized and non-parasitized forest tent caterpillars (*Malacosoma disstria*) on two quaking aspen (*Populus tremuloides*) genotypes (216, which is O_3-tolerant, and 259, which is O_3-sensitive) alone and in combination, also at the Aspen FACE site in northern Wisconsin, where trees were exposed to ambient air, ambient air + 200 ppm extra CO_2, ambient air + 50% extra ozone, and ambient air + 200 ppm extra CO_2 and 50% extra O_3 during the daylight hours of one full growing season. They found "elevated CO_2 had little effect on both primary and secondary metabolites of aspen." Thus, "elevated CO_2 had few biologically significant effects on forest tent caterpillar performance." Elevated O_3, on the other hand, altered foliar composition much more than did elevated CO_2; and, as they discovered, it improved tent caterpillar performance under ambient CO_2 conditions, but not in CO_2-enriched air. In addition, elevated O_3 decreased the larval survivorship of the parasite of the caterpillar.

These findings suggest the ongoing rise in the air's CO_2 content likely will be very important to the future well-being of quaking aspen trees, especially when atmospheric O_3 concentrations are increasing concurrently. Elevated levels of atmospheric CO_2 are known to significantly increase the productivity of aspen trees, making them more robust (Percy *et al.* (2002). Moreover, the extra CO_2 of this study totally thwarted the positive impact of the extra O_3 on caterpillar performance, thus eliminating a major negative consequence for the trees. As the authors note, "aspen growth is significantly increased under high CO_2, but decreased under high O_3," and "that difference is likely to be exacerbated by the impacts of CO_2 and O_3 on herbivorous insects and parasitoids as documented in this study." Without an increase in the air's CO_2 content commensurate with that projected for O_3 over the coming half-century, therefore, quaking aspen—the most widely distributed tree in North America—would suffer.

Johns *et al.* (2003) performed, in their words, "a factorial experiment to examine the effects of elevated CO_2 and increased temperature on both the leaf-chewing adults and leaf-mining larvae of two closely related beetle species, *Octotoma championi* Baly and *Octotoma scabripennis* Guerin-Meneville (Coleoptera: Chrysomelidae), feeding on the host plant *Lantana camara* L. (Verbenaceae)." The study was conducted in environment-controlled growth chambers maintained at atmospheric CO_2 concentrations of 360 or 700 ppm and at low (22°C/18°C) or high (25°C/21°C) day/night temperatures, where well-watered and fertilized plants were grown from cuttings for just over 13 months. Under the high temperature treatment, plants grown at ambient CO_2 suffered wilting and premature leaf loss, despite daily watering, but this effect was ameliorated at elevated CO_2. They also report "the wilting of plants in the ambient CO_2/high temperature treatment reduced the emergence success of the beetles," and "consumption rates of free-living beetles were not affected by either CO_2 or temperature," whereas "in short-term trials using excised foliage, beetles given no choice between ambient and elevated CO_2-grown foliage consumed more from ambient plants."

The authors state "this study indicates that under future conditions of higher temperatures, amelioration of water stress in host plants growing in elevated CO_2 may benefit some endophagous insects by reducing premature leaf loss," and they note "under some circumstances, this benefit may outweigh the deleterious effects of lower leaf nitrogen," which is typically described as posing a major problem for insects in a high-CO_2 world of the future. In addition, Johns *et al.* say their results indicate "foliage consumption under elevated CO_2 by mobile, adult insects on whole plants may not be significantly increased, as was previously indicated by short-term experiments using excised foliage."

According to Heagle (2003), the Western flower thrip (*Frankliniella occidentalis*) "is one of the most important and difficult to control plant pests," as "it feeds on numerous plant species and spreads the tomato spotted wilt virus, which also affects numerous plant species." In an effort to learn how this pest might respond to increasing concentrations of atmospheric CO_2, Heagle grew well-watered and fertilized white clover (*Trifolium repens*) plants from virus-free stolons in 1-liter pots filled with Metro Mix 220 and placed between two rows of thrip-invested plants growing in 15-liter pots, after which they were grown for either 27 or 35 additional days in continuous-stirred tank reactor chambers (CSTRs) maintained at either ambient or elevated atmospheric CO_2 concentrations (396 or 745 ppm) and located within a non-filtered-air greenhouse. The USDA researcher reports, "at elevated CO_2, clover shoot weight and laminae weight were ˜50% greater, and laminar area was ˜20% greater than at ambient CO_2." In addition, he notes the "thrips population size was not significantly affected by CO_2, but laminar area scarred by thrips feeding was ˜90% greater at elevated than at ambient CO_2." Nevertheless, because of the CO_2-induced increase in clover growth, "undamaged leaf area was approximately 15% greater at elevated than at ambient CO_2."

Barbehenn *et al.* (2004a) note "it has been hypothesized that herbivores will disproportionately increase their feeding damage on C_3 plants to compensate for the larger changes in C_3 plants in elevated CO_2 (Lincoln *et al.*, 1984, 1986; Lambers, 1993)." This is assumed because increases in the air's CO_2 content typically lead to greater decreases in the concentrations of nitrogen and, therefore, protein in the foliage of C_3 as compared to C_4 grasses (Wand *et al.*, 1999). In a test of this hypothesis, Barbehenn *et al.* grew *Lolium multiflorum* Lam. (Italian ryegrass, a common C_3 pasture grass) and *Bouteloua curtipendula* (Michx.) Torr. (sideoats gramma, a native C_4 rangeland grass) in chambers maintained at either the ambient atmospheric CO_2 concentration of 370 ppm or the doubled CO_2 concentration of 740 ppm for two months, after which grasshopper (*Melanoplus sanguinipes*) nymphs that had been reared to the fourth instar stage were allowed to feed on the grasses' foliage.

As expected, foliage protein concentration decreased much more in the C_3 grass than in the C_4 grass (22% vs. 7%) when the grasses were grown in CO_2-enriched air. However, and "contrary to the hypothesis that insect herbivores will increase their feeding rates disproportionately in C_3 plants under elevated atmospheric CO_2," Barbehenn *et al.* report "*M. sanguinipes* did not significantly increase its consumption rate when feeding on the C_3 grass grown under elevated CO_2," suggesting this observation implies "post-ingestive mechanisms enable these grasshoppers to compensate for variable nutritional quality in their host plants" and noting some of these post-ingestive responses may include "changes in gut size, food residence time, digestive enzyme levels, and nutrient metabolism (Simpson and Simpson, 1990; Bernays and Simpson, 1990; Hinks *et al.*, 1991; Zanotto *et al.*, 1993; Yang and Joern, 1994a,b)." Their data indicate, if anything, *M. sanguinipes* growth rates were increased, perhaps by as much as 12%, when they fed on the C_3 foliage that had been produced in the CO_2-enriched, as compared to the ambient-treatment, air.

As was also found by Barbehenn *et al.* (2004b), the CO_2-induced decrease in leaf protein concentration observed in this study did not induce an increase in foliage consumption in the C_3 plant studied, nor did it reduce the growth rate of the herbivore studied. The authors state "although compensatory feeding was commonly observed in early studies [of this subject], the absence of compensatory feeding on C_3 plants grown under elevated CO_2 has since been observed frequently among herbivorous insects (Bezemer and Jones, 1998)."

Noting the "detrimental effects of ozone on plants are well known," and "carbon dioxide [CO_2] generally affects trees in opposite ways to ozone [O_3]," Valkama *et al.* (2007) conducted a literature review they describe as "the first quantitative analysis of the interactive effects of elevated O_3 and elevated CO_2 on tree chemistry and herbivore performance," based on the results of "63 studies conducted on 22 tree species and 10 insect herbivore species and published between 1990 and 2005." With respect to ways by which elevated O_3 may benefit insect herbivores that tend to damage trees, Valkama *et al.* determined "elevated O_3 significantly shortened development time of insect herbivores [when they are exposed and vulnerable to attack by various enemies] and increased their pupal mass in the overall dataset." In addition, they found the "relative growth rate of chewers was significantly increased by 3.5% under elevated O_3." However, they discovered "these effects were counteracted by elevated CO_2," such that "elevated O_3 in combination with CO_2 had no effect on herbivore performance." When elevated CO_2 was added to the O_3-enriched air, it not only counteracted the O_3-induced increase in pupal biomass, but reduced it by 7% below what it was in ambient air.

Stiling and Cornelissen (2007) "report the results of the longest-known field study (9 years) to examine the effects of elevated carbon dioxide on leaf miner densities in a scrub-oak community at Kennedy Space Center, Florida [USA]." They then describe the results of various meta-analyses they employed to determine "the effects of elevated CO_2 on both plants (n = 59 studies) and herbivores (n = 75 studies)," where ambient CO_2 concentrations ranged between 350 and 420 ppm and elevated concentrations ranged between 550 and 1,000 ppm. With respect to the first subject of their review, Stiling and Cornelissen report "the densities of all leaf miner species (6) on all host species (3) were lower in every year in elevated CO_2 than they were in ambient CO_2." With respect to the second subject, they write, "elevated CO_2 significantly decreased herbivore abundance (-21.6%), increased relative consumption rates (+16.5%), development time (+3.87%) and total consumption (+9.2%), and significantly decreased relative growth rate (-8.3%), conversion efficiency (-19.9%) and pupal weight (-5.03%)." They also note "host plants growing under enriched CO_2 environments exhibited significantly larger biomass (+38.4%), increased C/N ratio (+26.57%), and decreased nitrogen concentration (-16.4%), as well as increased concentrations of tannins (+29.9%)." Thus with plant biomass increasing and herbivorous pest abundance decreasing (by +38.4% and -21.6%, respectively, in response to an approximate doubling of the atmosphere's CO_2 concentration), it appears plants will fare increasingly well as the air's CO_2 content continues to climb.

Kampichler *et al.* (2008) write, "since CO_2 enrichment alters the composition of live plant tissues, the ongoing global increase of atmospheric CO_2 concentration is expected to affect plant-animal interactions," but "systems studied so far have not included mature trees." They set out to determine "the abundance of dominant leaf-galls (spangle-galls induced by the cynipid wasps *Neuroterus* *quercusbaccarum* and *N. numismalis*) and leaf-mines (caused by the larvae of the moth *Tischeria ekebladella*) on freely colonized large oaks in a mixed forest in Switzerland, which received CO_2 enrichment [540 ppm vs. 375 ppm during daylight hours] from 2001 to 2004" by means of "the Swiss Canopy Crane (SCC) and a new CO_2 enrichment technique (web-FACE)" in a forest they describe as "80–120 years old with a canopy height of 32–38 m, consisting of seven deciduous and four coniferous species."

The German, Mexican and Swiss researchers report elevated CO_2 reduced various leaf parameters (water content, proteins, non-structural carbohydrates, tannins, etc.) at the SCC site, but "on the long term, their load with cynipid spangle-galls and leaf-mines of *T. ekebladella* was not distinguishable from that in oaks exposed to ambient CO_2 after 4 years of treatment." Kampichler *et al*. conclude, "CO_2 enrichment had no lasting effect in all three [animal] taxa, despite the substantial and consistent change in leaf chemistry of oak due to growth in elevated CO_2."

Rao *et al*. (2009) determined what foliage-mediated effects atmospheric CO_2 enrichment might have on another pernicious insect pest. They explain castor "is an important non-edible oilseed crop grown in many parts of the arid and semi-arid regions of India," and the castor semilooper (*Achaea janata*) and tobacco caterpillar (*Spodoptera litura*) "occur during early and late stages of growth of castor, respectively," when castor oil yields can be reduced "by 30–50% by the semilooper alone" and the tobacco caterpillar "can cause yield losses of 25–40%."

Rao *et al*. allowed larvae of both species to feed on castor foliage grown in present-day air (presumed to contain 350 ppm CO_2) and in air enriched with CO_2 to concentrations of 550 and 700 ppm. Their results indicate, "compared to the larvae fed on ambient CO_2 foliage, the larvae fed on 700 and 550 ppm CO_2 foliage exhibited greater consumption." However, the efficiency of conversion of both ingested and digested food into larval biomass "decreased in the case of larvae grown on 700 and 550 ppm CO_2 foliage," so they "grew slower and took longer time (two days more than ambient) to pupation," which would allow significantly more time (~13 percent) for them to be preyed upon by higher orders of creatures, many of which are considered to be much less of a threat to crop production than are insect larvae.

In the case of castor beans, then, it would appear in addition to the productivity enhancement likely to be provided by the stimulation of photosynthesis driven by atmospheric CO_2 enrichment—an approximate 34 percent increase in response to a 300 ppm increase in the air's CO_2 content (Grimmer and Komor, 1999; Grimmer *et al*., 1999)—a substantial increase in atmospheric CO_2 likely also would curtail yield losses currently caused by the castor semilooper and tobacco caterpillar.

Hillstrom *et al*. (2010) write, "natural forest systems constitute a major portion of the world's land area, and are subject to the potentially negative effects of both global climate change and invasion by exotic insects." They report, "a suite of invasive weevils has become established in the northern hardwood forests of North America," noting it is "unknown" how these insects will respond to continued increases in the air's CO_2 content.

Hillstrom *et al*. collected 200 mating pairs of *Polydrusus sericeus* weevils—which they describe as "the second most abundant invasive weevil species in northern hardwood forests"—from birch trees growing on the perimeter of the Aspen Face facility in Oneida County, Wisconsin (USA). They fed them leaves taken from the birch, aspen, and maple trees growing within either the facility's ambient-air rings or its CO_2-enriched rings (maintained at a target concentration of 560 ppm) under controlled laboratory conditions throughout the summer of 2007, while closely monitoring parameters affecting weevil longevity and fecundity.

According to the five researchers, all from the University of Wisconsin's Department of Entomology, the results indicate feeding the weevils with foliage produced on trees in the CO_2-enriched plots had no effect on male longevity, but it reduced female longevity by 19 percent. They also note, "*Polydrusus sericeus* egg production rate declined by 23% and total egg production declined by 29% for females fed foliage produced under elevated CO_2 compared with ambient CO_2."

Hillstrom *et al*. conclude, "concentrations of elevated CO_2 above 500 ppm have the potential to decrease *P. sericeus* populations by reducing female longevity and fecundity," which should be particularly beneficial for the northern hardwood forests of North America that are currently growing under atmospheric CO_2 concentrations of 390 ppm and rising.

The vast majority of pertinent experimental data suggest in the neverending battle between insect herbivores and the plants on whose foliage they feast, the ongoing rise in the air's CO_2 content likely plays an extremely important role in negating, and in some cases even more than negating, the damage otherwise capable of being done to Earth's vegetation by voracious insect pests.

References

Barbehenn, R.V., Karowe, D.N., and Chen, Z. 2004a. Performance of a generalist grasshopper on a C_3 and a C_4 grass: compensation for the effects of elevated CO_2 on plant nutritional quality. *Oecologia* **140**: 96–103.

Barbehenn, R.V., Karowe, D.N., and Spickard, A. 2004b. Effects of elevated atmospheric CO_2 on the nutritional ecology of C_3 and C_4 grass-feeding caterpillars. *Oecologia* **140**: 86–95.

Bernays, E.A. and Simpson, S.J. 1990. Nutrition. In: Chapman, R.F. and Joern, A. (Eds.) *Biology of Grasshoppers*. Wiley, New York, NY, pp. 105–127.

Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. *Oikos* **82**: 212–222.

Brooks, G.L. and Whittaker, J.B. 1999. Responses of three generations of a xylem-feeding insect, *Neophilaenus lineatus* (Homoptera), to elevated CO_2. *Global Change Biology* **5**: 395–401.

Docherty, M., Wade, F.A., Hurst, D.K., Whittaker, J.B., and Lea, P.J. 1997. Responses of tree sap-feeding herbivores to elevated CO_2. *Global Change Biology* **3**: 51–59.

Grimmer, C. and Komor, E. 1999. Assimilate export by leaves of *Ricinus communis* L. growing under normal and elevated carbon dioxide concentrations: the same rate during the day, a different rate at night. *Planta* **209**: 275–281.

Grimmer, C., Bachfischer, T., and Komor, E. 1999. Carbohydrate partitioning into starch in leaves of *Ricinus communis* L. grown under elevated CO_2 is controlled by sucrose. *Plant, Cell and Environment* **22**: 1275–1280.

Heagle, A.S. 2003. Influence of elevated carbon dioxide on interactions between *Frankliniella occidentalis* and *Trifolium repens*. *Environmental Entomology* **32**: 421–424.

Hillstrom, M.L., Vigue, L.M., Coyle, D.R., Raffa, K.F., and Lindroth, R.L. 2010. Performance of the invasive weevil *Polydrusus sericeus* is influenced by atmospheric CO_2 and host species. *Agricultural and Forest Entomology* **12**: 285–292.

Hinks, C.R., Cheeseman, M.T., Erlandson, M.A., Olfert, O., and Westcott, N.D. 1991. The effects of kochia, wheat and oats on digestive proteinases and the protein economy of adult grasshoppers, *Malanoplus sanguinipes*. *Journal of Insect Physiology* **37**: 417–430.

Holton, M.K., Lindroth, R.L., and Nordheim, E.V. 2003. Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO_2, O_3, and plant genotype. *Oecologia* **137**: 233–244.

Johns, C.V., Beaumont, L.J., and Hughes, L. 2003. Effects of elevated CO_2 and temperature on development and consumption rates of *Octotoma championi* and *O. scabripennis* feeding on *Lantana camara*. *Entomologia Experimentalis et Applicata* **108**: 169–178.

Kampichler, C., Teschner, M., Klein, S., and Korner, C. 2008. Effects of 4 years of CO_2 enrichment on the abundance of leaf-galls and leaf-mines in mature oaks. *Acta Oecologica* **34**: 139–146.

Kopper, B.J. and Lindroth, R.L. 2003. Responses of trembling aspen (*Populus tremuloides*) phytochemistry and aspen blotch leafminer (*Phyllonorycter tremuloidiella*) performance to elevated levels of atmospheric CO_2 and O_3. *Agricultural and Forest Entomology* **5**: 17–26.

Lambers, H. 1993. Rising CO_2, secondary plant metabolism, plant-herbivore interactions and litter decomposition. Theoretical considerations. *Vegetatio* **104/105**: 263–271.

Lincoln, D.E., Sionit, N., and Strain, B.R. 1984. Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. *Environmental Entomology* **13**: 1527–1530.

Lincoln, D.E., Couvet, D., and Sionit, N. 1986. Responses of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia* **69**: 556–560.

Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., and Karnosky, D.F. 2002. Altered performance of forest pests under atmospheres enriched by CO_2 and O_3. *Nature* **420**: 403–407.

Rao, M.S., Srinivas, K., Vanaja, M., Rao, G.G.S.N., Venkateswarlu, B., and Ramakrishna, Y.S. 2009. Host plant (*Ricinus communis* Linn.) mediated effects of elevated CO_2 on growth performance of two insect folivores. *Current Science* **97**: 1047–1054.

Simpson, S.J. and Simpson, C.L. 1990. The mechanisms of nutritional compensation by phytophagous insects. In: Bernays, E.A. (Ed.) *Insect-Plant Interactions*, Vol. 2. CRC Press, Boca Raton, FL, pp. 111–160.

Stiling, P. and Cornelissen, T. 2007. How does elevated carbon dioxide (CO_2) affect plant-herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology* **13**: 1–20.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2002. Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* DOI 10.1007/s00442-002-1075-5.

Stiling, P., Rossi, A.M., Hungate, B., Dijkstra, P., Hinkle, C.R., Knot III, W.M., and Drake, B. 1999. Decreased leaf-miner abundance in elevated CO_2: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* **9**: 240–244.

Valkama, E., Koricheva, J., and Oksanen, E. 2007. Effects of elevated O_3, alone and in combination with elevated CO_2, on tree leaf chemistry and insect herbivore performance: a meta-analysis. *Global Change Biology* **13**: 184–201.

Wand, S.J.E., Midgley, G.F., Jones, M.H., and Curtis, P.S. 1999. Responses of wild C_4 and C_3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* **5**: 723–741.

Whittaker, J.B. 1999. Impacts and responses at population level of herbivorous insects to elevated CO_2. *European Journal of Entomology* **96**: 149–156.

Yang, Y. and Joern, A. 1994a. Gut size changes in relation to variable food quality and body size in grasshoppers. *Functional Ecology* **8**: 36–45.

Yang, Y. and Joern, A. 1994b. Influence of diet quality, developmental stage, and temperature on food residence time in the grasshopper *Melanoplus differentialis*. *Physiological Zoology* **67**: 598–616.

Zanotto, F.P., Simpson, S.J., and Raubenheimer, D. 1993. The regulation of growth by locusts through post-ingestive compensation for variation in the levels of dietary protein and carbohydrate. *Physiological Entomology* **18**: 425–434.

5.6 Mammals

- The warming-induced extinctions of mammals that have been predicted to occur are highly unlikely to be realized in nature, and warming in fact opens new territories for mammal range expansions. In addition, rising atmospheric CO_2 concentrations may produce changes in the palatability of the trunk and branch tissues of certain trees that may protect them from being killed by hares and rabbits.

It has been projected global warming will lead to a mass demise, if not extinction, of species across Earth because they will not be able to migrate rapidly enough to keep up with the shifting climatic zones to which they are currently accustomed, or they will literally "run out of places to run," as in the case of mountain-top dwellers. As logical as that hypothesis might sound, more complex studies, such as the ones reviewed here, indicate it is wrong. Earth's plants and animals are not the simpletons the models often characterize them to be; they possess a wide array of strategies for coping with environmental change and re-colonizing former territories after having once been forced out of them.

Norment *et al.* (1999) summarized and compared the results of many surveys of mammal populations observed along the Thelon River and its tributaries in the Canadian Northwest Territories from the 1920s through much of the 1990s. Red squirrel, moose, porcupine, river otter, and beaver were found to have established themselves in the studied area in recent years, significantly increasing its biodiversity. Norment *et al.* suggest the primarily northward range expansions that produced these results may be explained by "a recent warming trend at the northern treeline during the 1970s and 1980s." Alternatively, they note the influx of new species also may be due to "increasing populations in more southerly areas." In either case, these several mammal species appear to be faring quite well, and perhaps thriving, in the face of increasing temperatures in this forest-tundra landscape.

Pockely (2001) report the results of a survey of the plants and animals on Australia's Heard Island, located some 4,000 kilometers southwest of Perth. Over the past 50 years this sub-Antarctic island has experienced a local warming of approximately 1°C that has resulted in a modest retreat of its glaciers; for the first time in a decade, scientists are documenting what this warming and melting has done to the ecology of the island. Pockley reports on the "rapid increases in flora and fauna" that have accompanied the warming, quoting Dana Bergstrom, an ecologist at the University of Queensland in Brisbane, as saying areas that previously were poorly vegetated are now "lush with large expanses of plants." He also notes populations of fur seals have expanded rapidly. He cites Eric Woehler of Australia's environment department as informing him fur seals have emerged from "near extinction" to a population of 28,000 adults and 1,000 pups.

Between these far-flung chilly regions (where warming would be expected to enhance the abilities of land mammals to survive and reproduce), Lawler (1998) examined biogeographic relationships of mammals typically found on mountaintops in the Great Basin of western North America, with the objective of determining their future well-being in the face of predicted climate-driven changes in their environment. Contrary to the conclusions of earlier, more simplistic studies that predicted dramatic global warming-induced reductions in the numbers of mammals in this region, Lawlor concludes "virtually no extinctions can be expected from a projected 3°C rise in temperature." The results of this study, as well as those of Grayson (2000) and Grayson and Madson (2000), stand in stark contrast to model-based extinction predictions.

Working with the entire population of about 325 red squirrels (*Tamiasciurus hudsonicus*) near Kluane Lake, Yukon (Canada), Reale *et al.* (2003) ear-tagged and monitored the reproductive activity of all females each year from 1989 to 2001, while identifying and similarly dealing with most of their young from birth to adulthood, and weather data were collected at a monitoring station located 50 km from their study site. In addition, noting "spruce cones stored in the autumn of a given year are an important source of food for reproductive females in the spring of the following year," they counted the number of cones on the top three meters of about 300 trees every August.

The four Canadian researchers report spring temperature rose by nearly 2°C over the course of their study, but there was "no particular trend for precipitation." They found the mean number of spruce cones available over a female's lifetime rose more than 35% over the 10 years of their observations, "a large increase in the abundance of food experienced by female squirrels." They also report the squirrels responded to these environmental changes by advancing breeding by 18 days over the 10-year study period, representing an advancement of six days per squirrel generation. Quoting Reale *et al.*, "this dramatic advancement in breeding comprised a plastic response to increased food abundance as well as a microevolutionary response to selection." Or as they write in the concluding sentence of their paper, "the combination of phenotypic changes within generations and microevolutionary changes among generations resulted in large phenotypic responses to rapid changes in environmental conditions experienced by this population of squirrels over the past ten years."

Mattson *et al.* (2004) grew one-year-old seedlings of silver birch trees in closed-top chambers for one summer and autumn in pots containing an unfertilized commercial peat maintained at three soil nitrogen levels and two temperature regimes in air of either 362 or 700 ppm CO_2. Feeding trials with caged Eurasian hares were carried out and a number of chemical analyses made of the tops of the seedlings and the basal parts of their stems. In a second experiment, they grew paper birch trees from seed for two 140-day growing seasons in well-watered and fertilized pots placed within FACE rings maintained at atmospheric CO_2 concentrations of either 362 or 562 ppm, after which (in an unplanned aspect of the study) North American eastern cottontail rabbits fed *ad libitum*, consuming bark tissue down to and scoring the wood, on the basal third of the seedlings, and these tissues were tested for the presence of various herbivore-deterring chemical constituents.

"As expected," the authors state, "elevated CO_2 substantially increased the above-ground woody biomass growth of both paper birch (63%) and silver birch (21%)." In addition, noting "numerous studies have shown that elevated atmospheric CO_2 often, but not always, elicits increases in carbon partitioning to carbon-based secondary plant compounds," which tend to act as deterrents to herbivory, they say their findings "confirm this general pattern in silver and paper birch." Finally, they report high CO_2 reduced hare feeding on silver birch shoots by as much as 48%, and it reduced rabbit feeding on paper birch stems by about 51%, while neither temperature nor severe early-season defoliation (another experimental treatment) affected tree resistance against these mammalian herbivores.

Calling the anti-herbivory effect of elevated CO_2 "remarkably strong," and noting rabbits "overwhelmingly preferred ambient CO_2 plants," Mattson *et al.* say their data "clearly suggest that the defensive biochemistry of paper birch twigs as well as the main stem were [positively] altered as the result of elevated CO_2."

Millar and Westfall (2010) studied American pikas, small generalist herbivores that are relatives of rabbits and hares, inhabit patchily distributed rocky slopes of western North American mountains, and are good at tolerating cold. Pikas are widely believed to have a physiological sensitivity to warming, which when "coupled with the geometry of decreasing area at increasing elevation on mountain peaks," in the words of the two scientists, "has raised concern for the future persistence of pikas in the face of climate change." They note the species "has been petitioned under California [USA] state and federal laws for endangered species listing."

In a study designed to investigate the validity of the basis for that classification, Millar and Westfall developed a rapid assessment method for determining pika occurrence and used it "to assess geomorphic affinities of pika habitat, analyze climatic relationships of sites, and evaluate refugium environments for pikas under warming climates." The researchers gathered data over two field seasons in the Sierra Nevada Mountains of California, the southwestern Great Basin of California and Nevada, and the central Great Basin of Nevada, as well as a small area in the central Oregon Cascades.

The two U.S. Forest Service researchers report, "whereas concern exists for diminishing range of pikas relative to early surveys, the distribution and extent in our study, pertinent to four subspecies and the Pacific southwest lineage of pikas, resemble the diversity range conditions described in early 20th-century pika records (e.g., Grinnell and Storer, 1924)." The lowest site at which they detected the current presence of pikas, at an elevation of 1,827 meters, "is below the historic lowest elevation of 2350 m recorded for the subspecies by Grinnell and Storer (1924) in Yosemite National Park; below the low elevation range limit for the White Mountains populations given by Howell (1924) at 2440 m; and below the lowest elevation described for the southern Sierra Nevada populations of 2134 m (Sumner and Dixon, 1953)." In addition, they write, "a similar situation occurred for another lagomorph of concern, pygmy rabbit (*Brachylagus idahoensis*), where a rapid assessment method revealed much wider distribution than had been implied from historic population databases or resurvey efforts (Himes and Drohan, 2007)."

Millar and Westfall thus conclude "pika populations in the Sierra Nevada and southwestern Great Basin are thriving, persist in a wide range of thermal environments, and show little evidence of extirpation or decline." Moreover, the documentation of a similar phenomenon operating among pygmy rabbits suggests still other animals also may be better able to cope with various aspects of climate change than we have been led to believe.

In a study of moose, Lowe *et al*. (2010) write, "intuitively, we would expect that a large northern ungulate with low tolerance for high temperatures would gradually be pushed out of the southern reaches of its range as the climate continues to warm and temperature conditions become increasingly unfavorable," because "persistent temperatures above the upper critical limit will suppress foraging time and consequently cause mass loss during the summer, and that this reduced condition could affect overwinter survival and productivity," citing Schwartz and Renecker (1998).

The authors "tested the hypothesis that climate limits the southern distribution of moose (*Alces alces*) by documenting space use and behavior of 36 females at the margin of the species' range in Ontario, Canada." They did this in 2006, 2007, and 2008 through the use of "global positioning system (GPS) telemetry to study their habitat use and movement," in an attempt "to document behavioral mechanisms indicative of adaptive responses to warm temperatures." This work was conducted during periods of the year when ambient temperatures frequently exceeded known critical thresholds (-5°C in winter and 14°C in summer) that had been demonstrated by Dussault *et al*. (2004) to induce heat stress in moose.

Lowe *et al*. "detected no differences in habitat use relative to thermoregulation thresholds," which they deemed to be particularly important during the summer, when they report the temperatures of all habitat classes greatly exceeded—by an average of 6°C, and by as much as 19°C in the first week of August 2006—the 14°C threshold for a large extent of the day and partially during the night. As a result, the three Canadian researchers conclude "moose in their southern range either ameliorate heat stress at a finer resolution than we measured or are more resilient to temperature than previously thought."

In a contemporaneous study, Garroway *et al*. (2010) write, "many species have responded to contemporary climate change through shifts in their geographic ranges," and "this could lead to increased sympatry [i.e., partially overlapping ranges] between recently diverged species, likely increasing the potential for hybridization." They further note this phenomenon "can be positive if it increases genetic variability and creates new gene combinations that increase the potential to adapt."

To test this hypothesis, between 2002 and 2004 Garroway *et al*. conducted more than 1,600 successful live-trappings of southern (*Glaucomys volans*) and northern (*Glaucomys sabrinus*) flying squirrels throughout portions of Ontario (Canada) and Pennsylvania (USA). From the hairs of these squirrels they extracted nuclear and mitochondrial DNA.

It already had been determined by Bowman *et al*. (2005) that *G. volans* had expanded its range from the south beginning in the mid–1990s in concert with a series of warm winters; the nine Canadian and U.S. researchers' new findings indicate "the expansion of *G. volans* north into the *G. sabrinus* range in Ontario has resulted in the formation of a new hybrid zone." In addition, their analyses suggest "the hybridization was recent, coinciding with the recent increase in sympatry." They state, to their knowledge "this is the first report of hybrid zone formation following a range expansion induced by contemporary climate change." These findings indicate yet another way in which living organisms can both physically (by shifting their ranges) and genetically (by hybridization) successfully confront the challenges global warming may present.

Coulson *et al*. (2011) write "environmental change has been observed to generate simultaneous responses in population dynamics, life history, gene frequencies, and morphology in a number of species." But they wonder, "how common are such eco-evolutionary responses to environmental change likely to be?" asking, "are they inevitable [and] do they require a specific type of change?"

The team of six researchers used theory and data obtained from a study of wolves in Yellowstone Park, which is located mostly in the U.S. state of Wyoming but also reaches into smaller parts of Montana and Idaho. They "used survival and reproductive success data, body weights, and genotype at the K locus (*CBD103*, a β-defensin gene that has two alleles and determines coat color), which were collected from 280 radio-collared wolves living in the park between 1998 and 2009." They note "body weight and genotype at the K locus vary across U.S. wolf populations" and both traits influence fitness, citing the studies of Schmitz and Kolenosky (1985), Anderson *et al*. (2009), and MacNulty *et al*. (2009).

The four researchers say their results "do reveal that, for Yellowstone wolves, (i) environmental change will inevitably generate eco-evolutionary responses; (ii) change in the mean environment will have more profound population consequences than changes in the environmental variance; and (iii) environmental change affecting different functions can generate contrasting eco-evolutionary dynamics," which suggests "accurate prediction of the consequences of environmental change will probably prove elusive."

The general principles Coulson *et al*. found to apply to Yellowstone wolves should clearly apply to all other animals as well, suggesting the "climate envelope" approach used to predict shifts in the ranges of Earth's many animal species—and sometimes their extinction—in response to IPCC-predicted global warming fails to accurately describe the way real animals respond to climate change in the real world.

Hof *et al*. (2012) note "it is supposed that the large expected climate change at high northern latitudes ... makes species in (sub)arctic regions particularly susceptible (Virkkala *et al*., 2008; Sala *et al*., 2000; Jetz *et al*., 2007), especially the European part of the (sub)arctic, since this region is the most geographically complex with the most infrastructure and great cultural, social, and political heterogeneity (Nilsson *et al*., 2010)." Hof *et al*. "assessed potential changes in the geographic distribution of all terrestrial mammal species currently present in (sub)arctic Europe," along with additional species that might possibly colonize the region from the south. They used "species distribution modeling, incorporating projections of future climate and vegetation, in order to provide a better insight into the magnitude of the risk mammal species are facing, and the potential community level changes they have to endure due to climate change."

"Contrary to expectation," the three Swedish researchers report their modeling of species distributions suggests "predicted climate change up to 2080 will favor most mammals presently inhabiting (sub)arctic Europe," and "no species is predicted to go extinct." Hof *et al*. conclude, "for most (sub)arctic mammals it is not climate change per se that will threaten them, but possible constraints on their dispersal ability and changes in community composition."

Canale *et al*. (2012) say, "understanding whether, and to what extent, females can flexibly adjust their energetic investment to reproduction according to unpredicted food shortages is essential to predict whether organisms could compensate climate changes by plastic phenotype adjustments," citing Bronson (2009), Moreno and Moller (2011), and Wingfield *et al*. (2011). The three researchers "experimentally tested the consequences of chronic-moderate and short-acute food shortages on the reproductive output of a small seasonally breeding primate, the grey mouse lemur (*Microcebus murinus*) under thermo-neutral conditions," where "two food treatments were respectively designed to simulate the energetic constraints imposed by a lean year (40% caloric restriction over eight months) or by a sudden, severe climatic event occurring shortly before reproduction (80% caloric restriction over a month)." During this time they "assessed the resilience of the early stages of reproduction (mating success, fertility, and gestation to these contrasted food treatments, and on the later stages (lactation and offspring growth) in response to the chronic food shortage only."

They found "food deprived mouse lemurs managed to maintain constant ... reproductive parameters, including oestrus timing, estrogenization level at oestrus, mating success, litter size, and litter mass as well as their overall number of surviving offspring at weaning," although "offspring growth was delayed in food restricted mothers." The three researchers say their results suggest "heterothermic, fattening-prone mammals display important reproductive resilience to energetic bottlenecks," and "more generally, species living in variable and unpredictable habitats may have evolved a flexible reproductive physiology that helps buffer environmental fluctuations."

Tveraa *et al*. (2013) write, "for caribou in Greenland earlier springs have been suggested to result in a lower reproductive success," based on the assumption "*Rangifer* (caribou/reindeer) might be unable to adjust their timing of reproduction to the earlier surge of high quality food," and this potential failure could "cause a mismatch between optimal forage conditions and the timing of reproduction." Therefore, they state, "concerns have been raised regarding the future viability of *Rangifer* in Arctic and sub-Arctic tundra ecosystems."

Tveraa *et al*. "analyzed a 10-year dataset of satellite derived measures of vegetation green-up, population densities, calf body masses and female reproductive success in 19 reindeer (*Rangifer tarandus*) populations in Northern Norway." The four Norwegian researchers report "an early onset of spring and high peak plant productivity had positive effects on calf autumn body masses and female reproductive success," and "the quantity of food available, as determined by the onset of vegetation green-up and plant productivity over the summer, were the main drivers of body mass growth and reproductive success." Hence, they found no evidence for a negative effect of the speed of spring green-up, nor did they detect "a negative mismatch between early springs and subsequent recruitment." Tveraa *et al*. conclude the "effects of global warming on plant productivity and onset of spring are likely to positively affect sub-Arctic reindeer."

The studies presented above show the warming-induced extinctions of mammals that have been predicted to occur are highly unlikely to be realized in nature, and warming in fact opens new territories for mammal range expansions. In addition, rising atmospheric CO_2 concentrations may produce changes in the palatability of the trunk and branch tissues of certain trees that may protect them from being killed by hares and rabbits.

References

Anderson, T.M., vonHoldt, B.M., Candille, S.I., Musiani, M., Greco, C., Stahler, D.R., Smith, D.W., Padhukasahasram, B., Randi, E., Leonard, J.A., Bustamante, C.D., Ostrander, E.A., Tang, H., Wayne, R.K, and Barsh, G.S. 2009. Molecular and evolutionary history of melanism in North American gray wolves. *Science* **323**: 1339–1343.

Bowman, J., Holloway, G.L., Malcolm, J.R., Middel, K.R., and Wilson, P.J. 2005. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Canadian Journal of Zoology* **83**: 1486–1494.

Bronson, F.H. 2009. Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences* **364**: 3331–3340.

Canale, C.I., Huchard, E., Perret, M., and Henry, P.-Y. 2012. Reproductive resilience to food shortage in a small heterothermic primate. *PLoS ONE* **7**: 10.1371/journal.pone.0041477.

Coulson T., MacNulty, D.R., Stahler, D.R., vonHoldt, B., Wayne, R.K., and Smith, D.W. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science* **334**: 1275–1278.

Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton L., and Larochelle, J. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* **11**: 321–328.

Garroway, C.J., Bowman, J., Cascaden, T.J., Holloway, G.L., Mahan, C.G., Malcolm, J.R., Steele, M.A., Turner, G., and Wilson, P.J. 2010. Climate change induced hybridization in flying squirrels. *Global Change Biology* **16**: 113–121.

Grayson, D.K. 2000. Mammalian responses to Middle Holocene climatic change in the Great Basin of the western United States. *Journal of Biogeography* **27**: 181–192.

Grayson, D.K. and Madson, D.B. 2000. Biogeographic implications of recent low-elevation recolonization by *Neotoma cinerea* in the Great Basin. *Journal of Mammalogy* **81**: 1100–1105.

Grinnell, J. and Storer, T.I. 1924. *Animal Life in the Yosemite*. Berkeley, CA: University of California Press.

Himes, J.G. and Drohan, P.J. 2007. Distribution and habitat selection of the pygmy rabbit, *Brachylagus idahoensis*, in Nevada (USA). *Journal of Arid Environments* **68**: 371–382.

Hof, A.R., Jansson, R., and Nilsson, C. 2012. Future climate change will favor non-specialist mammals in the (Sub)Arctics. *PLOS ONE*: 10.1371/journal.pone.0052574.

Howell, A.H. 1924. *Revision of the American Pikas*. North American Fauna No. 47. Washington, DC: USDA Bureau of Biological Survey.

Jetz, W., Wilcove, D., and Dobson, A. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* **5**: 1211–1219.

Lawlor, T.E. 1998. Biogeography of great mammals: Paradigm lost? *Journal of Mammalogy* **79**: 111–1130.

Lowe, S.J., Patterson, B.R., and Schaefer, J.A. 2010. Lack of behavioral responses of moose (*Alces alces*) to high ambient temperatures near the southern Periphery of their range. *Canadian Journal of Zoology* **88**: 1032–1041.

MacNulty, D.R., Smith, D.W., Mech, L.D., and Eberly, L.E. 2009. Body size and predatory performance in wolves: is bigger better? *Journal of Animal Ecology* **78**: 532–539.

Mattson, W.J., Kuokkanen, K., Niemela, P., Julkunen-Tiitto, R., Kellomaki, S., and Tahvanainen, J. 2004. Elevated CO_2 alters birch resistance to Lagomorpha herbivores. *Global Change Biology* **10**: 1402–1413.

Millar, C.I. and Westfall, R.D. 2010. Distribution and climatic relationships of the American Pika (*Ochotona princeps*) in the Sierra Nevada and Western Great Basin, U.S.A.: periglacial landforms as refugia in warming climates. *Arctic, Antarctic, and Alpine Research* **42**: 76–88.

Moreno, J. and Moller, A.P. 2011. Extreme climatic events in relation to global change and their impact on life histories. *Current Zoology* **57**: 375–389.

Nilsson, C., Jansson, R., Keskitalo, E.C.H., Vlassova, T., Sutinen, M.L., Moen, J., and Chapin III, F.S. 2010. Challenges to adaptation in northernmost Europe as a result of global climate change. *AMBIO* **39**: 81–84.

Norment, C.J., Hall, A., and Hendricks, P. 1999. Important bird and mammal records in the Thelon River Valley, Northwest Territories: Range expansions and possible causes. *The Canadian Field-Naturalist* **113**: 375–385.

Pockely, P. 2001. Climate change transforms island ecosystem. *Nature* **410**: 616.

Reale, D., McAdam, A.G., Boutin, S., and Berteaux, D. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society B* **270**: 591–596.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**: 1770–1774.

Schmitz, O.J. and Kolenosky, G.B. 1985. Wolves and coyotes in Ontario: morphological relationships and origins. *Canadian Journal of Zoology* **63**: 1130–1137.

Schwartz, C.C. and Renecker, L.A. 1998. Nutrition and energetics. In Franzmann, A.W. and Schwartz, C.C. (Eds.) *Ecology and Management of the North American Moose*. Washington, DC: Smithsonian Institution, pp. 441–478.

Sumner, L. and Dixon, J.S. 1953. *Birds and Mammals of the Sierra Nevada*. Berkeley, Ca: University of California Press.

Tveraa, T., Stien, A., Bardsen, B.-J., and Fauchald, P. 2013. Population densities, vegetation green-up, and plant productivity: Impacts on reproductive success and juvenile body mass in reindeer. *PLoS ONE* **8**: 10.1371/journal.pone.0056450.

Virkkala, R., Heikkinen, R.K., Leikola, N., and Luoto, M. 2008. Projected large-scale range reductions of northern-boreal land bird species due to climate change. *Biological Conservation* **141**: 1343–1353.

Wingfield, J.C., Kelley, J.P., and Angelier, F. 2011. What are extreme environmental conditions and how do organisms cope with them? *Current Zoology* **57**: 363–374.

5.7 Parasites and Other Diseases

One of the perceived great tragedies of CO_2-induced global warming is that rising temperatures will increase the development, transmission, and survival rates of parasites and other diseases in general, leading to biological interactions that will raise the prevalence of disease among animals in the future. This section examines that claim.

In a provocative paper analyzing the intricacies of this complex issue, Hall *et al.* (2006) begin by asking, "Will an increasingly warmer world necessarily become a sicker world?" They pose this question because "increased temperatures can accelerate the fitness of parasites, reduce recruitment bottlenecks for parasites during winter, and weaken hosts," and "warmer temperatures may allow vectors of parasites to expand their range," which would enable them to "introduce diseases to novel habitats," which is frequently claimed about mosquitoes and malaria (see Section 7.2, this volume). They continue, "these doom-and-gloom scenarios do not necessarily apply to all taxa or all situations," and "warming does not necessarily increase the fitness of all parasites."

The four biologists and their statistician coauthor note the "virulence of parasites may not change, may decrease, or may respond unimodally to increasing temperatures (Stacey *et al*., 2003; Thomas and Blanford, 2003)." They also observe, "vital rates increase with temperature until some optimum is reached," and "once temperature exceeds this optimum, vital rates decline gradually with increasing temperature for some taxa, but rapidly for others," such that "in some host-parasite systems, a parasite's optimum occurs at cooler temperatures than the optimum of its host," citing Carruthers *et al*. (1992), Blanford and Thomas (1999), and Blanford *et al*. (2003) on fungus-grasshopper associations. In such cases, "a host can use warmer temperatures to help defeat its parasites through behavioral modification of its thermal environment."

The situation sometimes can be even more complex than this: "warmer temperatures can also lead to shifts in temperature optima (Huey and Hertz, 1984; Huey and Kingsolver, 1989, 1993)," and "the exact evolutionary trajectory of host-parasite systems in a warmer world may depend sensitively upon underlying genetic correlation structures and interactions between host genotypes, parasite genotypes, and the environment (Blanford *et al*., 2003; Thomas and Blanford, 2003; Stacey *et al*., 2003; Mitchell *et al*., 2004)." Consequently, they conclude, "longer-term response of the physiology of host-parasite systems to global warming becomes difficult to predict."

The researchers also note "other species can profoundly shape the outcome of parasitism in host populations," and "predators provide an important example" because predators "can actually inhibit epidemics by selectively culling sick hosts and/or by maintaining host densities below levels required for parasites to persist (Hudson *et al*., 1992; Packer *et al*., 2003, Lafferty, 2004; Ostfeld and Holt, 2004; Duffey *et al*., 2005; Hall *et al*., 2005)." Therefore, Hall *et al*. conclude, "global warming does not necessarily mean that disease prevalence will increase in all systems."

Morgan and Wall (2009) echo many of the salient points raised in the Hall *et al*. paper and further elucidate the complex nature of this topic. With respect to the relationship between temperature and parasitic development, the two authors note, "just as development rates of many parasites of veterinary importance increase with temperature, so [too] do their mortality rates [increase]." They reiterate, "temperature will also affect mortality indirectly through the action of predators, parasitoids, pathogens and competitors, whose development and abundance are also potentially temperature sensitive," so "the net effect of climate change could be complex and far from easily predicted."

The two UK researchers suggest "several biological mechanisms (including increased parasite mortality and more rapid acquisition of immunity), in tandem with changes in husbandry practices (including reproduction, housing, nutrition, breed selection, grazing patterns and other management interventions), might act to mitigate increased parasite development rates, preventing dramatic rises in overall levels of diseases." Because "optimum mitigation strategies will be highly system specific and depend on detailed understanding of interactions between climate, parasite abundance, host availability and the cues for and economics of farmer intervention," they conclude "there is a need for research that considers likely effects of climate change and mitigation strategies in terms of the whole host-parasite system, including anthropogenic responses, and not just in terms of parasite population dynamics." One year later, two such papers were published, both attempting to account for the response of human behavior on parasite abundance and disease incidence.

Focusing on cutaneous myiasis (blowfly strike) in sheep, Wall and Ellse (2011) employed a stochastic simulation model "to examine the changes in the seasonal incidence of ovine cutaneous myiasis on farms in the United Kingdom and the likely effects of changes in husbandry and control strategies" in the face of projected changes in climate. The authors note "the ability of this model to successfully account for observed patterns of strike has been confirmed previously by comparison of predicted with observed strike incidence patterns observed on 370 farms in England and Wales," citing Wall *et al*. (2002).

The two UK researchers report, "the simulations show that the range of elevated temperatures predicted by current climate change scenarios result in an elongated blowfly season with earlier spring emergence and a higher cumulative incidence of strike," and "overall, higher temperatures increased strike incidence disproportionately in ewes in early summer, but had relatively less direct effect on the pattern of lamb strike incidence," noting "a 3°C increase in average temperature approximately doubles the cumulative incidence of strike in lambs but results in four times more strikes in ewes." However, as the researchers conclude in the abstract of their paper, "the simulations suggest that integrated changes in husbandry practices are likely to be able to manage expected increases in strike, given the range of climate changes currently predicted." They explain in the body of the paper, "modest changes in husbandry practices should be able to manage expected increases in strike, under the range of climate changes currently predicted," demonstrating "consideration of the likely impact of climate change must take into account animal management practices as well as parasite biology (Morgan and Wall, 2009)."

Working with two additional co-authors on the same host and parasite, Wall *et al*. (2011) came to a similar conclusion, reporting, "the models suggest that simple changes in some husbandry practices, such as shearing or trap use, could have an important effect in reducing early season ewe strike incidences," and "practical measures exist which, with modest changes in husbandry practices, should be able to manage expected increases in strike." The key message of this latter work is the authors' conclusion that "simple extrapolations of the known effects of temperature on ectoparasite development," in an attempt to "predict changes in disease incidence in a warmer climate," is simply "too simplistic." They emphasize "attempts to predict the likely impact of climate change on disease incidence must take into account changes in farmer behavior and animal management practices as well as parasite biology."

Baffoe *et al*. (2012) write, "with the prospect of warmer temperatures as a consequence of ongoing climate change, it is important to investigate how such increases will affect parasitoids and their top-down suppression of herbivory in agroecosystems." They studied a parasitoid that afflicts a common beetle that feeds on several short-rotation species of commercially coppiced willow trees in northern and central Europe, a trophic cascade described in more detail by Peacock *et al*. (1999), Bjorkman *et al*. (2003), and Dalin (2011). Baffoe *et al*. conducted laboratory experiments in which they "studied how the performance and biocontrol efficiency of the willow 'bodyguard' *Perilitus brevicollis* Haliday (Hymenoptera: Braconidae) were affected at different constant temperatures (10, 15, 20, 25°C) when parasitizing a pest insect, the blue willow beetle (*Phratora vulgatissima* L., Coleoptera: Chrysomelidae)." They did this by focusing on "the parasitoid's thermal threshold for development, development rate, adult body size, survival rate and the herbivore's consumption rate."

The four Swedish scientists report parasitism had no impact on herbivory at 10°C, but "parasitoid performance (survival and development rate) generally increased with increasing temperature up to 20°C." In addition, "the feeding capacity of the studied parasitized herbivores is reduced more at high than low temperatures." Thus, "these data suggest that *P. brevicollis* should become a better biocontrol agent if temperatures increase," a transformation that should have substantial positive consequences for willow trees in northern and central Europe, as well as for the enterprise of their commercial harvesting.

Bentley and Burgner (2011) examined the host/parasite relationship between juvenile sockeye salmon (*Oncorhynchus nerka*) and the tapeworm *Triaenophorus crassus* in an Alaskan watershed that had experienced a 1.9°C increase in summer water temperature over the prior 46 years. At the beginning of their experiment, Bentley and Burgner hypothesized the warming of the region "would have resulted in a corresponding increase in fish metabolism, and thus potential consumption rates, that would increase infestation rates of the tapeworm *Triaenophorus crassus*." To test their hypothesis, they compared infestation rate data for *T. crassus* collected between 1948 and 1960 with similar data obtained in 2008 and 2009 from the Wood River system of Bristol Bay, Alaska.

The two U.S. researchers from the University of Washington's School of Aquatic and Fishery Sciences report, "comparing the average summer air temperature to the parasite prevalence of juvenile sockeye salmon, we found no significant relationship over the fifteen years of collected data." Moreover, "evaluating the influence of average summer air temperature on the parasite infestation rates of juvenile sockeye salmon, we again found no significant relationship for either parasite abundance or parasite intensity." They note, "when we compared the 13 years of historic parasite prevalence to equivalent data collected in 2008 and 2009, we did not find a statistically significant positive long-term trend in the data," and "the parasite abundance of examined sockeye salmon smolts also did not exhibit a statistically significant long-term trend using the eight years of historic data and the two years of contemporary data." Finally, "evaluating the relationship between time and parasite intensity produced similar results as the other five comparisons, with there not being a statistically significant positive relationship."

Bentley and Burgner conclude their data demonstrate "the complex effects of warming have not summed to generate a measurable change in the infestation rates of juvenile sockeye salmon in the Wood River system." Given the many factors involved in host/parasite interrelationships, together with their great complexities, it is quite possible global warming will never significantly impact parasite infestation rates in the animals they attack.

Shifting from parasites to infectious diseases, Kampen and Werner (2010) write, "with few exceptions, vector-borne diseases have long been considered of minor importance in central and northern Europe." However, they note, "since the advent of bluetongue disease (BTD) in 2006, and the 2007 chikungunya fever outbreak in Italy, this attitude has changed." Focusing on BTD, a non-contagious insect-borne viral disease of ruminants (mainly sheep, but also affecting antelope, buffalo, cattle, deer, dromedaries, and goats) caused by the bluetongue virus (BTV), Kampen and Werner describe what is known about the outbreak of this serious animal disease in central Europe.

The two German researchers report "BTD was the first 'exotic' disease to arrive," but "it did not slowly spread northwards but jumped in through a still unknown entry point." It all started, as they describe it, "with about 2000 affected ruminant farming facilities in 2006 in the central western part of Europe," where the BTV–8 virus—which they say "had never been observed in Europe before," and for which DNA sequencing data suggested sub-Saharan Africa as its most likely point of origin—"managed to overwinter and spread in all directions in 2007, producing almost 60,000 outbreaks (farms affected) in ten European countries up to early 2008." And now, they say, the BTV–1 virus strain "appears to be approaching from the south, with some 4900 outbreaks in France in 2008," reiterating, "nobody had expected a novel and independent virus introduction into central Europe together with indigenous biting midges able to transmit BTV."

As for possible routes of introduction of the virus, they mention BTV-positive ruminants imported either legally or illegally, virus-carrying midges transported by wind over hundreds of kilometers, accidental importation by ship or aircraft, contaminated vaccines, and trade with the products of infected animals.

Kampen and Werner conclude, "it is due to continuing globalization rather than to climate change that even central and northern Europe are at risk of new pathogens as well as vectors of disease entering and establishing."

Conte *et al*. (2009) note, "the midge *Culicoides imicola* is the principal vector of bluetongue virus (BTV) that causes an infectious disease of domestic and wild ruminants," and "over the last ten years, BTV has invaded Mediterranean countries and much of Northern Europe," inducing several scientists to contend the BTV vector had expanded its range northward "because of rising temperatures," as suggested by Mellor (2004), Purse *et al*. (2005), and Mellor *et al*. (2008). However, Goffredo *et al*. (2003) made a careful examination of *Culicoides* population data in Italy prior to 2000 and determined "trapping conditions of previous collections would have had very little chance of catching *C. imicola*" or detecting its presence, suggesting there was insufficient evidence for a warming-induced northward expansion of the BTV vector because it already may already been present there but undetected.

In response to even earlier fears of a potential BTV invasion, a national surveillance program for *C. imicola* had been established in Italy in 2000, where 70,000 light-trap collections were made at about 3,800 sites. Using the first year of data obtained from this program, Conte *et al*. defined the spatial distributions of three *C. imicola* infection zones: zone I (endemicity), zone II (transition), and zone III (absence). Using data from 2002–2007, they quantified how *C. imicola* populations evolved through time in these three zones, working under the logical assumption that "a species that is undergoing geographical range expansion should have a population that remains stable over time in zone I and increases in zones II and III."

The three researchers say their results indicate there was "no detectable range expansion of *C. imicola* population in Italy over the past six years." They report "a weak, but significant reduction was observed in the transition zone." Conte *et al*. therefore conclude their data "support the hypothesis that the spread of BTV in Italy is not because of the geographical expansion of its main vector, but to a modification of the interaction between the virus, the vector and the environment, as may also have been the case in northern Europe." They say their results show "precautions should be taken when inferring range progression for species requiring highly targeted forms of sampling and for which a constant probability of detection over time should be established." This research demonstrates it is easy to blame global warming for the poleward expansion of a vector-spread disease, but quite another thing to prove that claim.

References

Baffoe, K., Dalin, P., Nordlander, G., and Stenberg, J.A. 2012. Importance of temperature for the performance and biocontrol efficiency of the parasitoid *Perilitus brevicollis* (Hymenoptera: Braconidae) on *Salix*. *BioControl* **57**: 611–618.

Bentley, K.T. and Burgner, R.L. 2011. An assessment of parasite infestation rates of juvenile sockeye salmon after 50 years of climate warming in southwest Alaska. *Environmental Biology of Fishes* **92**: 267–273.

Bjorkman, C., Dalin, P., and Eklund, K. 2003. Generalist natural enemies of a willow leaf beetle (*Phratora vulgatissima*): abundance and feeding habits. *Journal of Insect Behavior* **16**: 747–764.

Blanford, S. and Thomas, M.B. 1999. Host thermal biology: the key to understanding host-pathogen interactions and microbial pest control? *Agricultural and Forest Entomology* **1**: 195–202.

Blanford, S., Thomas, M.B., Pugh, C., and Pell, J.K. 2003.

Temperature checks the Red Queen: Resistance and virulence in a fluctuating environment. *Ecology Letters* **6**: 2–5.

Carruthers, R.I., Larkin, T.S., Firstencel, H., and Feng, Z. 1992. Influences of thermal ecology on the mycosis of a rangeland grasshopper. *Ecology* **73**: 190–204.

Conte, A., Gilbert, M., and Goffredo, M. 2009. Eight years of entomological surveillance in Italy show no evidence of *Culicoides imicola* geographical range expansion. *Journal of Applied Ecology* **46**: 1332–1339.

Dalin, P. 2011. Diapause induction and termination in a commonly univoltine leaf beetle (*Phratora vulgatissima*). *Insect Science* **18**: 443–450.

Duffy, M.A., Hall, S.R., Tessier, A.J., and Huebner, M. 2005. Selective predators and their parasitized prey: top-down control of epidemics. *Limnology and Oceanography* **50**: 412–420.

Goffredo, M., Conte, A., Cocciolito, R., and Meiswinkel, R. 2003. Distribution and abundance of *Culicoides imicola* in Italy. *Veterinaria Italiana* **47**: 22–32.

Hall, S.R., Duffy, M.A., and Caceres, C.E. 2005. Selective predation and productivity jointly drive complex behavior in host-parasite systems. *American Naturalist* **180**: 70–81.

Hall, S.R., Tessier, A.J., Duffy, M.G., Huebner, M., and Caceres, C.E. 2006. Warmer does not have to mean sicker: temperature and predators can jointly drive timing of epidemics. *Ecology* **87**: 1684–1695.

Hudson, P.J., Dobson, A.P., and Newborn, D. 1992. Do parasites make prey vulnerable to predation? Red Grouse and parasites. *Journal of Animal Ecology* **61**: 681–692.

Huey, R.B. and Hertz, P.E. 1984. Is a jack-of-all-temperatures a master of none? *Evolution* **38**: 441–444.

Huey, R.B. and Kingsolver, J.G. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology and Evolution* **4**: 131–135.

Huey, R.B. and Kingsolver, J.G. 1993. Evolution of resistance to high temperature in ectotherms. *American Naturalist* **142**: S21-S46.

Kampen, H. and Werner, D. 2010. Three years of bluetongue disease in central Europe with special reference to Germany: what lessons can be learned? *Wiener Klinische Wochenschrift* **122** (Suppl. 3): 31–39.

Lafferty, K.D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecological Applications* **14**: 1566–1573.

Mellor, P.S. 2004. Infection of the vectors and bluetongue epidemiology in Europe. *Veterinaria Italiana* **40**: 167–174.

Mellor, P.S., Carpenter, S., Harrup, L, Baylis, M., and Mertens, P.P.C. 2008. Bluetongue in Europe and the Mediterranean Basin: History of occurrence prior to 2006. *Preventive Veterinary Medicine* **87**: 4–20.

Mitchell, S.E., Halves, J., and Lampert, W. 2004. Coexistence of similar genotypes of *Daphnia magna* in intermittent populations: response to thermal stress. *Oikos* **106**: 469–478.

Morgan, E.R. and Wall, R. 2009. Climate change and parasitic disease: farmer mitigation? *Trends in Parasitology* **25**: 308–313.

Ostfeld, R.S. and Holt, R.D. 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. *Frontiers in Ecology and the Environment* **2**: 13–20.

Packer, C., Holt, R.D., Hudson, P.J., Lafferty, K.D., and Dobson, A.P. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecology Letters* **6**: 797–802.

Peacock, L., Herrick, S., and Brain, P. 1999. Spatio-temporal dynamics of willow beetle (*Phratora vulgatissima*) in short-rotation coppice willows grown as monocultures or a genetically diverse mixture. *Agricultural and Forest Entomology* **1**: 287–296.

Purse, B.V., Mellor, P.S., Rogers, D.J., Samuel, A.R., Mertens, P.P.C., and Baylis, M. 2005. Climate change and the recent emergence of bluetongue in Europe. *Nature Reviews Microbiology* **3**: 171–181.

Stacey, D.A., Thomas, M.B., Blanford, S., Pell, J.K., Pugh, C., and Fellowes, M.D. 2003. Genotype and temperature influence pea aphid resistance to a fungal entomopathogen. *Physiological Entomology* **28**: 75–81.

Thomas, M.B. and Blanford, S. 2003. Thermal biology in insect-parasite interactions. *Trends in Ecology and Evolution* **18**: 344–350.

Wall, R., Cruickshank, I., Smith, K.E., French, N.P., and Holme, A.S. 2002. Development and validation of a simulation model for sheep blowfly strike. *Medical and Veterinary Entomology* **16**: 335–346.

Wall, R. and Ellse, L.S. 2011. Climate change and livestock parasites: integrated management of sheep blowfly strike in a warmer environment. *Global Change Biology* **17**: 1770–1777.

Wall, R., Rose, H, Ellse, L., and Morgan, E. 2011. Livestock ectoparasites: Integrated management in a changing climate. *Veterinary Parasitology* **180**: 82–89.

5.8 Polar Bears

- Polar bears have survived historic changes in climate that have exceeded those of the twentieth century or are forecast by computer models to occur in the future. In addition, some populations of polar bears appear to be stable despite rising temperatures and summer sea ice declines. The biggest threat they face is not from global warming, but commercial hunting by humans, which has historically taken a huge toll on polar bear populations.

In its contribution to IPCC's *Fourth Assessment Report*, Working Group II claimed global warming is "inducing declining survival rates, smaller size, and cannibalism among polar bears" (IPCC, 2007-II). It predicted a bleak future for the species if atmospheric CO_2 concentrations continue to rise. However, polar bears have survived historic changes in climate that have exceeded those of the twentieth century or are forecast by computer models to occur in the future. In addition, some populations of polar bears appear to be stable despite rising temperatures and summer sea ice declines. The biggest threat they face is not from global warming, but commercial hunting by humans, which has historically taken a huge toll on polar bear populations.

Polar bears evolved from brown bears (*Ursus arctos*). While it was formerly thought this speciation event occurred sometime in the past 400,000 years and probably no more than 200,000 years ago (Arnason *et al.*, 1995; Davis *et al.,* 2008; Harington, 2008), that picture has now changed. The oldest polar bear fossil ever found (dated to 110,000–130,000 years old) was reported in 2008 (Ingolfsson *et al.*, 2008) and a complete mitochondrial DNA (mtDNA) sequence of it was generated two years later (Lindqvist *et al.,* 2010). This discovery spawned a suite of papers on polar bear genetics that fail to agree when polar bears arose as a distinct species: Edwards *et al.* (2011) suggest a possible range of 400,000 to two million years ago; Hailer *et al.* (2012), suggest a date of about 600,000 years ago; and Miller *et al.* (2012), suggest this event occurred four to five million years ago.

Although there is some disagreement about the onset of this species, it is clear that because the oldest polar bear fossil is at least 110,000–130,000 years old, polar bears have survived at least one glacial-interglacial cycle and perhaps as many as 10 or more.. Focusing on the last major interglacial (MIS 5e, the Eemian, which lasted from ca. 130,000–115,000 years ago), there not only appears to have been less winter Arctic ice than today (including no ice in the Bering Sea), but late summer ice was reduced to a remnant off northern Greenland and Ellesmere Island (Polyak *et al.,* 2010). During the current interglacial, or Holocene, there were at least two warm periods (the Early Holocene Climatic Optimum and the Medieval Warm Period) when sea ice was less extensive than it is now (Atkinson, 2009; Dyke and England, 2003; Dyke *et al.,* 1996; Kaufman *et al.,* 2004; Polyak *et al.,* 2010; Steffensen *et al.,* 2008).

Polar bears obviously survived large-scale and often sudden climate changes in the historic past, such as those described above. This does not mean their populations remained constant throughout this period; their numbers likely rose in some periods and declined in others. But past changes in climate have not led to their extinction, which leads to the question: Why would temperature changes predicted to be of the same scale or less than those that occurred in the past be projected to cause a near-future extinction of polar bears?

In order to ascertain whether there are indeed risks to polar bears from model-predicted increases in global temperature and associated sea ice decline, researchers have examined various aspects of polar bear population dynamics and life history traits as they relate to temperature changes that have taken place over the past 30 years. Several of their findings are presented in the subsections below, where it is seen that polar bears are well-equipped to adapt with the challenges they may face as a result of any CO_2-induced global warming.

References

Arnason, U., Bodin, K., Gullberg, A., Ledje, C., and Mouchaty, S. 1995. A molecular view of pinniped relationships with particular emphasis on the true seals. *Journal of Molecular Evolution* **40**: 78–85.

Atkinson, N. 2009. A 10400-year-old bowhead whale (*Balaena mysticetus*) skull from Ellef Ringnes Island, Nunavut: implications for sea-ice conditions in high Arctic Canada at the end of the last glaciation. *Arctic* **62:** 38–44.

Davis, C.S., Stirling, I., Strobeck, C., and Coltman, D.W. 2008. Population structure of ice-breeding seals. *Molecular Ecology* **17**: 3078–3094.

Dyke, A.S. and England, J.H. 2003. Canada's most northerly postglacial bowhead whales (*Balaena mysticetus*): Holocene sea-ice conditions and polynya development. *Arctic* **56:**14–20.

Dyke, A.S., Hooper, J., and Savelle, J. M. 1996. A history of sea ice in the Canadian Arctic Archipelago based on postglacial remains of bowhead whale (*Balaena mysticetus*). *Arctic* **49:** 235–255.

Edwards, C.J., Suchard, M.A., Lemey, P., Welch, J.J., Barnes, I., Fulton, T.L., Barnett, R., O'Connell, T.C., Coxon, P., Monoghan, N., Valdiosera, C.E., Lorenzen, E.D., Willerslev, E., Baryshnikov, G.F., Rambaut, A., Thomas, M.G., Bradley, D.G., and Shapiro, B. 2011. Ancient hybridization and an Irish origin for the modern polar bear matriline. *Current Biology* **21**: 1251–1258.

Hailer, F., Kutschera, V.E., Hallstrom, B.M., Klassert, D., Fain, S.R., Leonard, J.A., Arnason, U., and Janke, A. 2012. Nuclear genomic sequences reveal that polar bears are an old and distinct bear lineage. *Science* **336**: 344–347.

Harington, C.R. 2008. The evolution of Arctic marine mammals. *Ecological Applications* **18** : S23-S40.

Ingolfsson, Ó. and Wiig, Ø. 2008 Late Pleistocene fossil find in Svalbard: the oldest remains of a polar bear (*Ursus maritiumus* Phipps, 1744) ever discovered. *Polar Research* **28:**455–462.

IPCC. 2007-II. *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., and Hanson, C.E. (Eds.) Cambridge University Press, Cambridge, UK.

Kaufman, D.S., Ager, T.A., Anderson, N.J., Anderson, P.M., Andrews, J.T., Bartlein, P.J., Brubaker, L.B., Coats, L.L., Cwynar, L.C., Duvall, M.L., Dyke, A.S., Edwards, M.E, Eisner, W.R., Gajewski, K., Geirsdóttir, A., Hu, F.S., Jennings, A.E., Kaplan, M.R., Kerwin, M.W., Lozhkin, A.V., MacDonald, G.M., Miller, G.H., Mock, C.J., Oswald, W.W., Otto-Bliesner, B.L., Porinchu, D.F., Rühland, K., Smol, J.P., Steig, E.J., and Wolfe, B.B. 2004. Holocene thermal maximum in the western Arctic (0–180°W). *Quaternary Science Reviews* **23:** 529–560.

Lindqvist, C., Schuster, S.C., Sun, Y., Talbot, S.L., Qi, J., Ratan, A., Tomsho, L., Kasson, L., Zeyl, E., Aars, J., Miller, W., Ingólfsson, Ó., Bachmann, L., and Wiig, Ø. 2010. Complete mitochondrial genome of a Pleistocene jawbone unveils the origin of polar bear. *Proceedings of the National Academy of Sciences USA* **107:** 5053–5057.

Miller, W., Schuster, S.C., Welch, A.J., Ratan, A., Bedoya-Reina, O.C., Zhao, F., Kim, H.L., Burhans, R.C., Drautz, D.I., Wittekindt, N.E., Tomsho, L.P., Ibarra-Laclette, E., Herrera-Estrella, L., Peacock, E., Farley, S., Sage, G.K., Rode, K., Obbard, M., Montiel, R., Bachmann, L., Ingolfsson, Ó., Aars, J., Mailund, T., Wiig, Ø., Talbot, S.L., and Lindqvist, C. 2012. Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change. *Proceedings of the National Academy of Sciences* **109:** 14295–14296.

Polyak, L., Alley, R.B., Andrews, J.T., Brigham-Grette, J., Cronin, T.M., Darby, D.A., Dyke, A.S., Fitzpatrick, J.J., Funder, S., Holland, M., Jennings, A.E., Miller, G.H., O'Regan, M., Savelle, J., Serreze, M., St. John, K., White, J.W.C., and Wolff, E. 2010. History of sea ice in the Arctic. *Quaternary Science Reviews* **29:** 1757–1778.

Steffensen, J.P., Andersen, K.K., Bigler, M., Clausen, H., Dahl-Jensen, D., Fischer, H., Goto-Azuma, K., Hansson, M., Johnsen, S.J., Jouzei, J., Masson-Delmotte, V., Popp, T., Rasmussen, S.O., Röthlisberger, R., Ruth, U., Stauffer, B., Siggaard-Andersen, M.-L., Sveinbjörnsdóttir, Á.E., Svensson, A., and White, J.W.C. 2008. High-resolution Greenland ice core data show abrupt climate change happens in few years. *Science* **321:** 680–684.

5.8.1 Population

The world's polar bear populations live in the wild only in the Northern Hemisphere on land and sea ice in the area surrounding the North Pole. Polar bears tend to stay in, or return to, local areas (Taylor and Lee, 1995; Bethke *et al.,* 1996; Taylor *et al.,* 2001), although some migration is known to occur (Messier *et al.,* 2001; Amstrup *et al.,* 2004). Their range expands and contracts with the accretion and contraction of sea ice with the seasons, with bears moving south during the winter as sea ice advances (Amstrup *et al.,* 2000). In some areas (e.g., Hudson Bay, Foxe Basin, Baffin Bay, and James Bay) polar bears move from sea ice to land for several months during the summer open-water season (Ferguson *et al.,* 1997; Lunn *et al.,* 1997; Taylor *et al.,* 2001, 2005).

The total polar bear population is unknown, since its numbers in the Arctic Basin, East Greenland, Chukchi Sea, and the Kara Sea have never been counted (Aars *et al.,* 2006; Obbard *et al.,* 2010). The official estimate has been given as 20,000–25,000 since 2005 (Aars *et al.,* 2006; Obbard *et al.,* 2010), despite claims of declining numbers. The total has remained stable despite the fact that the former estimate for the Chukchi Sea was reduced from 2,000 to zero between 2005 and 2009.

There is even less certainty regarding the number of polar bears in the 1950s and 1960s, with most estimates around 5,000 to 10,000. Virtually all scientists agree polar bear populations have grown since the 1970s. For example, Derocher (2009) has stated, "after the signing of the International Agreement on Polar Bears in the 1970s, harvests were controlled and the numbers increased. There is no argument from anyone on this point." Ramsay and

Stirling (1988) wrote, "if a population was reduced in the past and the causal agent was no longer in effect, then the population would be expected to recover to its approximate pre-decline level."

Even though polar bear populations grew during the second half of the twentieth century, a time when IPCC claims there was a rapid increase in global temperatures and loss of sea ice, Derocher and others say this population growth is evidence of the effects of hunting bans and quotas and does not contradict their claim that warming temperatures and melting sea ice have hurt polar bear populations. They point, with apparent merit, to negative demographic impacts on polar bear populations identified in the Southern Beaufort Sea and in Western Hudson Bay, and possible adverse nutritional impacts in the Northern Beaufort Sea and Southern Hudson Bay, due to changes in local sea ice conditions.

But this observation falls short of providing evidence global warming threatens polar bears with extinction. If anthropogenic global warming were a real threat to polar bears, its effects should be observable throughout the Current Warm Period, not just the last few years, and the warming would have to affect more than only a small number of subpopulations, as appears to have been the case (see discussion below). The modified argument—that global warming only in recent years is negatively affecting only some subpopulations of polar bears but not others—is not what is being reported in daily newspapers or even what IPCC claims. The real-world long-term trends in polar bear populations contradict what would be expected if the theory of anthropogenic global warming were true.

The polar bear population is divided into 19 subpopulations for management purposes (see Figure 5.8.1.1). In 2005, according to the IUCN Polar Bear Specialist Group, five subpopulations were declining, five were stable, two were increasing, and on seven there was insufficient data on which to base a decision (Aars *et al.*, 2006). Significantly, four of the five subpopulations listed as declining were at risk due to hunting, not reduced sea ice (Aars *et al.,* 2006). This is hardly a picture of a species in steep decline, or even in decline at all. It certainly does not provide an empirical basis for predictions of imminent extinction.

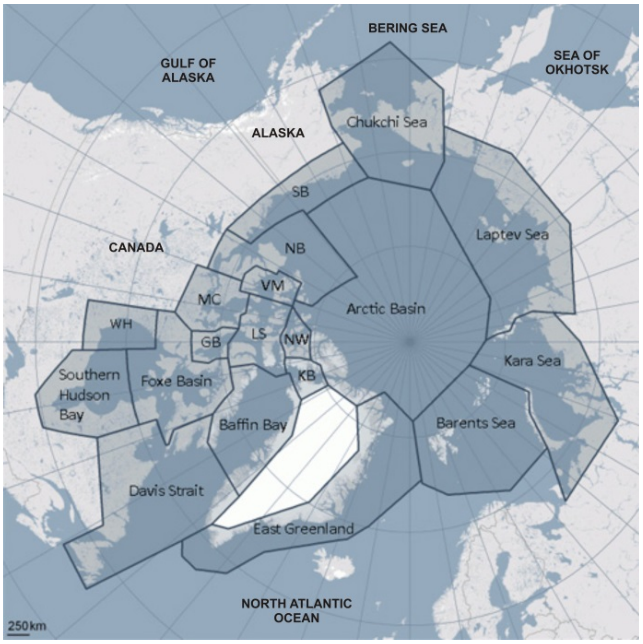

Figure 5.8.1.1. Polar bear subpopulations, as defined by the IUCN Polar Bear Specialist Group. Modified from map provided by the PBSG (2009). GB, Gulf of Boothia; KB, Kane Basin; LS, Lancaster Sound; MC, M'Clintock Channel; NB, Norwegian Bay; VM, Viscount Melville; NB, Northern Beaufort; SB, Southern Beaufort; WHB, Western Hudson Bay.

More recently, this view has changed somewhat (Obbard *et al.,* 2010). Seven subpopulations are now considered data-deficient (no trend given, including one that was rated as increasing in 2005), seven are listed as declining (including one subpopulation considered to have 'data deficient' status and another—the Chukchi—that has never been surveyed but is determined to have a "reduced" status and declining trend based on sea ice reductions and suspected poaching), three are considered stable, and one is considered to be increasing. Suspected overhunting and/or poaching are considered the primary reason five of the seven declining populations are at risk, based on modeled projections over the next 10 years. For another, declines in body condition, modeled over the next 10 years, are the basis for it being given a "declining" trend (Southern Beaufort).

Only one of the seven declining populations (Western Hudson Bay) has documented a statistically significant decline in population numbers. Obbard *et al.* state, "our status report currently indicates that two subpopulations (WH [Western Hudson Bay] and SB [Southern Beaufort]) have likely declined due to climate change. It is thought that there may also be some impacts of climate change in other populations (CS [Chukchi Sea], SH [Southern Hudson Bay]), however data are not conclusive or available." New research in the Chukchi by Rode *et al.* (2014) suggests bears there are in good condition and reproducing very well, indicating projected negative effects due to declining summer sea ice have not materialized.

In addition, whereas the decline in Western Hudson Bay polar bear numbers (about 22%) is stated to have occurred between 1987 and 2004 (Regehr *et al.,* 2007a), Obbard *et al.* (2010) acknowledge this population had been stable prior to 1998 (Stirling *et al.,* 1999). This means the statistically significant decline really occurred between 1998 and 2004 (seven years), during which there was no apparent trend in sea ice breakup dates (Regehr *et al.,* 2007a), although both 1998 and 2003 were relatively early breakup years (occurring about June 14 both years, according to the new method used by Cherry *et al.,* 2013). If the population was still on a declining trend after 2004, there should be fewer polar bears in Western Hudson Bay now than in 2004.

No data have yet been made available from mark-recapture studies undertaken between 2005 and 2011, but an aerial survey, similar to those conducted in the Barents Sea and Baffin Bay, was conducted by the Nunavut Government in 2011 (Stapleton *et al.,* 2012a). Stapleton and colleagues' estimate of the current population number is about 1,000 (95% confidence interval, range of 715–1398). Although the two methods (mark-recapture and aerial survey) cannot be directly compared, the authors say the aerial survey was "consistent with the 2004 capture-based estimate but inconsistent with projections suggesting continued decreases in abundance." So while Obbard *et al.* (2010) say "data from this subpopulation [WHB] provide the best indications of how polar bears respond to the negative effects of climate warming," it appears the population has not continued to decline as predicted.

Similar aerial surveys have been done to the north, in Foxe Basin by Stapleton *et al.* (2012b). In that study, the authors undertook a helicopter survey throughout the territory of Foxe Basin polar bears in the summers of 2009 and 2010, concluding "our abundance estimates were highly consistent between years and survey methods, (~2,580 bears (95% CI: about 2,100–3,200), and were comparable to an estimate from the early 1990s. Our results suggest that Nunavut's management regime has enabled polar bear abundance in FB to remain relatively stable."

Hunting historically has been the greatest threat to polar bear populations. The arrival of snowmobiles, helicopters, and high-powered rifles led to "harvest" levels that were not sustainable (Taylor *et al.,* 2002; Taylor *et al.,* 2006; Taylor *et al.,* 2008). Hunting was largely unregulated until passage of the 1974 International Agreement for the Conservation of Polar Bears and Their Habitat. Greenland didn't institute a quota for polar bear hunting until 2006 (Polar Bear Technical Committee, 2006). Annual kills for most populations now have been substantially reduced, but it will take at least 20 years for populations to recover.

The range of polar bears is affected by changes in climate but not in a linear fashion with temperature or the extent or thickness of sea ice. Sea ice extent and thickness are only indirectly related to polar bear populations. Only two subpopulations—the Western Hudson Bay (WH) and Southern Beaufort Sea (SB) populations—may have declined (Ferguson *et al.,* 2005; Regehr *et al.,* 2006, 2007a,b; Rode *et al.,* 2007; Hunter *et al.,* 2007); one of these (WH) is disputed (Dyck *et al.,* 2007), and the other (SB) is not a statistically significant decline.

Taylor and Dowsley (2008) summarized recent population surveys as follows: Of six polar bear populations recently evaluated during the climate warming period, two populations appear to have been reduced (WH, SB), two populations appear to have remained constant (SH, NB), one population appears to have increased (DS), and one was abundant but the information was not sufficient to estimate a trend (BS). Seven other populations (VM, LS, NW, BB, KB, MC, GB) surveyed during the period of climate warming had vital rates sufficient to sustain substantial rates of harvest (*i.e.*, hunting) at the time they were studied. Information from a Foxe Basin (FB) population survey was sufficient to document the population had remained abundant although it had been harvested at a relatively high rate and the survival and recruitment estimates necessary to determine trend were not available. The biological information on the remaining four populations (CS, LS, KS, EG) and the few bears that may inhabit the Arctic Basin is insufficient to suggest anything about current numbers or trend.

Taylor and Dowsley say "the increase to current high numbers of polar bears in the Davis Strait has occurred during the current warming period, and has occurred with declining sea ice conditions that are sometimes less than 40% coverage at winter maximum (Stirling and Parkinson, 2006). Clearly the DS bears do manage to hunt successfully in unconsolidated pack ice." They comment, as do Dyck *et al.* (2007), that polar bears have been observed to successfully hunt seals in tidal flats along shores during ice-free periods. "Considered together," Taylor and Dowsley conclude, "these demographic data do not suggest that polar bears as a species are headed for extinction in the next three generations (45 years) or the foreseeable future. The demographic data do support increased monitoring, and augmenting periodic population surveys with ecological and behavioral studies." They also observe, "to date, no population has been expatriated due to climate change effects, so the effect of decreased densities, alternative food sources, or behavioral adaptation to less ice on population persistence is not known."

Stirling and Derocher (2012) contend "polar bears will largely disappear from the southern portions of their range by mid-century." Western Hudson Bay is clearly included in this subset of all polar bear territory, as it lies below the Arctic Circle. But what other portions of the range lie below this point? Southern Hudson Bay, the Bering Sea, most of the Chukchi Sea, and most of Davis Strait also lie below the Arctic Circle; their population status already has been discussed. However, Southern Hudson Bay (SH), which extends to about 52°N, should presumably show more pronounced effects from global warming than even Western Hudson Bay to the north.

Obbard *et al.* (2010) say in their summary, "recent analysis of coastal survey data (Stirling *et al.* 2004) suggests polar bear numbers in SH have remained unchanged in recent years" and they consider this population to be one of three "stable" polar bear subpopulations. In a more comprehensive study of Southern Hudson Bay bears, Obbard *et al.* (2007) state, "reductions in survival of juvenile, subadult and senescent polar bears were demonstrated for the WH population (Regehr *et al*., 2007), but were only weakly supported by our data." Obbard *et al.* (2007) also note, "abundance in the Southern Hudson Bay population was unchanged between two intensive capture-recapture periods, which were separated by almost 20 years (1984–86 *vs.* 2003–05. This was so despite the evidence for a decline of 22% in abundance for the neighboring Western Hudson Bay population over roughly the same period (*i.e.*, 1987–2004; Regehr *et al*., 2007)." They conclude, "it appears that changes in environmental factors such as sea ice distribution and duration … have not yet resulted in unambiguous changes in survival or to a consequent reduction in population size in the SH population to this date." This is in spite of the fact that Obbard *et al.* (2006), in a dedicated study of Southern Hudson Bay polar bears, found body condition (fatness) was "significantly poorer for bears captured from 2000 to 2005 than for bears captured from 1984 to 1986," and concluded, "the significance of a trend toward poorer body condition over time is unknown." Nonetheless, in 2009 the province of Ontario listed Southern Hudson Bay polar bears as a "threatened" species (Obbard *et al.,* 2010).

The deep water over the Arctic Basin is often assumed to be of such low productivity (e.g., Amstrup *et al*., 2007; Fischbach *et al*., 2007; Obbard *et al*., 2010) that it is largely unsuitable for polar bears except as a transit corridor. This assumption is contradicted by measurements of significant amounts of phytoplankton and ice algae (e.g., Gosselin *et al*., 1997; Stirling, 1997) as well as reports at the North Pole of "small fish" (estimated as 5–8cm, presumably young polar cod, *Boreogadus saida*) thrown up by icebreakers, and algal growth visible on the underside of broken ice chunks (Todd *et al*., 1992). Polar cod and their prey are the food of ringed seals and are known to live under ice of all types, including multiyear and first-year drifting sea ice regardless of the ocean depth (Lønne and Gulliksen, 1989). The cracks ("leads") that continuously develop in moving multiyear ice allow thinner first-year ice to form, creating habitat for seals and thus potential food for polar bears (Stirling, 1997). Although the Arctic Basin is undoubtedly less productive than continental shelf areas, it may be more productive than has been assumed.

Ovsyanikov (2010) summarizes preliminary results of two distinct pieces of polar bear research conducted by Russian biologists from 2005–2008: on Wrangel Island in the Chukchi Sea and in the central Arctic Basin. Although the Wrangel Island work was a continuation of population monitoring that has been ongoing since 1990, the Arctic Basin surveys conducted in 2005 and 2007 were the first of this kind.

The late-summer Arctic Basin surveys were split between two years, each taking a different route: the 2005 expedition surveyed northward from Wrangel Island (in the far eastern Russian Arctic), on both sides of the 180° meridian up to 79°15' N, and the 2007 trip surveyed north from Franz Joseph Land (in the far western Russian Arctic, at about 81°N, 60°E), to the North Pole and back. Observations were taken 24 hours/day from the ship bridge for the duration of the trips, and sightings of both bears and ringed seals were recorded.

In 2005, 18 bears were seen north of Wrangel, 12 of these above 75°N, which marks the edge of the continental shelf at this location. Ten of the bears seen were in four family groups, and three of these families were observed north of the continental shelf. All were in good physical condition. A female and her single cub-of-the-year were observed feeding on a ringed seal at 78°50.20' N, 177°27.40' W, where water depth under the ice was 1,500 m. In addition, seven tracks of lone bears were recorded north of the continental shelf. A total of 48 ringed seals were observed from Wrangel Island to 79°15' N, more than half of these between 78°–79° N.

In 2007, the survey ship worked the other side of the Arctic Basin, north of Franz Joseph Land, where the continental shelf ends at around 82°–83° N (Weber, 1983). Seven polar bears were sighted beyond 81° N, all of them in good condition and all recorded on fields of substantial ice. One female was observed and photographed at the North Pole on 1–2 August 2007. A total of 61 tracks of single bears were also recorded, with a concentration around 82° N. Eleven ringed seals also were observed, five between 82° and 83° N, three between 83° and 87° N, and three between 89° and 90° N (including one at the North Pole). A lower proportion of the observations of seals and bears were noted beyond the continental shelf north of Franz Joseph Land than were sighted north of Wrangel Island but a few seals and at least one bear were recorded close to, or at, the North Pole.

Ovsyanikov suggests ringed seals living at the periphery of the Arctic Ocean move into the central Arctic Basin as the pack ice recedes in late summer and polar bears that choose to stay on the pack ice (rather than moving onto land) move along with the seals and the ice into the central Arctic beyond the continental shelves. Previous reports also have documented the presence of both ringed seals (Todd *et al*., 1992) and polar bears in the central Arctic Basin (Van Meurs and Splettstoesser, 2003), and in 1992–1993, a female tracked via satellite by Durner and Amstrup (1995) migrated from Prudhoe Bay in the southern Beaufort to northern Greenland via the central Arctic Basin (going as far north as 88°).

Ovsyanikov's Arctic Basin survey confirms ringed seals and polar bears do not require ice that is positioned over shallow, continental shelf waters, although higher densities of both species undoubtedly exist in such areas (e.g., Derocher *et al*., 2004). Ovsyanikov's study, although limited, is the first systematic look at polar bears and ringed seal abundance within the Arctic Basin. Further surveys may reveal the Arctic Basin is a more important habitat for polar bears than has been assumed, especially given the new finds of significant blooms of phytoplankton under thick annual ice (Arrigo *et al.*, 2011), discussed previously.

Years prior to the discovery reported by Arrigo and colleagues in 2011, Amstrup (2003) said, "Despite apparent preferences for the more productive waters near shorelines and polynyas (areas of persistent open water), polar bears occur throughout the polar basin including latitudes >88°N (Stefansson 1921; Papanin 1939; Durner and Amstrup 1995)." Amstrup also notes "the frequency of recent observations deep in the polar basin, however, mandates recognition that a separate stock could occur there." Although polar bear research in the remote and formidable Arctic Basin has so far been marginal, evidence to date suggests a significant population of polar bears live their entire lives in the Arctic Basin, although their official contribution to the global population estimate is still zero (Obbard *et al.,* 2010).

Polar bears are adapted to extremes of both warming and cooling that can and do occur. Under hostile climate conditions, polar bears will move out of affected areas and return when conditions improve and when the sea ice is neither too thick nor too ephemeral. If local sea ice changes continue for whatever reason, some subpopulations may be expatriated or decline to low numbers. However, polar bears as a species are not in danger of extinction and have not reached worrying levels of population decline.

References

Aars J., Lunn N.J., and Derocher, A.E. (Eds) 2006. Polar Bears: Proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 20–24 June 2005, Seattle, Washington, USA. *Occasional Paper of the IUCN Species Survival Commission.* Gland (Switzerland) and Cambridge (UK).

Amstrup, S.C. 2003. Polar bear (*Ursus maritimus*). In: Feldhamer, G.A., Thompson, B.C., and Chapman, J.A. (Eds.) *Wild Mammals of North America.* Baltimore, MD: Johns Hopkins University Press, pp. 587–610.

Amstrup, S.C., Durner, G., Stirling, I., Lunn, N.J., and Messier, F. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Canadian Journal of Zoology* **78**: 948–966.

Amstrup, S.C., McDonald, T.L., and Durner, G.M. 2004. Using satellite radio telemetry data to delineate and manage wildlife populations. *Wildlife Society Bulletin* **32**: 661–679.

Amstrup, S.C., Marcot, B.G., and Douglas, D.C. 2007. *Forecasting the rangewide status of polar bears at selected times in the 21st century*. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M.M., Palmer, M.A., Balch, W.M., Bahr, F., Bates, N.R., Benitez-Nelson, C., Bowler, B., Brownlee, E., Ehn, J.K., Frey, K.E., Garley, R., Laney, S.R., Lubelczyk, L., Mathis, J., Matsuoka, A., Mitchell, B.G., Moore, G.W.K., Ortega-Retuerta, E., Pal, S., Polashenski, C.M., Reynolds, R.A., Schieber, B., Sosik, H.M., Stephens, M., and Swift, J.H. 2012 Massive phytoplankton blooms under Arctic Sea ice. *Science* **336**: 1408.

Bethke, R., Taylor, M.K., Amstrup, S., and Messier, F. 1996. Population delineation of polar bears using satellite collar data. *Ecological Applications* **6**: 311–317.

Cherry, S.G., Derocher, A.E., Thiemann, G.W., and Lunn, N.J. 2013**.** Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology* **82:** 912–921.

Derocher, A. 2009. Ask the experts: Are polar bear populations increasing? Polar Bears International. Web site, last accessed April 30, 2009. http://www.polarbears international.org/ask-the-experts/ population/

Derocher, A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* **44**: 163–176.

Durner, G.M. and Amstrup, S.C. 1995. Movements of a polar bear from northern Alaska to northern Greenland. *Arctic* **48**: 338–341.

Dyck, M.G., Soon, W., Baydack, R.K., Legates, D.R., Baliunas, S., Ball, T.F., and Hancock, L.O. 2007. Polar bears of western Hudson Bay and climate change: Are warming spring air temperatures the 'ultimate' survival control factor? *Ecological Complexity* **4**: 73–84.

Ferguson, S.H., Taylor, M.K., and Messier, F. 1997. Space use by polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. *Canadian Journal of Zoology* **75**: 1585–1594.

Ferguson, S.H., Stirling, I., and McLoughlin, P. 2005. Climate change and ringed seal (Phoca hispida) recruitment in western Hudson Bay. *Marine Mammal Science* **21**: 121–135.

Fischbach, A.S., Amstrup, S.C., and Douglas, D.C. 2007. Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. *Polar Biology* **30**: 1395–1405.

Gosselin, M., Levasseur, M., Wheeler, P.A., Horner, R.A., and Booth, B.C. 1997. New measurements of phytoplankton and ice algae production in the Arctic Ocean. *Deep-Sea Research II* **44**: 1623–1644.

Hunter, C.M., Caswell, H., Runge, M.C., Amstrup, S.C., Regehr, E.V., and Stirling, I. 2007. Polar bears in the southern Beaufort Sea II: Demography and population growth in relation to sea ice conditions. USGS Alaska Science Center, Anchorage, Administrative Report.

Lønne, O.J. and Gulliksen, B. 1989. Size, age and diet of polar cod, Boreogadus saida (Lepechin 1773), in ice covered waters. *Polar Biology* **9**: 187–191.

Lunn, N.J., Stirling, I., and Nowicki, S.N. 1997. Distribution and abundance of ringed (Phoca hispida) and bearded seals (Erignathus barbatus) in western Hudson Bay. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 914–921.

Messier, F., Taylor, M.K., Plante, A., and Romito, T. 2001. Atlas of polar bear movements in Nunavut, Northwest Territories, and neighboring areas. Nunavut Wildlife Service and University of Saskatchewan, Saskatoon, SK.

Obbard, M.E., Cattet, M.R.L., Moody, T., Walton, L.R., Potter, D., Inglis, J., and Chenier, C. 2006. Temporal trends in the body condition of southern Hudson Bay polar bears. Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste, Marie, Canada. Climate Change Research Information Note 3. Available from http://sit.mnr.gov.on.ca.

Obbard, M.E., McDonald, T.L., Howe, E.J., Regehr, E.V., and Richardson, E.S. 2007. Polar bear population status in southern Hudson Bay, Canada. Administrative Report, U.S. Department of the Interior- U.S. Geological Survey, Reston, VA.

Obbard, M.E., Theimann, G.W., Peacock, E., and DeBryn, T.D. (Eds.) 2010. *Polar Bears: Proceedings of the 15th meeting of the Polar Bear Specialists Group IUCN/SSC, 29 June–3 July, 2009*, Copenhagen, Denmark. Gland, Switzerland and Cambridge UK, IUCN.

Ovsyanikov, N. 2010. Polar bear research on Wrangel Island and in the central Arctic Basin. In: Obbard, M.E., Theimann, G.W., Peacock, E., and DeBryn, T.D. (Eds.) *Proceedings of the 15th meeting of the Polar Bear Specialists Group IUCN/SSC, 29 June–3 July, 2009*. Gland, Switzerland and Cambridge UK, IUCN, pp. 171–178.

Papanin, I. 1939. *Life on an Ice-floe*. Hutchinson, London.

Polar Bear Technical Committee. 2006. Minutes of the 2006 Federal/Provincial/Territorial Polar Bear Technical Committee Meeting, St. John's, Newfoundland and Labrador, 6–8 February 2006. Canadian Wildlife Service, Edmonton, AB.

Ramsay, M.A. and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology London* **214:** 601–624.

Regehr, E.V., Amstrup, S.C., and Stirling, I. 2006. Polar bear population status in the Southern Beaufort Sea. U.S. Geological Survey Open-File Report 2006–1337.

Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2007a. Survival and population size of polar bears in western Hudson Bay in relation to earlier sea ice breakup. *Journal of Wildlife Management* **71**: 2673–2683.

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C., and Stirling, I. 2007b. Polar bears in the southern Beaufort Sea I: survival and breeding in relation to sea ice conditions, 2001–2006. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Rode, K.D., Amstrup, S.C., and Regehr, E.V. 2007. Polar bears in the southern Beaufort Sea III: stature, mass, and cub recruitment in relationship to time and sea ice extent between 1982 and 2006. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Rode, K.D., Regehr, E.V., Douglas, D., Durner, G., Derocher, A.E., Thiemann, G.W., and Budge, S. 2014. Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. *Global Change Biology* **20:** 76–88.

Stapleton, S., Atkinson, S., Hedman, D., and Garshelis, D. 2012a. Western Hudson Bay polar bear aerial survey, 2011. Final report, May 14, 2012, prepared for the Government of Nunavut, Igloolik.

Stapleton, S., Peacock, E., and Garshelis, D. 2012b. Foxe Basin polar bear aerial survey. Nunavut Wildlife Research Trust, Government of Nunavut, Igloolik.

Stefansson, V. 1921. *The Friendly Arctic.* Macmillan, New York.

Stirling, I. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. *Journal of Marine Systems* **10**: 9–21.

Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climate change. *Arctic* **52:** 294–306.

Stirling, I. and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* **59**: 261–275.

Taylor, M. and Dowsley, M. 2008. Demographic and ecological perspectives on the status of polar bears. Science & Public Policy Institute, Washington D.C.

Todd, F.S., Headland, R.K., and Lasca, N. 1992. Animals at the North Pole. *Polar Record* **28**: 321–322.

Taylor, M.K. and Lee, L.J. 1995. Distribution and abundance of Canadian polar bear populations: a management perspective. *Arctic* **48**: 147–154.

Taylor, M.K., Akeeagok, S., Andriashek, D., Barbour, W., Born, E.W., Calvert, W., Cluff, H.D., Ferguson, S., Laake, J., Rosing-Asvid, A., Stirling, I., and Messier, F. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. *Canadian Journal of Zoology* **79:** 690–709.

Taylor, M.K., Laake, J., Cluff, H.D., Ramsay, M., and Messier, F. 2002. Managing the risk of harvest for the Viscount Melville Sound polar bear population. *Ursus* **13**: 185–202.

Taylor, M.K., Laake, J., McLoughlin, P.D., Born, E.W., Cluff, H.D., Ferguson, S.H., Rosing-Asvid, A., Schweinsburg, R., and Messier, F. 2005. Demography and viability of a hunted population of polar bear. *Arctic* **58**: 203–214.

Taylor, M.K., Laake, J.L., McLoughlin, P.D., Cluff, H.D., and Messier, F. 2006. Demographic parameters and harvest-explicit population viability analysis for polar bears in M'Clintock Channel, Nunavut. *Journal of Wildlife Management* **70**: 1667–1673.

Taylor, M.K., Laake, J., McLoughlin, P.D., Cluff, H.D., Born, E.W., Rosing-Asvid, A., and Messier, F. 2008. Population parameters and harvest risks for polar bears (*Ursus maritimus*) in Kane Basin, Nunavut and Greenland. *Polar Biology* **31**: 491–499.

Todd, F.S., Headland, R.K., and Lasca, N. 1992. Animals at the North Pole. *Polar Record* **28**: 321–322.

Van Meurs, R. and Splettstoesser, J.F. 2003. Farthest north polar bear. *Arctic* **56**: 309.

Weber, J.R. 1983. Maps of the Arctic Basin sea floor: A history of bathymetry and its interpretation. *Arctic* **36**: 121–142.

5.8.2 Life History

5.8.2.1 Choice of Den Location by Females

In the fall, pregnant polar bear females make maternity dens in drifted snow, either on land or drifting pack ice, where they hibernate over the winter (Mauritzen *et al.*, 2001). The tiny cubs are born during hibernation (from mid-November to January) and are nursed within the den for at least two months. Mothers and cubs emerge around March-April. Individual females appear to have preferences for den location: females that den on land and those that den on ice are known in most subpopulations studied, except western Hudson Bay and around Svalbard in the Barents Sea, where all females appear to den on land (Mauritzen *et al.*, 2001; Ferguson *et al.*, 2000; Fischbach *et al.*, 2007; Lentfer, 1975; Zeyl *et al.*, 2010). According to Amstrup (2003), although it was once believed there were several high-density "core" areas for denning, "over much of their range, we now know, polar bears den in a more diffuse pattern where individual dens are scattered over broad reaches of habitat at low density." And as Zeyl *et al*. (2010) have stated, "long-term fidelity of denning areas and faithfulness to denning substrate (*i.e*., land vs. ice) has been observed."

Do females switch their den locations from one year to the next? If so, what is the level of loyalty ("fidelity") to either the area (the particular place on land) or the substrate (land vs. ice)? As all Svalbard-area females appear to den on land, the issue addressed in the paper by Zeyl *et al.* was whether mothers switched from one denning area to another within the Svalbard region, and whether related individuals (especially mothers and daughters) tended to den in the same area.

The authors used data collected from a technique called "mark-recapture," along with results from analysis of mitochondrial DNA (mtDNA, the kind inherited from mothers) to investigate the amount of loyalty individual female polar bears had to five denning areas around Svalbard. They also used these data to address whether any loyalty to a specific area was transmitted from mothers to daughters to such an extent that it would result in genetic clustering of mtDNA haplotypes in different den areas.

The results of the study indicate female polar bears have a moderate degree of loyalty to their chosen den areas (3/13 females switched areas from one year to the next) and daughters had a tendency to den in the same areas as their mothers (only 2/8 did not). There was not, however, the kind of genetic clustering expected if such loyalty had been ongoing over a long period of time. Although the distances between successive mark-recapture locations for Svalbard females were similar to distances reported for land-denning females in western Hudson Bay (23.7 km vs. 34 km, respectively), these were much lower than documented for females in the Beaufort Seas (308 km), where a significant proportion of bears den on sea ice (Amstrup and Gardner, 1994), the authors note. Zeyl and colleagues also note the level of denning site loyalty demonstrated by female polar bears on Svalbard is markedly lower than recorded for brown bears, their closest living relatives (who of course always den on land).

Zeyl and colleagues suggest female polar bears may switch the precise location of their dens from one year to the next depending on prevailing snow or sea ice conditions. In a similar study, Fischbach *et al.* (2007) documented some females who switched between pack ice dens and land dens (*i.e*., a switch of substrate type). Zeyl *et al.* suggest there is more flexibility than previously assumed in den site choice among polar bear females.

The demonstrated willingness of polar bear females to switch den locations from one year to the next, despite a general tendency towards den site loyalty, almost certainly gives them the flexibility they need as a species to persist in the face of sea ice conditions that vary from year to year. The ability of polar bear females to shift from one den site location to another or one substrate to another is just one aspect of the kind of plasticity needed to survive in this habitat.

Amstrup and Gardner (1994) stated, "contrary to previous hypotheses (Stirling and Andriashek, 1992), substantial polar bear denning occurs in the Beaufort Sea region of northern Alaska and adjacent Canada. Bears that den on pack ice are subject to risks not encountered by bears that den on land. Unstable, moving ice caused early abandonment of dens and, apparently, loss of cubs. However, the persistence of pack-ice denning indicated that those risks are not overwhelming."

As one Russian polar bear researcher commented years ago regarding bears in the eastern Russian Arctic (Kochnev, 2006), "our investigations on Wrangel Island have shown the polar bear is a very plastic animal: it can rapidly change its way of life, spatial distribution and behavior according to new ecological conditions." Zeyl and colleagues (2010) seem to agree, stating, "females are likely able to change denning locations if unsuitable ice conditions prevent them from reaching their preferred denning areas. We consider this plasticity an important attribute of polar bears when facing climate change."

Working in the same Southern Beaufort region as Fischbach *et al.* (2007), Schliebe *et al.* (2008) found in 2000–2005 an average of 3.7% of polar bears spent time on land between mid-September and the end of October; the rest were on the pack ice. They state, "across all years and survey dates between mid-September and the end of October, an average of 4 ± 2 bears/100 km (57 ± 28 bears total) were observed. Thus, a maximum of 8.0% and an average of 3.7% of the estimated 1,526 bears in the SBS population (Regehr *et al*., 2006) were observed on land." This means there were, on average, only 56 bears on land in the fall each year (out of 1,526 bears), suggesting most pregnant females in the Southern Beaufort made their dens in the pack ice and never came to land in fall. Schliebe *et al.* conclude, "overall, we did not detect an increasing trend in polar bear densities along the Beaufort Sea coast of Alaska during the six years of this study," indicating bears were not being forced on land due to declining summer ice coverage.

These studies make it apparent an unknown number of polar bear females den in the offshore pack ice and many Southern Beaufort bears never set foot on land. Amstrup (2003), in his discussion of pack-ice denning in the Beaufort Sea, says this about offshore denning: "despite the absence of conclusive reports, sea-ice denning probably occurs at some level in other areas." Amstrup suggests these areas include the Arctic Basin, given "the recent recognition of a possible polar basin stock of polar bears." In addition, he suggests the "linear coastline of central Arctic Russia may be more similar to the Beaufort Sea than other areas, and hence may be another area where sea-ice denning is common."

Given the known and predicted use of offshore ice for denning, it is rather astonishing that the report supplied in support of the listing of the polar bear as a threatened species in the United States (Bergen *et al*., 2007) modeled only future changes to terrestrial denning habitat. Since those models did not address offshore sea ice denning habitat at all, it means those studies ignored a huge amount of polar bear habitat that is likely critical to their resilience to changing sea ice conditions.

References

Amstrup, S.C. 2003. Polar bear (*Ursus maritimus*). In: Feldhamer, G.A., Thompson, B.C., and Chapman, J.A. (Eds.) *Wild Mammals of North America*. Baltimore, MD: Johns Hopkins University Press, pp. 587–610.

Amstrup, S.C. and Gardner, C. 1994. Polar bear maternity denning in the Beaufort Sea. *The Journal of Wildlife Management* **58**: 1–10.

Bergen, S., Durner, G.M., Douglas, D.C., and Amstrup, S.C. 2007. Predicting movements of female polar bears between summer sea ice foraging habitats and terrestrial denning habitats of Alaska in the 21st century: Proposed methodology and pilot assessment. Administrative Report, USGS Alaska Science Center, Anchorage, AK.

Ferguson, S.H., Taylor, M.K., and Messier, F. 2000. Influence of sea ice dynamics on habitat selection by polar bears. *Ecology* **81**: 761–772.

Fischbach, A.S., Amstrup, S.C., and Douglas, D.C. 2007. Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. *Polar Biology* **30**: 1395–1405.

Kochnev, A.A. 2006. Research on polar bear autumn aggregations on Chukotka, 1989–2004. In: Aars, J., Lunn, N.J., and Derocher, A.E. (Eds.) Polar Bears: Proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 20–24 June 2005, Seattle, Washington, USA. *Occasional Paper of the IUCN Species Survival Commission 32*. Gland, Switzerland, and Cambridge, UK: IUCN, pp. 157–165.

Lentfer, J.W. 1975. Polar bear denning on drifting sea ice. *Journal of Mammalogy* **56**: 716–718.

Mauritzen, M., Derocher, A.E., and Wiig, Ø. 2001. Space-use strategies of female polar bears in a dynamic sea ice habitat. *Canadian Journal of Zoology* **79**: 1704–1713.

Regehr, E.V., Amstrup, S.C., and Stirling, I. 2006. Polar bear population status in the Southern Beaufort Sea. U.S. Geological Survey Open-File Report 2006–1337.

Schliebe, S., Rode, K.D., Gleason, J.S., Wilder, J., Proffitt, K., Evans, T.J., and Miller, S. 2008. Effects of sea ice extent and food availability on spatial and temporal distribution of polar bears during the fall open-water period in the southern Beaufort Sea. *Polar Biology* **31:** 999–1010.

Stirling, I. and Andriashek, D. 1992. Terrestrial maternity denning of polar bears in the eastern Beaufort Sea area. *Arctic* **45:** 363–366.

Zeyl, E., Ehrich, D., Aars, J., Bachmann, L., and Wiig, Ø. 2010. Denning-area fidelity and mitochondrial DNA diversity of female polar bears (*Ursus maritimus*) in the Barents Sea. *Canadian Journal of Zoology* **88**: 1139–1148.

5.8.2.2 Mortality Due to Den Collapse

In a list of suggested risks to polar bears in a warmer world, Derocher *et al.* (2004) state, "An additional concern specific to female polar bears in dens with altricial cubs is the possibility that rain might become more frequent in late winter and cause the snow cover over dens to collapse and suffocate the occupants." Stirling and Derocher (2012) provide more up-to-date and detailed information on this concern. Their paper summarizes all of the known anecdotal reports of rain on snow events that led to the collapse of polar bear maternity dens and/or ringed seal birthing lairs. They state "such rain on snow events are predicted to increase as the climate warms in the Arctic."

Stirling and Derocher describe four incidents: one case of a maternity den collapse (involving a six-year-old, probably first-time mother and two cubs three to four weeks old) in the southern Beaufort in 1989, apparently caused by warm weather followed by heavy snow in late January, reported originally by Clarkson and Irish (1991); a rain event in early March 1990 in western Hudson Bay that was not associated with den collapses and which led to "no evidence of dead bears the following summer"; rain and warm weather in early April 1979 in southeastern Baffin Island that resulted in "increased predation mortality of ringed seal pups" by polar bears and Arctic foxes; a warm period, also in southeastern Baffin Island, in late April 1990, that was reported to have generated a tripling of polar bear predation success on newborn ringed seal pups because ringed seal birthing lairs were easier to break or had melted and collapsed.

These details indicate each of the den collapse incidents occurred in 1990 or before, not in more recent years as might be expected if such events were associated with warmer temperatures. It appears there has not been a single documented event of this kind since 1990, despite increasing temperatures and "progressive unidirectional changes to sea ice distribution" (Stirling and Derocher, 2012). Instead, it appears warm spells in winter and rain in the spring occur rarely in the Arctic, even in a warming world, and do not pose a significant risk to polar bears or their ringed seal prey. Anecdotal reports such as these are not evidence and do not contribute to our understanding of how polar bears respond to unidirectional climate change.

References

Clarkson, P.L. and Irish, D. 1991. Den collapse kills female polar bear and two newborn cubs. *Arctic* **44:** 83–84.

Derocher, A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* **44**: 163–176.

Stirling, I. and Derocher, A.E. 2012. Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology* **18:** 2694–2706

5.8.3 Nutrition and Reproductive Success

Researchers have expressed concern over the relationships between temperature and sea ice breakup and the nutrition and physical condition of polar bears and reproductive success. Closer scrutiny of these claims suggests they lack empirical bases.

5.8.3.1 Nutritional Stress and Declines in Body Condition

According to Stirling and Derocher (2012), "the most comprehensive long-term research on polar bear demography, body condition, subpopulation size, abundance, and reproductive success has been conducted on the Western Hudson Bay subpopulation." For bears in this subpopulation, they found "statistically significant relationships have been documented between progressively earlier dates of sea ice breakup (which shortens the feeding time for polar bears at the most important time of the year just before coming ashore, and lengthens the fasting period)," and declines in the following parameters: mean body condition during the fall ice-free period; mean weights of suspected pregnant females prior to denning in fall; and survival of juvenile, subadult, and old (senescent) adult bears.

These claimed correlations between these life history parameters and "progressively earlier dates of sea ice breakup" in Western Hudson are based on published sea ice data only up to 1998. As their figure caption notes, data after that time (1999 to 2007) is attributed to "N.J. Lunn and I. Stirling, unpublished data." In contrast, the figure they include showing global sea ice declines, based on Stroeve *et al.* (2007), is updated to 2011 with publicly available data provided by the U.S. National Snow and Ice Data Center. Moreover, although Stirling and Derocher say "the mean mass of adult females declined (by about 20%) between 1980 and 2007" (mass being a "proxy" for body condition, which they say is tied closely to litter size, age at weaning, and cub survival), the data used to reach this conclusion are for 1980 to 2004 only: the data from 2006 to 2007 are not available in the peer-reviewed literature. This means the data on which these claims are made are strikingly out of date and/or unavailable, and the conclusions may no longer be valid.

Stirling and Derocher's claim of "progressive unidirectional changes to sea ice distribution" may be accurate for global sea ice coverage but not for ice on Hudson Bay. In a recent paper on breakup in Western Hudson Bay, Cherry *et al.* (2013) show between 1991 and 2009, there was considerable variability in breakup dates. Polar bears left the ice later in 2009 than in 1992, indicating breakup dates have not been progressively earlier since 1992. Only nine of 19 breakup dates in this period fell in June (with none falling in the first half of the month), suggesting there was little or no impact on the critical November–June feeding period. And although some bears apparently chose a favorite location to come ashore even if there was enough ice to spend more time hunting, many bears were flexible enough in their choice of where and when they left the ice to adapt to yearly variability in conditions. Overall, it appears variability may be the most prominent feature of sea ice breakup dates for Western Hudson Bay and most polar bear females can and do take these variations in stride.

Polar bears in the Southern Beaufort region have also been reasonably well-studied. This subpopulation is shared between the United States and Canada and comprises most of the north coast of Alaska and about an equal length of the western Canadian Arctic coastline. It is characterized by a dynamic mix of annual and multiyear sea ice. Bears in the Southern Beaufort routinely den on the sea ice rather than on land and reach their maximum weights in the fall, rather than in summer, as do bears in Western Hudson Bay—probably because they spend little, if any, time on land during the summer.

Durner and Amstrup (1996) note, "polar bears in western Hudson Bay differ from other populations because the sea ice substrate required for hunting melts completely by late summer (Ramsay and Stirling, 1988), and all members of the population fast or consume only low-energy food (Derocher *et al*., 1992). On the other hand, polar bears inhabiting certain areas of the Canadian Arctic archipelago (e.g., Viscount Melville Sound) may be food deprived because of stable sea ice conditions during winter and low seal densities (Messier *et al*., 1994). Because polar bears in Alaska [*i.e.*, the Southern Beaufort] follow seasonal changes in dynamic pack ice (Amstrup and DeMaster, 1988), they may not face the food scarcity that characterizes the Hudson Bay population during summer and the northern Canadian population during the winter."

In other words, even before there were declines in sea ice coverage purportedly caused by global warming, polar bear biologists saw marked differences among subpopulations in patterns of body condition changes from season to season. In light of that understanding, do reports that blame global warming for declines in polar bear size and body condition (and associated declines in cub production and/or survival) stand up to scrutiny?

Rode *et al.* (2010) studied polar bears in the Southern Beaufort between 1982 and 2006. They used a subjective definition of sea ice conditions, called "optimal ice habitat," which is not a quality measured by satellites but "resource selection function (RSF) models" that use data from satellite-collared polar bears (1985–1995) to show where the bears that researchers captured on land or near shore moved throughout the year. Using this method, a decline in area (km^2-months) of "optimal ice habitat" (ice neither too thin nor too thick) could mean sea ice got thicker, got thinner, or disappeared—it is not possible to tell which. Rode *et al.* (2010) conclude, "the decline over time in the availability of sea ice corresponded with declining trends in most measures of bear sizes and condition." But because their "decline over time in availability" is not a straightforward decline in sea ice extent or timing of the ice-free period, but a decline in "optimal ice habitat," it is unlikely this parameter is really useful in addressing whether reduced levels of summer sea ice in the Southern Beaufort are the proximate cause of negative impacts on polar bears.

In direct contraction of a statement made by Obbard *et al.* (2010), discussed in more detail near the end of this section, Rode *et al.* (2010) say, "declines in the size of bears in this population have occurred during a time period when the number of bears in the region also appears to be lower than previously thought (Regehr *et al.,* 2006), and the trend in numbers appears to be downward (Regehr *et al.,* 2010). Though the mechanism associated with population-level change is not clear, nutritional limitations in the population are apparent as a result of the observed declines in bear skull sizes and body lengths. … Thus, nutritional factors may also have played a role in the observed population-level changes." Although nutritional stress has indeed been documented for this area, there has not been a statistically significant decline in the population, a point reiterated by Regehr *et al.* (2007): "changes in the sea ice have not yet been associated with changes in the size of the SB polar bear population (Regehr *et al.,* 2006)." Obbard *et al.* (2010) concur.

Even more surprising is recent research on polar bears in the neighboring Chukchi Sea subpopulation (shared between the United States and Russia), which has shown either no negative effects or marked improvement despite at least twice as much summer sea ice loss as in the Southern Beaufort. Rode *et al.* (2014) captured, measured, and released polar bears on the sea ice between mid-March and early May, 2008–2011; others did similar work in 1986–1994. Rode *et al.* compared data collected on body condition, litter size, and juvenile survival ("reproductive indices") in the Chukchi Sea between the two periods (1986–1994 and 2008–2011). They also compared body condition and reproduction in the Chukchi and neighboring Southern Beaufort for the period 2008–2011. They evaluated these metrics in relation to sea ice loss and prey availability; for Chukchi bears in 2008–2011 only, they also determined diet composition from analysis of fat samples ("fatty acid signatures") and fasting behavior from analysis of blood samples ("levels of blood urea nitrogen and creatinine").

The authors found "in 2008–2011, CS [Chukchi] bears were either larger and in better condition, or similar in size and condition, to CS bears in 1986–1994." They also found "no difference in the number of yearlings per female, yearling litter size, or the annual percentage of females with yearlings between periods in the CS. … Overall, CS bears in 2008–2011 were larger and in better condition than SB [Southern Beaufort] bears during the same period." The number of yearlings per female in spring was also higher in the Chukchi Sea than in the Southern Beaufort.

Most surprisingly, Chukchi bears were larger and heavier than virtually all other subpopulations studied. Rode *et al.* (2014) found "spring COY litter sizes are among the highest reported for 18 of 19 polar bear populations. … [S]pring litter sizes of CS yearlings from the study were also higher than other populations." The authors note, "the larger body mass of adult females in the CS corresponded not only with larger litter sizes, but also with heavier yearlings (Fig.5 [in original document]) which have a greater chance of survival." Rode *et al.* state, "body size, condition, and reproductive indices of CS polar bears did not decline over time between 1986–1994 and 2008–2011 despite a 44-day increase in the number of reduced-ice days. Furthermore, CS bears were larger, in better condition, and appeared to have higher recruitment compared to the adjacent SB population during 2008–2011. These differences were biologically significant."

In the Chukchi subpopulation, the authors conclude, "body condition was maintained or improved when sea ice declined" and "continued high biological productivity in the Chukchi and northern Bering seas may be allowing polar bears and their prey to prosper despite habitat loss." Regarding Southern Beaufort bears, they state, "Our evaluation of nutritional ecology for polar bears is consistent with lower prey availability in the SB compared to the CS."

These results were unexpected because the Southern Beaufort and Chukchi Seas are considered similar ice ecoregions and polar bears were predicted to respond similarly to summer sea ice loss. Both have been classified as "divergent" ice ecoregions by researchers attempting to predict how polar bear habitat might fare over the next 25 to 95 years based on computer-projected sea ice declines (Amstrup, 2011; Amstrup *et al.,* 2008, 2010; Durner *et al.,* 2009). Durner and colleagues, for example, state, "within the Divergent ecoregion, rates of decline are projected to be greatest in the Southern Beaufort, Chukchi, and Barents Sea subpopulations." Two conclusions can be drawn from this study: Declines in summer sea ice extent can markedly benefit polar bear survival, and extent of sea ice loss in summer is not the paramount determiner of polar bear health and population status, at least over the short term.

In the eastern Arctic, there also has been recent work done on Davis Strait polar bears, the most southerly polar bear subpopulation. Whereas the southernmost portion of the Southern Hudson Bay region (James Bay) lies at about 52°N and the southernmost portion of Western Hudson Bay lies at about 55°N, bears in the Davis Strait polar bear subpopulation occur regularly to at least 50°N, with some moving as far south in spring as 47°N.

Based on mark-recapture studies undertaken from 1974 to 1979 and from 2005 to 2007, Peacock *et al.* (2013) state, "the overall amount of sea ice declined and breakup has become progressively earlier" since the 1970s. Nonetheless, they "estimated the abundance of the Davis Strait polar bear subpopulation to 2,158, which results in a relatively high population density of polar bears of approximately 5.1 bears/1,000 km^2 of sea ice habitat (Taylor and Lee, 1995). This density is greater than polar bear densities in other seasonal-ice subpopulations, which are approximately 3.5 bears/1,000 km^2." So despite declining sea ice since the 1970s, the density of bears in this region has reached a higher level than any other subpopulation known that loses ice completely in summer. The authors conclude, "survival and reproduction of bears in southern Davis Strait was greater than in the north and tied to a concurrent dramatic increase in breeding harp seals (*Pagophilus groenlandicus*) in Labrador."

They suggest the Davis Strait polar bear sub-population is characterized by "low recruitment rates, average adult survival rates, and high population density." The high density of bears in this region may be affecting recruitment (*i.e.,* reproduction), the authors conclude, "low reproductive rates may reflect negative effects of greater densities or worsening ice conditions." In other words, polar bear populations with a high density of animals may show changes to life history parameters similar to those expected in populations affected by declines in sea ice. However, effects of high density and less time spent feeding due to reduced sea ice appear to be viable explanations for the observed conditions in Davis Strait, and these factors are not necessarily mutually exclusive. Nevertheless, polar bears in Davis Strait appear to be increasing in number, not declining as reported by the IUCN/SSC Polar Bear Specialist Group (Obbard *et al.,* 2010) and others, despite the declines in sea ice.

In a similar study that compared Davis Strait polar bears to those in Baffin Bay to the North, Rode *et al.* (2012) "examined trends in body condition metrics of captured bears and relationships with summertime ice concentration between 1977 and 2010 for the Baffin Bay (BB) and Davis Strait (DS) polar bear populations." Both of these regions are dominated by annual (first year) ice. They conclude, "we suggest that declining body condition in BB may be a result of recent declines in sea ice habitat. In DS, high population density and/or sea ice loss may be responsible for the declines in body condition. ... Though a decline in body condition was observed for DS between 1978 and 1994, there was no relationship between body condition and sea ice concentrations at that time." In other words, the decline in condition of polar bears in Davis Strait may be evidence the population has reached "carrying capacity" despite the declining trend in annual sea ice extent. This result suggests declines in body condition may not necessarily be the harbinger of doom for polar bears some researchers have proposed but instead a signal more bears exist than the local habitat can support.

One of the presumed repercussions of polar bears that end up in poor condition due to nutritional stress, especially if they get to the point of starving, is an increase in propensity for infanticide and cannibalism. These phenomena are well-known in all bears (Taylor *et al.,* 1985), but there have been no long-term, carefully designed scientific studies on infanticide or cannibalism among polar bears, so no baseline data exist with which to compare recent anecdotal reports. This has not stopped some polar bear researchers and conservation advocates from using these anecdotal observations as a kind of "supporting evidence" for contending polar bears are already being negatively impacted by global warming.

Stirling and Derocher (2012) state, "There have been several well-publicized observations that are consistent with predictions of the effects of climate warming on polar bears, but cannot be statistically linked. For example, intraspecific aggression and cannibalism were predicted to increase in polar bears with climate warming (Derocher *et al*., 2004, Table 1). Observations of infanticide and cannibalism by thin adult males on land during the open water period have been documented (e.g., Lunn and Stenhouse, 1985; Derocher and Wiig, 1999; Amstrup *et al*., 2006; Stone and Derocher, 2007)."

However, of the references cited, only Lunn and Stenhouse (1985) report a confirmed instance of a thin (*i.e.,* starving) adult male killing and consuming another adult bear during the open water period, and that event occurred in 1984. Amstrup *et al.* (2006), who report three incidents of cannibalism in the Southern Beaufort, did not know the condition of the bears that killed and partially consumed other bears, as no one witnessed these attacks. In addition, contrary to the notion that cannibalism is associated with starvation, in the most recent case published (one not mentioned by Stirling and Derocher), Stirling and Ross (2011) report three cases of cannibalism on the sea ice around Svalbard, all of which involved males in good or very good condition killing other young bears. They say "the three observations we describe are different from most other reports of infanticide and cannibalism in polar bears because they took place between midsummer and early autumn. … All three adult males appeared to be in good physical condition (*i.e.*, not obviously thin), and one was both very large and very fat."

Stirling *et al.* (2008), in a follow-up to the report of Amstrup *et al.* (2006), state, "these observations, along with cannibalized and starved polar bears found on the sea ice in the same general area in the springs of 2004 through 2006, suggest that during those years, polar bears in the southern Beaufort Sea were nutritionally stressed." They point out several severe winter storms piled up thick ridges of sea ice in the landfast ice zone, which made seal hunting difficult for polar bears. They acknowledge the nutritional stress was caused by heavy ice conditions in 2004 and 2005 (confirmed by Harwood *et al.,* 2012 and Melling *et al.,* 2005) but suggest the heavy ice may have been caused by open water many months prior in the Chukchi Sea far to the west. However, there have been heavy ice years in this region every decade since the 1960s (long before there was increased open water in the fall) and starving bears in spring were documented in most of those heavy ice years (Stirling, 2002; Stirling and Lunn, 1997; Stirling *et al.,* 2008), suggesting the cause of heavy spring ice is something other than increased open water in the summer.

The impact of the most recent heavy ice years on ringed seals is documented by Harwood *et al.* (2012), for the Amundson Gulf, which lies in the south half of the Northern Beaufort polar bear subpopulation (and immediately east of the Southern Beaufort areas discussed above). They examined "the relationship between ringed seal body condition and reproduction and spring sea ice conditions in prime ringed seal habitat" in the western Canadian Arctic between 1992 and 2011. They found "failure to ovulate was obvious in 2005, the most extreme late ice clearance year in our series, when only 30.0% of the mature adult females sampled ovulated." The authors conclude, "Seals sampled in years of late ice clearing had, on average, lower body condition than those sampled in years of earlier ice clearing, particularly in the case of subadults" and for mature females, "marked declines were seen in 1974 (Smith, 1987), in 1987 (Kingsley and Byers, 1998), and in 2005 (this study), all times when seals were in significantly poorer body condition. ... Signals were detected in the most extreme ice years (e.g., when fast ice breakup occurred 3–8 weeks later than the average since 1970) and were linked to the degree of severity of winters, as indicated by the annual ice regime." They note, "In the Beaufort/Amundsen regions, for example, observations over the last 40 years have revealed large fluctuations in ice presence and thickness over intervals of years to decades, with so far only small trends towards earlier ice clearance and longer open water seasons (Melling and Riedel, 2004; Melling *et al*., 2005)."

Pilfold *et al.* (2012) corroborate the declines in ringed seal pup production documented by Harwood *et al.* (2012) in their study of the age composition of ringed seals killed by polar bears in the eastern Beaufort from 1971 to 2006. They show, in their Figure 3, a higher proportion of pups were killed during the low or average spring ice years of 1971–1973 (when about 45% of seals killed were pups) and 2007–2011 (about 80% pups) than in the heavy spring ice years of 1974 to 1975 (none killed were pups), 1985 to 1987 (about 10% pups), or in 2003 to 2006 (about 40% pups). In other words, since the early 1970s, polar bears killed fewer seal pups in springs with heavy sea ice conditions, suggesting fewer seal pups were available.

Another perspective on these events is provided by Cherry *et al.* (2009), who compared the fasting physiology of eastern Beaufort Sea polar bears during two known heavy spring ice periods: 1985–1986 and 2005–2006. In their analysis of the proportion of urea vs. creatinine (considered an indicator of fasting) from blood samples drawn in the eastern Beaufort Sea (which include the southern portion of the Northern Beaufort subpopulation) in April-May 1985–1986 and 2005–2006, they found "the proportions of polar bears fasting were 9.6% in 1985, 10.5% in 1986, 21.4% in 2005, and 29.3% in 2006. … The increased number of polar bears in a physiological fasting state from all sex, age, and reproductive classes in 2005 and 2006 corresponded with broad scale changes in Arctic sea ice composition, which may have affected prey availability." They write, "none of the bears displayed physical or behavioral traits indicative of an animal in the advanced stages of starvation." This seems to corroborate the finding by Amstrup *et al.* (2006), who found in the spring of 2004, the year before Cherry *et al.* took their samples, "70 of 148 (47%) of bears captured as independent animals (*i.e.*, not including cubs captured with their mothers) were in the lean condition classes 1 and 2*.*" This is perhaps not very surprising, as polar bears are generally at their leanest in March, and if they are slow to put on weight for any reason over the spring months, by April or May they would not yet be in optimum condition (although they might be so a few months later).

Cherry *et al.*'s discussion of the "changes in Arctic sea ice" in their introduction attempts to imply the changes over time in the percentage of fasting bears was caused by reduced ice and more open water. They say, for example, "the Arctic ice-ocean system has been warming faster than global averages since the 1960s." They conclude, "Beaufort Sea bears reach their lightest weights in late March and rely on a 2–3 month spring feeding period, when fat and naïve ringed seal pups are available, to gain the fat reserves necessary for survival and reproduction (Stirling and Øritsland, 1995; Stirling, 2002). ... [T]he recent increase in bears fasting during April and May suggests that there has been a decrease in prey availability at that time of year. ... [T]he precise means through which prey have apparently become less available to polar bears in the Beaufort Sea remains unknown." But as discussed above, "the precise means" have been documented—evidence from this region suggests heavy sea ice in the spring during 2004–2006, which resulted in precipitous declines in ringed seal pup production, was almost certainly the cause of more bears fasting (Harwood *et al.,* 2012; Melling *et al.,* 2005; Stirling, 2002; Stirling *et al.,* 2008).

Regehr *et al.* (2010) provide another attempt to shift attention from heavy ice conditions in spring to low sea ice conditions in late summer. These researchers "evaluated the effects of sea ice conditions on vital rates (survival and breeding probabilities) for polar bears in the southern Beaufort Sea" with models, based on data collected from 2001 to 2006 on polar bears and the number of ice-free days each year. They conclude, "in the most supported models, polar bear survival declined with an increasing number of days per year that waters over the continental shelf were ice free. In 2001–2003, the ice-free period was relatively short (mean 101 days) and adult female survival was high (0·96–0·99, depending on reproductive state). In 2004 and

2005, the ice-free period was longer (mean 135 days) and adult female survival was low (0·73–0·79, depending on reproductive state). Breeding rates and cub litter survival also declined with increasing duration of the ice-free period. Confidence intervals on vital rate estimates were wide."

Regehr *et al.* did not include possible effects of heavy sea ice conditions in spring in their models, which, as shown above, tends to have a direct negative impact on polar bear life history parameters in the eastern Beaufort (Harwood *et al.,* 2012; Melling *et al.,* 2005; Stirling, 2002; Stirling and Lunn, 1997). Regehr *et al.*'s models considered only number of ice-free days in summer as a possible association. As a consequence their results and conclusions add little to our understanding of changes in polar bear survival or body condition in the Southern Beaufort.

It should be noted that despite the repeated bouts of less-than-optimum conditions every decade or so, polar bear numbers in the Southern Beaufort appear to have remained remarkably stable. Obbard *et al.* (2010) note,

> through the 1980s and early 1990s, observations suggested that the SB subpopulation was increasing. Amstrup *et al.* (2001) found the SB subpopulation may have reached as many as 2,500 polar bears in the late 1990s. However, that estimate was not considered reliable due to methodological difficulties, and management decisions continued to be based on a population size of 1,800. Results from an intensive mark-recapture study conducted from 2001–2006 in both the USA and Canada indicated that the SB subpopulation included 1,526 (95% CI = 1,211–1,841) polar bears in 2006 (Regehr *et al.,* 2006). This suggests that the size of the SB subpopulation declined between the late 1990s and 2006, although low precision in the previous estimate of 1,800 precluded a statistical determination."

In other words, although there is evidence of nutritional stress in 2004–2006, it did not result in a statistically significant decline in numbers of polar bears in the Southern Beaufort region.

In addition, polar bears that live in the region around Banks Island and the Amundsen Gulf in the past were often included in studies of the "eastern Beaufort," but they now are considered part of the Northern Beaufort subpopulation, one of the few subpopulations some researchers consider as having a stable population trend (Obbard *et al.,* 2010; Stirling *et al.,* 2011).

Surprisingly, one question seldom addressed in studies on nutritional stress and associated behaviors such as cannibalism is this: Do polar bears ever starve under conditions that cannot be blamed on sea ice changes? Indeed, they do. Amstrup (2003) notes

> starvation of independent young as well as very old animals must account for much of the natural mortality among polar bears. … Also, age structure data show that subadults aged 2–5 years survive at lower rates than adults (Amstrup, 1995), probably because they are still learning hunting and survival skills. … I once observed a 3-year-old subadult that weighed only 70 kg in November. This was near the end of the autumn period in which Beaufort Sea bears reach their peak weights (Durner and Amstrup, 1996), and his cohorts at that time weighed in excess of 200 kg. This young animal apparently had not learned the skills needed to survive and was starving to death.

It appears the anecdotal reports of cannibalism, infanticide, and den collapses due to spring rain are being included for their emotional appeal to the public but are not associated with recent declines in local or global sea ice or with recent increases in temperature. Data supporting claims of declines in body condition for Western Hudson Bay polar bears are seriously out of date and/or unpublished, and in the Southern Beaufort, declines in body condition due to heavy ice conditions in spring have been documented every decade since the 1960s. Despite attempts to blame these phenomena on global warming, peer-reviewed research suggest otherwise.

References

Amstrup, S.C. 2003. Polar bear (*Ursus maritimus*). In: Feldhamer, G.A., Thompson, B.C., and Chapman, J.A. (Eds.) *Wild Mammals of North America.* Baltimore, MD: Johns Hopkins University Press, pp. 587–610.

Amstrup, S.C. 1995. Movements, distribution, and population dynamics of polar bears in the Beaufort Sea. Ph.D. dissertation, University of Alaska Fairbanks, Fairbanks.

Amstrup, S.C. 2011. Polar bears and climate change: certainties, uncertainties, and hope in a warming world. In: Watson, R.T., Cade, T.J., Fuller, M., Hunt, G., and Potapov, E. (Eds.) *Gyrfalcons and Ptarmigan in a Changing World, Volume 1.* Boise, ID: The Peregrine Fund, pp. 11–20.

Amstrup, S.C. and DeMaster, D.P. 1988. Polar Bear. In: Lentfer, J.W. (Ed.) *Selected Marine Mammals of Alaska: Species Accounts with Research and Management*

Recommendations. Washington, DC: Marine Mammal Commission, pp. 39–56.

Amstrup, S.C., DeWeaver, E.T., Douglas, D.C., Marcot, B.G., Durner, G.M., Bitz, C.M., and Bailey, D.A. 2010. Greenhouse gas mitigation can reduce sea-ice loss and increase polar bear persistence. *Nature* **468:** 955–958.

Amstrup, S.C., Marcot, B.G., and Douglas, D.C. 2008. A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. In: DeWeaver, E.T., Bitz, C.M., and Tremblay, L.B. (Eds.) *Arctic Sea Ice Decline: Observations, Projections, Mechanisms, and Implications,* Geophysical Monograph 180. Washington, DC: American Geophysical Union, pp. 213–268.

Amstrup, S.C., McDonald, T.L., and Stirling, I. 2001. Polar bears in the Beaufort Sea: A 30-year mark-recapture case history. *Journal of Agricultural, Biological, and Environmental Statistics* **6:** 221–234.

Amstrup, S.C., Stirling, I., Smith, T.S., Perham, C., and Thiemann, B.W. 2006. Recent observations of intraspecific predation and cannibalism among polar bears in the Southern Beaufort Sea. *Polar Biology* **29**: 997–1002.

Cherry, S.G., Derocher, A.E., Stirling, I., and Richardson, E.S. 2009. Fasting physiology of polar bears in relation to environmental change and breeding behavior in the Beaufort Sea. *Polar Biology* **32:** 383–391.

Cherry, S.G., Derocher, A.E., Thiemann, G.W., and Lunn, N.J. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology* **82:** 912–921.

Derocher, A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* **44**: 163–176.

Derocher, A.E., Stirling, I., and Andriashek, D. 1992. Pregnancy rates and progesterone levels of polar bears in western Hudson Bay. *Canadian Journal of Zoology* **70:** 561–566.

Derocher, A.E. and Wiig, Ø. 1999. Infanticide and cannibalism of juvenile polar bears (*Ursus maritimus*) in Svalbard. *Arctic* **52:** 307–310.

Durner, G.M. and Amstrup, S.C. 1996. Mass and body-dimension relationships of polar bears in northern Alaska. *Wildlife Society Bulletin* **24:** 480–484.

Durner, G.M., Douglas, D.C., Nielson, R.M., Amstrup, S.C., McDonald, T.L., Stirling, I., Mauritzen, M., Born, E.W., Wiig, Ø., DeWeaver, E., Serreze, M.C., Belikov, S.E., Holland, M.M., Maslanik, J., Aars, J., Bailey, D.A., and Derocher, A.E. 2009**.** Predicting 21st-century polar bear habitat distribution from global climate models. *Ecological Monographs* **79:** 25–58.

Harwood, L.A., Smith, T.G., Melling, H., Alikamik, J., and Kingsley, M.C.S. 2012. Ringed seals and sea ice in Canada's western Arctic: harvest-based monitoring 1992-2011. *Arctic* **65:** 377–390.

Kingsley, M.C.S. and Byers, T.J. 1998. Failure of reproduction in ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories in 1984–1987. In: Heide-Jørgensen, M.P. and Lydersen, C. (Eds.) *Ringed Seals in the North Atlantic.* NAMMCO Scientific Publication 1. Tromsø: The North Atlantic Marine Mammal Commission, pp. 197–210.

Lunn, N.J. and Stenhouse, G.B. 1985. An observation of possible cannibalism by polar bears (*Ursus maritimus*). *Canadian Journal of Zoology* **63:** 1516–1517.

Melling, H. and Riedel, D.A. 2004. Draft and movement of pack ice in the Beaufort Sea: A time-series presentation April 1990–August 1999. *Canadian Technical Report of Hydrography and Ocean Sciences* **238.**

Melling, H., Riedel, D.A., and Gedalof, Z. 2005. Trends in the draft and extent of seasonal pack ice, Canadian Beaufort Sea. *Geophysical Research Letters* **32:** L24501.

Messier, F., Taylor, M.K., and Ramsay, M.A. 1994. Denning ecology of polar bears in the Canadian High Arctic. *Journal of Mammalogy* **75:** 420–430.

Obbard, M.E., Theimann, G.W., Peacock, E., and DeBryn, T.D. (Eds.) 2010. *Polar Bears: Proceedings of the 15th meeting of the Polar Bear Specialists Group IUCN/SSC, 29 June-3 July, 2009*. Copenhagen, Denmark. Gland, Switzerland and Cambridge UK, IUCN.

Peacock, E., Taylor, M.K., Laake, J., and Stirling, I. 2013. Population ecology of polar bears in Davis Strait, Canada and Greenland. *Journal of Wildlife Management* **77:** 463–476.

Pilfold, N.W., Derocher, A.E., Stirling, I., Richardson, E., and Andriashek, D. 2012. Age and sex composition of seals killed by polar bears in the eastern Beaufort Sea. *PLoS ONE* **7**: e41429.

Ramsay, M.A. and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology London* **214:** 601–624.

Regehr, E.V., Amstrup, S.C., and Stirling, I. 2006. *Polar bear population status in the southern Beaufort Sea*. U.S. Geological Survey Open-File Report 2006-1337.

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C., and Stirling, I. 2010. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. *Journal of Animal Ecology* **79**: 117–127.

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C., and Stirling, I. 2007. Polar bears in the southern Beaufort Sea I: survival and breeding in relation to sea ice conditions, 2001–2006. Administrative Report, U.S. Department of the Interior- U.S. Geological Survey, Reston, VA.

Rode, K.D., Amstrup, S.C., and Regehr, E.V. 2010. Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications* **20:** 768–782.

Rode, K.D., Peacock, E., Taylor, M., Stirling, I., Born, E.W., Laidre, K.L., and Wiig, Ø. 2012. A tale of two polar bear populations: ice habitat, harvest, and body condition. *Population Ecology* **54:** 3–18.

Rode, K.D., Regehr, E.V., Douglas, D., Durner, G., Derocher, A.E., Thiemann, G.W., and Budge, S. 2014. Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. *Global Change Biology* **20:** 76–88.

Smith, T.G. 1987. The ringed seal, *Phoca hispida,* of the Canadian western Arctic. *Canadian Bulletin of Fisheries and Aquatic Sciences* **216**.

Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic* **55** (Suppl. 1)**:** 59–76.

Stirling, I. and Derocher, A.E. 2012. Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology* **18:** 2694–2706

Stirling, I. and Lunn, N.J. 1997. Environmental fluctuations in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. In: Woodin, S.J. and Marquiss, M. (Eds.) *Ecology of Arctic Environments.* Blackwell Science, UK, pp. 167–181.

Stirling, I., McDonald, T.L., Richardson, E.S., Regehr, E.V., and Amstrup, S.C. 2011. Polar bear population status in the northern Beaufort Sea, Canada, 1971–2006. *Ecological Applications* **21:** 859–876.

Stirling, I. and Øritsland, N.A. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* **52:** 2594–2612.

Stirling, I., Richardson, E., Thiemann, G.W., and Derocher, A.E. 2008. Unusual predation attempts of polar bears on ringed seals in the southern Beaufort Sea: possible significance of changing spring ice conditions. *Arctic* **61:** 14–22.

Stirling, I. and Ross, J.E. 2011. Observations of cannibalism by polar bears (*Ursus maritimus*) on summer and autumn sea ice at Svalbard, Norway. *Arctic* **64:** 478–482.

Stone, I.R. and Derocher, A.E. 2007. An incident of polar bear infanticide and cannibalism on Phippsøya, Svalbard. *Polar Record* **43:** 171–173.

Stroeve, J., Holland, M.M., Scambos, T., and Serreze, M. 2007. Arctic sea ice decline: faster than forecast. *Geophysical Research Letters* **34:** L09501, doi: 10.1029/2007/GL029703.

Taylor, M., Larsen, T., and Schweinsburg, R.E. 1985. Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). *Arctic* **38:** 303–309.

Taylor, M., and Lee, J. 1995. Distribution and abundance of Canadian polar bear populations: a management perspective. *Arctic* **48:** 147–154.

5.8.3.2 Changes in Reproductive Success

A warmer Arctic portending dramatic declines in sea ice is predicted to have significant effects on the reproductive success of polar bears, based on changes already documented in some subpopulations. Stirling and Derocher (2012) have this to say about reproductive success in the western Hudson Bay subpopulation: “the proportion of independent yearlings fell from over 81% before 1980 to a mean of 34% in 1980–1992 (Derocher and Stirling, 1995). By the late 1990s, the proportion of independent yearlings dropped to <10% (Stirling *et al.*, 1999) and by the early 2000s was almost nonexistent (I. Stirling, unpublished data).”

In the 1999 paper the authors cite, Stirling *et al.* say this: “The proportion of yearlings that were independent in the annual capture samples fluctuated widely at 3–4 year intervals, but overall the maximum proportions have declined from about 60% in 1982 to 15–20% since 1991 (Fig. 6). There was no statistically significant relationship between the proportion of lone yearlings and the time of [sea ice] breakup in the same year (r =- 0.205, n = 14, p = 0.46).” More importantly, Stirling *et al* (1999) also point out, “for about the last 12 years [ending 1998], estimates of population size have remained relatively constant (Lunn *et al.*, 1997; this study), indicating that the declines in condition and natality have not led to a decline in population.” In other words, the well-documented change from weaning at 2.5 years rather than 1.5 years had no immediate negative impact on the population up to 1992, and any additional data collected on this phenomenon are not available in the peer-reviewed literature.

Derocher and Stirling (1995) state: “the results of our analyses suggest that the unique reproductive characteristics of polar bears in western Hudson Bay in the 1960s and 1970s were either a function of a population increasing from a depleted state and feeding on a relatively abundant prey base, or density-independent fluctuations in prey population size, or availability due to sea ice variation." Therefore, declining sea ice is not the only reason reproductive parameters, such as age at weaning, might change. And since the assertion that the proportion of independent yearlings was "almost nonexistent" by the early 2000s is based on unpublished data, we cannot be sure the claimed further decline in proportion of independent yearlings has had any significant impact on population size, since previous changes did not.

In addition, it should be noted the proportion of independent yearlings being approximately zero is the norm for virtually all other polar bear subpopulations studied (Ramsay and Stirling, 1988; Van de Velde *et al.,* 2003). Western Hudson Bay always has been anomalous in this feature. In that respect, in weaning their cubs at 2.5 years rather than 1.5 years, Western Hudson Bay polar bears may simply be returning to normal.

Stirling and Lunn (1997) perhaps put it best:

> In the early to mid-1980s, the natality [cub production] of female polar bears in western Hudson Bay was the highest recorded anywhere in polar bear range, and nowhere else did females successfully wean cubs at 1.5 years of age instead of at the normal age of 2.5 years. Subsequently, a long-term decline in condition of adult female polar bears and survival of their cubs was documented from the 1970s through the late 1980s (Derocher and Stirling, 1992), as reflected by a significant decline in condition indices. This decline did not constitute a threat to the population because even when natality was at its lowest in the late 1980s, the rates were still higher than the upper range of values for bears elsewhere in the Arctic (e.g., Stirling *et al*., 1976, 1980). … The more important (but unanswered) question is probably not why natality declined from the early 1980s but how could natality have been sustained at a level so much higher than other polar bear populations in the first place, what facilitated the successful weaning of yearlings there but nowhere else in their range, and how could females manage these physiological feats in a habitat where pregnant females must also fast for 8 months or more?"

They did not answer their question.

Rode *et al*. (2014), in their recent study of Chukchi Sea polar bears, found "spring COY litter sizes are among the highest reported for 18 of 19 polar bear populations. ... [S]pring litter sizes of CS yearlings from the study were also higher than other populations." The authors note, "the larger body mass of adult females in the CS corresponded not only with larger litter sizes, but also with heavier yearlings (Fig.5) which have a greater chance of survival" and "body size, condition, and reproductive indices of CS polar bears did not decline over time between 1986–1994 and 2008–2011 despite a 44-day increase in the number of reduced-ice days." In other words, contrary to predictions, reproductive parameters of Chukchi Sea polar bears did not decline, despite marked declines in summer sea ice.

References

Derocher, A.E. and Stirling, I. 1992. The population dynamics of polar bears in western Hudson Bay. In: McCullogh, D. R. and Barrett, R.H. (Eds.) *Wildlife 2001: Populations*. London: Elsevier Applied Science, pp. 1150–1159.

Derocher, A.E. and Stirling, I. 1995. Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. *Canadian Journal of Zoology* **73:** 1657–1665.

Lunn, N.J., Stirling, I., Andriashek, D., and Kolenosky, G.B. 1997. Re-estimating the size of the polar bear population in western Hudson Bay. *Arctic* **50:** 234–240.

Ramsay, M.A. and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology London* **214:** 601–624.

Stirling, I., Calvert, W., and Andriashek, D. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. *Canadian Wildlife Service Occasional Papers* **44.**

Stirling, I. and Derocher, A.E. 2012. Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology* **18:** 2694–2706.

Stirling, I. and Lunn, N.J. 1997. Environmental fluctuations in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. In: Woodin, S.J. and Marquiss, M. (Eds.) *Ecology of Arctic Environments.* UK: Blackwell Science, pp. 167–181.

Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climate change. *Arctic* **52:** 294–306.

Stirling, I., Pearson, A.M., and Bunnell, F.L. 1976. Population ecology studies of polar and grizzly bears in northern Canada. *Transactions of the North American Wildlife and Natural Resources Conference* **41:** 421–429.

Van de Velde, F., Stirling, I., and Richardson, E. 2003. Polar bear (*Ursus maritimus*) denning in the area of the Simpson Peninsula, Nunavut. *Arctic* **56:** 191–197.

5.8.4 Effects of more open water

Polar bears use sea ice as a platform for hunting, traveling, and denning. They are known to be excellent swimmers, capable of swimming long distances between ice flows. But what happens during the late summer, when the edge of the pack ice is many kilometers offshore for months at a time? Although some polar bears spend this "open water" period on land, is it because they are incapable of swimming to the ice edge once it gets beyond a certain point? Or are polar bears, particularly females with cubs, able to swim hundreds of kilometers from land to the ice edge during the "open water" season if they choose to do so?

Working from three points along the coast of the Beaufort and Chukchi Seas, Alaska (Barrow, Prudhoe Bay, Kaktovik) between 2004 and 2009, Pagano *et al.* (2012) attached radio collars during March through May (but also in August 2008) to 62 female polar bears, some of which had cubs with them. The number of bears successfully monitored for this study varied each year; as only two collars were deployed in 2007 and one of these failed, data from 2007 were excluded. The authors analyzed global positioning system (GPS) data from the 52 radio collars that successfully transmitted signals between 1 June and 31 October each year and compared these to the position of the sea ice edge determined from satellite imagery. Some additional data from bears collared between 1985 and 2009 were used to assess whether an early cessation of signal transmission during the open water period (July through September), from bears that had been at sea and were not later re-sighted, could be assumed to indicate the bears had drowned while swimming.

The authors found 50 "long-distance" swimming events (>50 km) were made by 20 of the bears monitored (38% of the total), and 12 of the 20 bears that swam long distances did so multiple times in the same year. The researchers found the majority of the long-distance swims were from unconsolidated sea ice (ice concentration <50%) to the main pack ice (mean distance 155.9 km, range 114.5–197.4 km, 25 swims). Relatively few bears swam from land to another area of land (mean distance 106.2 km, range 53.7–288.3 km, 7 swims) or from unconsolidated sea ice to land (mean distance 169.1 km, range 69.9–302.6 km, 6 swims). Only three swims involved bears moving from land to unconsolidated sea ice (mean distance 102.3 km, range 68.3–113.7 km), and only two were bears moving from land to the main pack ice (mean distance 402.5 km, range 117.9–687.1 km).

There were no long-distance swimming data prior to 2004 with which to compare this study's data, and sampling differences among years precluded the researchers from determining any trend in their results.

They also found there was no significant difference in the rate of cub mortality between females with cubs that undertook long-distance swims and those that did not. It also appeared premature cessation of radio collar signal transmission did not necessarily indicate a bear had drowned; some bears whose signals stopped prematurely probably drowned, but drowning was not the only explanation for signal failure.

Pagano *et al.* calculated the mean distance between the mainland coast and the sea ice edge at the end of September for each year of the study period. This distance varied from a low of about 200 km (achieved in 2005, 2006, and 2009) and a high of about 430 km (achieved in 2008). Mean distance from the shore to the ice in 2004 was about 300 km, and in 2007 it was about 380 km. Each of these measurements varied somewhat depending on the configuration of the shoreline, but in 2008 the ice edge was definitely farther away than in any other year since 1979. However, the largest number of long-distance swimming events took place in 2009, when the ice edge in this region was about the same distance offshore as in 2005 and 2006. The longest swim was recorded in late August/early September of 2008 at a point where the sea ice was >500 km offshore: a female with a year-old cub swam 687.1 km in just over nine days, as described in detail by Durner *et al.* (2011). This bear was one of only two individuals in the Pagano *et al.* study that swam from land to the main pack ice edge; after a few weeks meandering around at the edge of the pack ice, this bear then walked back to shore on the rapid-forming ice, arriving on land at the end of October. The second-longest swim (366.0 km) was recorded in 2005, when the pack ice edge was about the same distance offshore as in 2009.

Pagano *et al.* state, "we show that both adult female polar bears and their dependent young possess an ability to swim long distances." They also observe, "most of the long-distance swimming events that we identified involved bears swimming from unconsolidated sea ice to the main pack ice or to land." In other words, few swims recorded were from land to sea ice, indicating that during the open water season most southern Beaufort and Chukchi Sea polar bears are on the sea ice, not on land—a point also made by Durner *et al.* (2011). In addition, the results of this study suggest that despite there being little or nothing for female polar bears and their cubs to eat on shore during the late summer months in the southern Beaufort Sea, the few bears that remain on shore are apparently not hungry enough to undertake long-distance swims to the pack ice to relieve their fast, although they appear able to do so. Despite an overall decline in September sea ice levels between 1979 and 2010, this study found no significant correlation between increased long-distance swims and increased amounts of open water in this region over time.

Although polar bears are clearly accomplished swimmers, an anecdotal account of polar bears that apparently drowned in open water, purported to be evidence of global warming and declining sea ice effects, has garnered remarkable media attention. Monnett and Gleason (2006) report what appeared at the time to be four dead polar bears that drowned in open water in 2004. The bodies were observed from aircraft while surveying for bowhead whales (*Balaena mysticetus*) after a September storm. However, like the anecdotal accounts of cannibalism and den collapses attributed to global warming by Stirling and Derocher (2012) discussed previously, no baseline scientific studies have quantified the number of swimming polar bears that have drowned under any conditions vs. those that have not. So while these isolated events continue to be touted as probable effects of global warming, there is no scientific evidence they are anything of the sort. Scientists do controlled, well-designed studies precisely because anecdotes cannot be trusted to give an unbiased picture of events. The inclusion of anecdotal events as supporting evidence of global warming is an appeal to emotions, rather than scientific reasoning.

References

Durner, G.M., Whiteman, J.P., Harlow, H.J., Amstrup, S.C., Regehr, E.V., and Ben-David, M. 2011. Consequences of long-distance swimming and travel over deep-water pack ice for a female polar bear during a year of extreme sea ice retreat. *Polar Biology* **34**: 975–984.

Monnett, C. and Gleason, J.S. 2006. Observations of mortality associated with extended open-water swimming by polar bears in the Alaskan Beaufort Sea. *Polar Biology* **29:** 681–687.

Pagano, A.M., Durner, G.M., Amstrup, S.C., Simac, K.S., and York, G.S. 2012. Long-distance swimming by polar bears (Ursus maritimus) of the southern Beaufort Sea during years of extensive open water. *Canadian Journal of Zoology* **90**: 663–676.

Stirling, I. and Derocher, A.E. 2012. Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology* **18:** 2694–2706.

5.9 Reptiles

- Studies of the effects of rising temperatures on reptiles find they often are able to tolerate a greater range of environmental conditions than they have been exposed to in the recent past, demonstrate abilities to thermo-regulate to achieve body temperatures close to their preferred temperatures, and often benefit from warmer temperatures.

Many are the predictions of species decline and possible extinction arising from warming-induced changes in the characteristics of regions to which the species are endemic. Concerns over the fate of reptiles are no exception, yet the results of several research studies conducted on this topic suggest these animals are in no such danger.

Chamaille-Jammes *et al*. (2006) studied four discontinuous subpopulations of the common lizard (*Lacerta vivipara*), a small live-bearing lacertid that lives in peat bogs and heath lands across Europe and Asia, concentrating on a small region near the top of Mont Lozere in southeast France, at the southern limit of the species' range. From 1984 to 2001 they monitored several life-history traits of the sub-populations, including body size, reproduction characteristics, and survival rates, while local air temperatures rose by approximately 2.2°C. They found individual body size increased dramatically in all four lizard populations over the 18-year study period, with snout-vent length expanding by roughly 28 percent. This increase in body size occurred in all age classes and, as they describe it, "appeared related to a concomitant increase in temperature experienced during the first month of life (August)." As a result, they found "adult female body size increased markedly, and, as fecundity is strongly dependent on female body size, clutch size and total reproductive output also increased." In addition, for a population where capture-recapture data were available, they learned "adult survival was positively related to May temperature."

Since all fitness components investigated responded positively to the increase in temperature, the French researchers state, "it might be concluded that the common lizard has been advantaged by the shift in temperature." This finding, they write, stands in stark contrast to the "habitat-based prediction that these populations located close to mountain tops on the southern margin of the species range should be unable to cope with the alteration of their habitat." They conclude, "to achieve a better prediction of a species persistence, one will probably need to combine both habitat and individual-based approaches." Furthermore, they note individual responses, such as those documented in their study (which were all positive), represent "the ultimate driver of a species response to climate change."

Noting tropical species long have been thought to be "especially sensitive to climatic fluctuations because their narrow thermal tolerances and elevational ranges can restrict their ability to persist in, or disperse across, alternate habitats," Bell *et al.* (2010) compared "responses to historical climate fluctuation in a montane specialist skink, *Lampropholis robertsi*, and its more broadly distributed congener, *L. coggeri*, both endemic to rainforests of northeast Australia." They combined "spatial modeling of potential distributions under representative palaeoclimates, multi-locus phylogeography and analyses of phenotypic variation." The seven scientists write, "both species exhibit pronounced phylogeographic structuring for mitochondrial and nuclear genes, attesting to low dispersal and high persistence across multiple isolated regions." Referring specifically to *L. robertsi*, the researchers state their evidence demonstrates "persistence and isolation" of most populations of the montane species "throughout the strong climate oscillations of the late Pleistocene, and likely extending back to the Pliocene."

Noting many of the isolated refugia they studied "are particularly rich in narrowly endemic species," Bell *et al.* state this characteristic has been attributed to "their relative stability during recent episodes of climate change (Williams and Pearson, 1997; Yeates *et al*., 2002; Graham *et al*., 2006; VanDerWal *et al*., 2009)." Furthermore, they say these observations "support the general hypothesis that isolated tropical montane regions harbor high levels of narrow-range taxa because of their resilience to past climate change," citing Fjeldsa and Lovett (1997) and Jetz *et al.* (2004). Thus, "at first sight, species such as *L. robertsi* would seem especially prone to local extinction and loss of considerable genetic diversity with any further warming; yet, these populations and those of other high-montane endemic species (*Cophixalus* frogs; Hoskin, 2004) have evidently persisted through past warming events."

Rodder *et al.* (2010) state, "if the climate changes, island endemics may be restricted in their ability to conduct range shifts depending on the topographic variability and the size of the island," and "species that inhabit islands characterized by low altitudinal variation may be the ones most strongly affected by climate change due to the lack of possibilities for horizontal or upward range shifts." However, they note only a small part of the fundamental niche of a species may currently be available to it, and the species may possess a hitherto-unknown ability to tolerate a much greater range of environmental conditions than that to which it may have been exposed in the recent past. Therefore, in determining what climatic conditions a species may be able to tolerate in the future, they state "a comparison between conditions tolerated in the present and in the past may be helpful."

Focusing on *Phelsuma parkeri*, an endemic gecko species native to the relatively flat (0 to < 100 m elevation) island of Pemba, Tanzania, Rodder *et al.* observed the species and provided information on its current spatial distribution in terms of both physical and environmental space, as well as its adaptability to habitat modification by humans. With respect to past climatic conditions, they employed simulations of the Last Glacial Maximum provided by the Community Climate System Model and the Model for Interdisciplinary Research on Climate, while with respect to the future, they employed climate change predictions based on three other models and the emission scenarios reported in the *Special Report on Emissions Scenarios* by the Intergovernmental Panel on Climate Change.

The three researchers report a comparison of current climatic conditions with those derived from model simulations for 21,000 years ago revealed "no climate conditions analogous to those of today existed during the Last Glacial Maximum," noting there were "decreases of between 1.4 and 2.8°C in the minimum temperature of the coldest month and of between 2.1 and 3.4°C in the maximum temperature of the warmest month throughout the island" compared to the corresponding temperatures of today. As for the future, the climate models they used suggested "the minimum temperature of the coldest month may increase about 1.2 to 3.8°C and the maximum temperature of the warmest month by about 2.0 to 3.7°C." Rodder *et al.* say their results suggest "*P. parkeri* is distributed over the largest part of the island, that it is well adapted to current land use, and that it is most likely not threatened by climate change."

Moreno-Rueda *et al*. (2011) "used data on the distributions of reptiles in Spain during the 20th century to analyze whether the distributions of these reptiles have changed as climate has changed." They compared "the distributions of reptile species before 1975"—the year, they say, according to IPCC (2007), the current period of warming began—"with distributions during 1991–2005." The authors report, "after controlling for sampling effort, geographic bias in sampling, phylogeny, and spatial autocorrelation, the northern limits of the distribution of reptiles in Spain shifted northward between 1940–1975 and 1991–2005," but "there was no similar shift southward in the southern limits of species' ranges." In addition, the mean latitude of the ranges of the species they examined "shifted northward by an equivalent of 0.5 km/year, which is similar to the magnitude of range shifts in other taxonomic groups (Parmesan and Yohe, 2003)."

Noting they were "the first to show there is a correlation between changes in latitudinal distribution and increases in temperature for a wide variety of species of reptiles in Spain," the four researchers say their "finding that reptiles are expanding their northern ranges, potentially in response to climate change, could mean the probability of extinction associated with increases in temperature may be lower than expected."

According to Amiel and Shine (2012), a hatchling reptile's sex, body size, and shape, as well as its locomotor performance, "can be influenced not only by its genes, but also by the temperature that it experiences during incubation." At the time of their study little was known about whether incubation temperature can also affect a hatchling's cognitive skills. Amiel and Shine examined "whether incubation temperature affects lizards' ability to learn the location of a safe retreat site during a predatory attack," because mastering this cognitive task "is directly relevant to individual survival and therefore fitness," citing Paulissen (2008).

The pair of Australian researchers worked with the scincid lizard *Bassiana duperreyi*, by first "randomly dividing eggs from each clutch between two incubation treatments ('hot' = diel cycle of 22 ± 7.5°C; 'cold' = diel cycle of 16 ± 7.5°C)," treatments that "mimic thermal regimes typical of natural nests at low (hot) versus high (cold) elevations." They then conducted a specific test designed to evaluate the young lizards' cognitive skills and their abilities to act appropriately to escape the perceived danger. Amiel and Shine report finding "hot-incubated lizards achieved higher learning scores than did cold-incubated lizards," and "the number of errors they made decreased more from the first to the second half of the trials than was the case for cold-incubated lizards." They speculate, based on Ahmad and Zamenhof (1978), Rissman *et al*. (2002), Valenzuela and Lance (2004), and Radder *et al*. (2008), "thermal effects on hormone levels during incubation may induce structural variation in parts of the brain that control behaviors such as learning." Amiel and Shine conclude, "climate change may simultaneously generate novel challenges for post-hatching organisms, while also modifying their ability to respond flexibly to such challenges." They specifically opine, "in *B. duperreyi*, hotter natural nests over recent decades (due to climate change) probably have produced hatchling lizards with enhanced learning abilities."

Clarke and Zani (2012) note observed real-world temperature increases typically have been "asymmetrically distributed over diurnal time frames, with daily minima increasing at a faster rate than daily maxima," citing Karl *et al*. (1991, 1993), Easterling *et al*. (1997, 2000), and DeGaetano and Allen (2002), whereas most previous studies of the effects of global warming on biological systems have boosted temperatures by the same amount during all hours of the day and night. Clarke and Zani conducted their study of the potential impact of global warming on the common side-blotched lizard (*Uta stansburiana*)—which they collected about 20 km south of Burns, Oregon (USA) at the northern edge of the Great Basin Desert—employing the latter, more-realistic imposed mode of asymmetric nighttime-only warming.

Working at their field laboratory, Clarke and Zani simulated observed trends in the asymmetric alteration of the local diurnal temperature range by increasing the nighttime temperatures in the incubators into which they transferred the female lizards (from their daytime cages) during their ovarian cycle. They treated the eggs the female lizards produced in a similar manner during their incubation period, carefully documenting the differences they detected throughout the entire reproductive process between the female parent and progeny lizards of the warmed and control treatments.

The two U.S. researchers discovered higher night-time temperatures during the female lizards' ovarian cycles "increased the probability of reproductive success and decreased the duration of the reproductive cycle." They found the higher temperatures had neither positive nor negative effects on "embryo stage or size at oviposition, clutch size, egg mass or relative clutch mass." They also report "higher incubation temperatures increased hatchling size and decreased incubation period," noting "subsequent hatchlings were more likely to survive winter if they hatched earlier."

Clarke and Zani state, "as our findings confirm that climate warming is likely to increase the rate of development as well as advance reproductive phenology, we predict that warmer nights during the breeding season will increase reproductive output as well as subsequent survival in many temperate ectotherms, both of which should have positive fitness effects." Thus, they conclude, "these effects are primarily beneficial for this population of northern lizards," and they predict "future changes will continue to benefit the reproduction, growth and survival of individuals at this site."

Leal and Gunderson (2012) write, "the general view is that climate change will have a major impact on biodiversity by increasing the extinction risk of many species or changing their distributions," based on "the implicit assumption that species are relatively fixed entities, unable to respond to rapid changes in ecological conditions, including climatic variables, over an ecological timescale." They state "evidence that some organisms are able to respond to climatic changes over short timescales has begun to emerge (e.g., Grant and Grant, 2002; Walther *et al.*, 2002; Bradshaw and Holzapfel, 2006)."

Nearly 40 years ago, the tropical Caribbean lizard *Anolis cristatellus*, native to an area of xeric forest in northeastern Puerto Rico, was found in Miami, Florida, by Schwartz and Thomas (1975) in a location where minimum temperatures in winter can average 10°C cooler than in Puerto Rico, but where maximum temperatures in summer are much more similar. Taking advantage of this situation, Leal and Gunderson set about to determine whether the cold tolerance or critical thermal minimum temperature (CT_{min}) of the introduced populations had diverged from that of the source populations of *A. cristatellus* since their physical separation in 1975. As a check on their experimental procedures, they also conducted studies to see whether the critical thermal maximum temperature (CT_{max}) of the two groups of lizards remained about the same.

They found "the introduced population tolerates significantly colder temperatures (by ~3°C) than does the Puerto Rican source population," while the maximum temperatures tolerated "did not differ." These observations "demonstrate that changes in thermal tolerance occurred relatively rapidly (~35 generations), which strongly suggests that the thermal physiology of tropical lizards is more labile than previously proposed." They conclude, "regardless of the mechanism, the adaptive lability of thermal tolerance in *A. cristatellus* over an ecological timescale" provides "a glimpse of hope for tropical lizards under the current conditions of rapid climate change."

Valdecantos *et al.* (2013) note "temperature has a great impact on ectotherms, affecting physiological, behavioral and life history traits such as reproductive timing (Zug *et al.*, 2001; Labra and Bozinovic, 2002), reproductive mode (Shine, 2004), growth rate, survivorship (Huey, 1982), locomotion (Hertz *et al.*, 1983; Angilleta *et al.*, 2002) and diet (Espinoza *et al.*, 2004)." They note late twentieth century global warming "has been suggested as a potential threat for lizards at a global scale," citing Sinervo *et al.* (2010).

The researchers studied four related species—*Liolaemus irregularis*, *L. albiceps*, *L. multicolor*, and *L. yanalcu*—that inhabit high-elevation desert areas in Northwestern Argentina, Northern Chile, and Southwestern Bolivia, working both in the laboratory and at four sites near San Antonio de los Cobres in Salta, Argentina, where they measured body temperatures (Tb), air temperatures (Ta), soil temperatures (Ts), operative temperatures in the field (Te), and preferred body temperatures (Tpref) for all four species.

The four Argentine researchers report their study revealed all four species, "despite living at high elevation and harsh climatic conditions," were able to "behaviorally or physiologically thermo-regulate to achieve body temperatures close to their preferred temperatures." They conclude, "as proposed by Labra *et al.* (2009)," "many species are conservative in some aspects (e.g. Tpref), yet labile in others (e.g. Tb)," thus "allowing them to inhabit a wide range of environments."

Moritz *et al.* (2012) note it is often assumed large central populations of a species have higher genetic diversity and, therefore, greater potential for adaptive response to environmental change. But they state "this is not always the case," and "lineages that have persisted as isolates in peripheral areas through past climate change might well have genotypes that will confer greater resistance to future warming and which could be exploited for genetic translocation," citing Chown *et al.* (2010).

Moritz *et al.* (2012) tested this hypothesis through comparative assays of minimum and maximum critical thermal limits (CT_{min} and CT_{max}), as well as optimal performance parameters, including CT_{opt}, across central and peripheral lineages of three species of ground-dwelling skinks (scincid lizards) endemic to the rainforests of northeast Australia:

Gnypetoscincus queenslandiae, *Carlia rubrigularis,* and *Saproscincus basiliscus*.

Results of the analysis indicate "peripheral lineages show significantly increased optimal performance temperatures (T_{opt}) relative to central populations, as well as elevated CT_{min}." Moritz *et al.* conclude the peripheral lineages they examined "appear to have evolved higher thermal optima relative to centrally located lineages," noting this finding "contrasts with the usual assumption that local adaptation of peripheral populations will be overwhelmed by gene flow from the center of the species range or, in the absence of immigration, will experience higher extinction rates." Thus the authors state, "long-isolated populations in peripheral rainforests harbor genotypes that confer resilience to future warming."

Sea turtles, like many other reptiles, have what is called "temperature-dependent sex determination" (TSD), which means the temperature experienced by each developing embryo (within its individual eggshell casing, laid within a nest built by the mother on a terrestrial beach) determines its sex (Janzen, 1994). In turtles, males require somewhat cooler embryonic conditions than females: a temperature of 29°C generates a sex ratio among hatchlings of about 50:50, whereas at higher temperatures, more females are produced (Hawkes *et al*., 2009). (Strangely enough, in the tuatara, another TSD reptile, the opposite is true: more males are produced at higher temperatures.) As a result, strongly skewed offspring sex ratios are common in TSD reptiles.

The amount of global warming predicted for the next century by some climate scientists is considered a threat to TSD-species because it is feared the higher temperatures will generate such extreme sex ratio biases (e.g. 100% females) that extinction will be inevitable (e.g. Fuentes *et al*., 2010; Janzen, 1994; Witt *et al*., 2010). As a highly female-skewed hatchling sex ratio already occurs in marine turtles (Hawkes *et al*. 2009), "predicted increases in global temperatures are expected to exacerbate this trend," say Wright *et al*., 2012.

Although living sea turtle species have survived substantial temperature fluctuations in the recent past (Janzen and Paukstis, 1988), Wright *et al*. (2012) investigated whether they will be able to adapt to future warming. Wright *et al*. examined the mating behavior of green sea turtles (*Chelonia mydas*) to see if it was compensating for the extreme female-skewed sex ratios of hatchlings currently produced in the Mediterranean (86–96% female). They undertook genetic typing of tissue samples taken in 2008 from 20 nesting females and 809 of their offspring (from 37 clutches of eggs), from a single rookery beach in northern Cyprus. Paternity analysis of the hatchlings allowed the researchers to determine how many males had mated with the females they sampled. They also put a satellite transmitter on a single male to map his movements during the breeding season.

Sea surface temperatures at the study site rose by, on average, less than 1°C over the past 50 years, and the female bias that exists today in adult green sea turtles is probably the result of a similar extent of female bias among hatchlings produced approximately 30 years ago (due to the late age at sexual maturity in this species)—that is, the authors assumed many more breeding-aged adult turtles in the population were female than were male.

They found, "despite an offspring sex ratio of 95 per cent females, there were at least 1.4 reproductive males to every breeding female"—28 males breeding with 20 females tested. The authors suggest males may breed more often than females (females breed every 2–4 years). In addition, the male they tracked visited a number of rookeries in the region, suggesting males may mate with females on a number of different beaches. Together, the authors suggest, these mating behaviors partially compensate for the lower abundance of males within the population, so "male mating patterns have the potential to buffer the disruptive effects of climate change on marine turtle populations, many of which are already seriously threatened." Furthermore, Wright *et al.* conclude, "current mating patterns will help to preserve genetic variation that may be critical if marine turtles are to adapt behaviorally or physiologically to a warming climate and have, no doubt, contributed to their persistence through historical climatic upheaval."

Citing Lavergne *et al.* (2010), Refsnider and Janzen (2012) also studied turtles, writing, "adaptation to climate change may be impossible even when high genetic variation is present if the rate of environmental change is too rapid and the population demography is insufficiently dynamic," adding, "species with temperature-dependent sex determination may be particularly threatened by climate change, because altered temperatures could skew sex ratios." Refsnider and Janzen experimentally tested nest-site choice in the long-lived turtle *Chrysemys picta*, to see whether nesting behavior "could compensate for potential skews in sex ratios caused by rapid climate change." They collected females from five populations spread across the species' range, housed them in a semi-natural common garden, and waited to see what would happen.

The two researchers report "females from transplanted populations showed similar choice of shade cover over nests to local females," which suggests, in their words, "behavioral phenotypic plasticity in female choice of shade cover over the nest site may comprise an immediate mechanism by which long-lived reptiles with temperature-dependent sex determination can avoid skews in sex ratio potentially caused by rapid climate change."

References

Ahmad, G. and Zamenhof, S. 1978. Serotonin as a growth factor for chick embryo brain. *Life Sciences* **22**: 963–970.

Amiel, J.J. and Shine, R. 2012. Hotter nests produce smarter young lizards. *Biology Letters* **8**: 372–374.

Angilleta Jr., M.J., Niewiarowski, P.H., and Navas, C.A. 2002. The evolutions of thermal physiology in ectotherms. *Journal of Thermal Biology* **27**: 249–268.

Bell, R.C., Parra, J.L., Tonione, M., Hoskin, C.J., Mackenzie, J.B., Williams, S.E., and Moritz, C. 2010. Patterns of persistence and isolation indicate resilience to climate change in montane rainforest lizards. *Molecular Ecology* **19**: 2531–2544.

Bradshaw, W.E. and Holzapfel, C.M. 2006. Evolutionary responses to rapid climate change. *Science* **312**: 1477–1478.

Chamaille-Jammes, S., Massot, M., Aragon, P., and Clobert, J. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* **12:** 392–402.

Chown, S., Hoffmann, A.A., Kristensen, T.N., Angilletta Jr., M.J., Stenseth, N.C., and Pertoldi, C. 2010. Adapting to climate change: a perspective from evolutionary physiology. *Climate Research* **43**: 3–15.

Clarke, D.N. and Zani, P.A. 2012. Effects of night-time warming on temperate ectotherm reproduction: potential fitness benefits of climate change for side-blotched lizards. *The Journal of Experimental Biology* **215**: 1117–1127.

DeGaetano, A.T. and Allen, R.J. 2002. Trends in twentieth-century temperature extremes across the United States. *Journal of Climate* **15**: 3188–3205.

Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, M.J., Razuvayev, V., Plummer, N., Jamason, P., and Folland, C.K. 1997. Maximum and minimum temperature trends for the globe. *Science* **277**: 364–367.

Easterling, D.R., Karl, T.R., Gallo, K.P., Robinson, D.A., Trenberth, K.E., and Dai, A. 2000. Observed climate variability and change of relevance to the biosphere. *Journal of Geophysical Research* **105**: 20,101–20,114.

Espinoza, R.R., Wiens, J.J., and Tracy, C.R. 2004. Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences USA* **101**: 16,819–16,824.

Fjeldsa, J. and Lovett, J.C. 1997. Biodiversity and environmental stability. *Biodiversity and Conservation* **6**: 315–323.

Fuentes, M.M.P.B., Hamann, M., and Limpus, C.J. 2010. Past, current and future thermal profiles of green turtle nesting grounds:implications from climate change. *Journal of Experimental Marine Biology and Ecology* **383**: 56–64.

Graham, C.H., Moritz, C., and Williams, S.E. 2006. Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences, USA* **103**: 632–636.

Grant, P.R. and Grant, R.B. 2002. Unpredictable evolution in 30-year study of Darwin's finches. *Science* **296**: 707–711.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H., and Godley, B.J. 2009. Climate change and marine turtles. *Endangered Species Research* **7**: 137–154.

Hertz, P.E., Huey, R., and Nevo, E. 1983. Homage to Santa Rita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* **37**: 1075–1084.

Hoskin, C.J. 2004. Australian microhylid frogs (*Cophixalus and Austrochaperina*): phylogeny, taxonomy, calls, distributions and breeding biology. *Australian Journal of Zoology* **52**: 237–269.

Huey, R.B. 1982. Temperature, physiology, and the ecology of the reptiles. In: Gans, C. (Ed.) *Biology of the Reptilia*, Vol. 12. Wiley, New York, New York, USA, pp. 25–91.

Janzen, F.J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Science USA* **91**: 7487–7490.

Janzen, F.J. and Paukstis, G.L. 1988. Environmental sex determination in reptiles. *Nature* **332**: 790.

Jetz, W., Rahbek, C., and Colwell, R.K. 2004. The coincidence of rarity and richness and the potential signature of history in centers of endemism. *Ecology Letters* **7**: 1180–1191.

Karl, T.R., Kukla, G., Razuvayev, V.N., Changery, M.J., Quayle, R.G., Helm Jr., R.R., Easterling, D.R., and Fu, C.B. 1991. Global warming: evidence for asymmetric diurnal temperature change. *Geophysical Research Letters* **18**: 2253–2256.

Karl, T.R., Jones, P.D., Knight, R.W., Kukla, G., Plummer, N., Razuvayev, V., Gallo, K.P., Lindseay, J., Charlson, P.J., and Peterson, T.D. 1993. Asymmetric trends of daily maximum and minimum temperature. *Bulletin of the American Meteorology Society* **74**: 1007–1023.

Labra, A. and Bozinovic, F. 2002. Interplay between pregnancy and physiological thermoregulation in *Liolaemus* lizards. *Ecoscience* **9**: 421–426.

Labra, A., Pienar, J., and Hansen, T.F. 2009. Evolution of thermal physiology in Liolaemus lizards: adaptation, phylogenetic inertia, and niche tracking. *American Naturalist* **174**: 204–220.

Lavergne, S., Mouquet, N., Thuiller, W., and Ronce, O. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution and Systematics* **41**: 321–350.

Leal, M. and Gunderson, A.R. 2012. Rapid change in the thermal tolerance of a tropical lizard. *The American Naturalist* **180**: 815–822.

Moreno-Rueda, G., Pleguezuelos, J.M., Pizarro, M., and Montori, A. 2011. Northward shifts of the distributions of Spanish reptiles in association with climate change. *Conservation Biology* **26**: 278–283.

Moritz, C., Langham, G., Kearney, M., Krockenberger, A., VanDerWal, J., and Williams, S. 2012. Integrating phylogeography and physiology reveals divergence of thermal traits between central and peripheral lineages of tropical rainforest lizards. *Philosophical Transactions of the Royal Society B* **367**: 1680–1687.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

Paulissen, M.A. 2008. Spatial learning in the little brown skink, *Scincella lateralis*: the importance of experience. *Animal Behavior* **76**: 135–141.

Radder, R., Quinn, A.E., Georges, A., Sarre, S.D., and Shine, R. 2008. Genetic evidence for co-occurrence of chromosomal and thermal sex-determining systems in a lizard. *Biology Letters* **4**: 176–178.

Refsnider, J.M. and Janzen, F.J. 2012. Behavioural plasticity may compensate for climate change in a long-lived reptile with temperature-dependent sex determination. *Biological Conservation* **152**: 90–95.

Rissman, E.F., Heck, A.L., Leonard, J.E., Shupnik, M.A., and Gustafsson, J. 2002. Disruption of estrogen receptor ß gene impairs spatial learning in female mice. *Proceedings of the National Academy of Sciences USA* **99**: 3996–4001.

Rodder, D., Hawlitschek, O., and Glaw, F. 2010. Environmental niche plasticity of the endemic gecko *Phelsuma parkeri* Loveridge 1941 from Pemba Island, Tanzania: a case study of extinction risk on flat islands by climate change. *Tropical Zoology* **23**: 35–49.

Schwartz, A. and Thomas, R. 1975. *A Check-List of West Indian Amphibians and Reptiles*. Carnegie Museum of Natural History Special Publication 1. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.

Shine, R. 2004. Does viviparity evolve in cold climate reptiles because pregnant females maintain stable (not high) body temperature? *Evolution* **58**: 1809–1818.

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M.L., Meza-Lazaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibarguengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., and Sites, J.W. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**: 894–899.

Valdecantos, S., Martinez, V., Lobo, F., and Cruz, F.B. 2013. Thermal biology of Liolaemus lizards from the high Andes: Being efficient despite adversity. *Journal of Thermal Biology* **38**: 126–134.

Valenzuela, N. and Lance, V. (Eds.) 2004. *Temperature-Dependent Sex Determination in Vertebrates*. Smithsonian Institution, Washington, DC, USA.

VanDerWal, J., Shoo, L.P., and Williams, S.E. 2009. New approaches to understanding late Quaternary climate fluctuations and refugial dynamics in Australian wet tropical rain forests. *Journal of Biogeography* **36**: 291–301.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.

Williams, S.E. and Pearson, R.G. 1997. Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rainforests of Australia's wet tropics. *Proceedings of the Royal Society of London Series B—Biological Sciences* **264**: 709–716.

Witt, M.J., Hawkes, L.A., Godfrey, M.H., Godley, B.J., and Broderick, A.C. 2010. Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *Journal of Experimental Biology* **213**: 901–911.

Wright, L.I., Stokes, K.L., Fuller, W.J., Godley, B.J., McGowan, A., Snape, R., Tregenza, T., and Broderick, A.C. 2012. Turtle mating patterns buffer against disruptive effects of climate change. *Proceedings of the Royal Society B: Biological Sciences* Published online before print January 25, 2012 doi: 10.1098/rspb.2011.2285.

Yeates, D.K., Bouchard, P., and Monteith, G.B. 2002. Patterns and levels of endemism in the Australian wet tropics rainforest: evidence from flightless insects. *Invertebrate Systematics* **16**: 605–661.

Zug, G.R., Vitt, L.J., and Caldwell, J.P. 2001. *Herpetology. An Introductory Biology of Amphibians and Reptiles*. Second Edition. Academic Press, San Diego, California, USA. 630 pp.

5.10 Worms

- It appears earthworms and soil nematodes respond to increases in the air's CO_2 content, via a number of plant-mediated phenomena, in ways that further enhance the positive effects of atmospheric CO_2 enrichment on plant growth and development, while helping to sequester more carbon more securely in the soil and thereby reducing the potential for CO_2-induced global warming.

"Earthworms," writes Edwards (1988), "play a major role in improving and maintaining the fertility, structure, aeration and drainage of agricultural soils." As noted by Sharpley *et al*. (1988), for example, "by ingestion and digestion of plant residue and subsequent egestion of cast material, earthworms can redistribute nutrients in a soil and enhance enzyme activity, thereby increasing plant availability of both soil and plant residue nutrients," as others also have demonstrated (Bertsch *et al*., 1988; McCabe *et al*., 1988; Zachmann and Molina, 1988). Kemper (1988) describes how "burrows opened to the surface by surface-feeding worms provide drainage for water accumulating on the surface during intense rainfall," noting "the highly compacted soil surrounding the expanded burrows has low permeability to water which often allows water to flow through these holes for a meter or so before it is absorbed into the surrounding soil."

Hall and Dudas (1988) report the presence of earthworms appears to mitigate the deleterious effects of certain soil toxins. Logsdon and Lindon (1988) describe a number of other beneficial effects of earthworms, including enhancement of soil aeration, since under wet conditions earthworm channels do not swell shut as many soil cracks do; enhancement of soil water uptake, since roots can explore deeper soil layers by following earthworm channels; and enhancement of nutrient uptake, since earthworm casts and channel walls have a more neutral pH and higher available nutrient level than bulk soil.

In light of these observations, there is great interest about what may happen to earthworms as the air's CO_2 content and temperature rise.

With respect to how rising atmospheric CO_2 concentrations might impact earthworms, Edwards (1988) writes, "the most important factor in maintaining good earthworm populations in agricultural soils is that there be adequate availability of organic matter." Hendrix *et al.* (1988) and Kladivko (1988) report greater levels of plant productivity promote greater levels of earthworm activity. Consequently, since the most ubiquitous and powerful effect of atmospheric CO_2 enrichment is its stimulation of plant productivity (see Chapter 1, this volume), which leads to enhanced delivery of organic matter to soils, it logically follows this aerial fertilization effect of the ongoing rise in the air's CO_2 content should increase earthworm populations and amplify the many beneficial services they provide for plants.

Then there's the second most significant and common impact of atmospheric CO_2 enrichment on plants: its antitranspirant effect, whereby elevated levels of atmospheric CO_2 reduce leaf stomatal apertures and slow the rate of evaporative water loss from the vast bulk of Earth's vegetation. Growth chamber studies and field experiments that have studied this phenomenon provide voluminous evidence it often leads to increased soil water content in many terrestrial ecosystems (see Section 2.33, this volume), which is something earthworms favor.

Zaller and Arnone (1997) fumigated open-top and -bottom chambers they established in a calcareous grassland near Basal, Switzerland with air of either 350 or 600 ppm CO_2 for an entire growing season. They found the mean annual soil moisture content in the CO_2-enriched chambers was 10% greater than that observed in the ambient-air chambers. They note cumulative surface earthworm cast production after only one year was 35% greater in the CO_2-enriched chambers than in the control chambers. In addition, because earthworm casts are rich in organic carbon and nitrogen, the cumulative amount of these important nutrients on a per-land-area basis was found to be 28% greater in the CO_2-enriched chambers than in the ambient-air chambers. In a subsequent study of the same grassland, Zaller and Arnone (1999) report plants growing in close proximity to the earthworm casts produced more biomass than similar plants growing further away from them. They also found the CO_2-induced growth stimulation experienced by the various grasses was greater for those plants growing nearer the earthworm casts.

These observations show atmospheric CO_2 enrichment sets in motion a self-enhancing cycle of positive biological phenomena whereby increases in the air's CO_2 content stimulate plant productivity and reduce plant evaporative water loss, which results in more organic matter entering the soil and a longer soil moisture retention time and/or greater soil water contents. All of this leads to the development of larger and more active earthworm populations, which enhance many important soil properties, including fertility, structure, aeration, and drainage. These improved properties further enhance the growth of the plants.

There are additional reasons for optimism regarding this process. As Jongmans *et al*. (2003) point out, "the rate of organic matter decomposition can be decreased in worm casts compared to bulk soil aggregates (Martin, 1991; Haynes and Fraser, 1998)." They conducted a micro-morphological investigation of structural development and organic matter distribution in two calcareous marine loam soils on which pear trees had been grown for 45 years. One of the soils exhibited little or no earthworm activity and the other exhibited high earthworm activity, due to different levels of heavy metal contamination of the soils as a consequence of the prior use of different amounts of fungicides. Based on their results and other studies they cite, they conclude, "earthworms play an important role in the intimate mixing of organic residues and fine mineral soil particles and the formation of organic matter-rich micro-aggregates and can, therefore, contribute to physical protection of organic matter, thereby slowing down organic matter turnover and increasing the soil's potential for carbon sequestration." That is, atmospheric CO_2 enrichment that stimulates the activity of earthworms also leads to more—and more secure—sequestration of carbon in Earth's soils, thereby reducing the potential for CO_2-induced global warming.

Cole *et al*. (2002) report, "in the peatlands of northern England, which are classified as blanket peat, it has been suggested that the potential effects of global warming on carbon and nutrient dynamics will be related to the activities of dominant soil fauna, and especially enchytraeid worms." Cole *et al*. say they hypothesized warming would lead to increased enchytraeid worm activity, which would lead to higher grazing pressure on microbes in the soil, and since enchytraeid grazing has been observed to enhance microbial activity (Cole *et al*., 2000), they further hypothesized more carbon would be liberated in dissolved organic form, "supporting the view that global warming will increase carbon loss from blanket peat ecosystems."

The scientists constructed small microcosms from soil and litter they collected near the summit of Great Dun Fell, Cumbria, England. Subsequent to "defaunating" this material by reducing its temperature to -80°C for 24 hours, they thawed and inoculated it with native soil microbes. Half of the microcosms were incubated in the dark at 12°C and half at 18°C, the former temperature being approximately equal to mean August soil temperature at a depth of 10 cm at the site of soil collection, and the latter being "close to model predictions for soil warming that might result from a doubling of CO_2 in blanket peat environments."

Ten seedlings of an indigenous grass of blanket peat were then transplanted into each of the microcosms, while 100 enchytraeid worms were added to each of half of the mini-ecosystems. These procedures resulted in the creation of four experimental treatments: ambient temperature, ambient temperature + enchytraeid worms, elevated temperature, and elevated temperature + enchytraeid worms. The resulting 48 microcosms—sufficient to destructively harvest three replicates of each treatment four times throughout the course of the 64-day experiment—were arranged in a fully randomized design and maintained at either 12 or 18°C with alternating 12-hour light and dark periods. In addition, throughout the course of the study the microcosms were given distilled water every two days to maintain their original weights.

Contrary to their hypothesis, the scientists found elevated temperature reduced the ability of the enchytraeid worms to enhance the loss of carbon from the microcosms. At the normal ambient temperature, for example, the presence of the worms enhanced dissolved organic carbon (DOC) loss by 16%, and at the elevated temperature expected for a doubling of the air's CO_2 content, the worms had no effect at all on DOC. In addition, Cole *et al*. note, "warming may cause drying at the soil surface, forcing enchytraeids to burrow to deeper subsurface horizons." Hence, since the worms are known to have little influence on soil carbon dynamics below a depth of 4 cm (Cole *et al*., 2000), the scientists conclude this additional consequence of warming would further reduce the ability of enchytraeids to enhance carbon loss from blanket peatlands.

Summarizing their findings, Cole *et al*. say, "the soil biotic response to warming in this study was negative." That is, it resulted in a reduced loss of carbon to the atmosphere, which would tend to slow the rate of rise of the air's CO_2 content, as was suggested by the study of Jongmans *et al*.

Maraldo *et al*. (2010) also studied enchytraeids, recognizing their important contribution "to the decomposition processes and nutrient mineralization." Such activities have been shown to lead to increased nutrient availability and uptake by plants (Laakso and Setala, 1999; Cragg and Bardgett, 2001). Enchytraeids provide these benefits directly, as Maraldo *et al*. describe it, "by consuming large amounts of organic matter," and indirectly "by their feeding activity and modifications of soil structure." They note, "the presence of enchytraeids is especially important in nutrient poor ecosystems" such as "temperate heathland and northern coniferous forests, where their biomass dominates the soil faunal community," citing Cragg (1961) and Swift *et al*. (1998).

Working on a hilly, nutrient-poor, sandy soil with a dry heath/grassland cover at Brandbjerg, Denmark, Maraldo *et al*. conducted an experiment beginning October 2005 and extending through 2007. The seven scientists studied the individual and combined effects of soil warming, drought, and atmospheric CO_2 enrichment.

They warmed the soil so as to achieve a mean daily temperature increase of 0.3°C in winter and 0.7°C in summer at a depth of 5 cm, using a scaffolding that carried a curtain, which reflected the outgoing infrared radiation from the soil/plant surface back toward the ground, that was automatically pulled over the vegetation at sunset and retracted at sunrise. They achieved drought conditions by reducing peak soil water content by 11 percent and 13 percent compared to control plots in 2006 and 2007, using waterproof curtains that were automatically pulled over the vegetation during rain events. And they used a free-air CO_2 enrichment (FACE) system to increase the air's CO_2 concentration from 382 to 481 ppm.

Maraldo *et al*. report their experimentally imposed warming had no significant impact on enchytraeid biomass production, but their drought treatment decreased it by 40 percent. The extra 99 ppm of CO_2 stimulated enchytraeid biomass by 40 percent. At certain times this latter phenomenon was "especially positive," as in the summer of 2007, when "the total enchytraeid biomass in the CO_2 plots was increased by 108% compared to ambient plots." They found no interactions among the three factors, so "the positive effect of increased CO_2 [+40%] and the negative effect of drought [-40%] were cancelled out when applied in combination."

Bossuyt *et al*. (2005) note "earthworms ingest large quantities of organic materials that are mixed and excreted as casts (Parmelee *et al*., 1990; Martin and Marinissen, 1993; Jegou *et al*., 1998) and improve stable macroaggregation (Guggenberger *et al*., 1996; Marinissen and Hillenaar, 1996; Scullion and Malik, 2000)," as also has been found by van Rhee (1977), De Vleesschauwer and Lal (1981), and McKenzie and Dexter (1987). In addition, they remark, "the retention of organic C in soil is becoming more important since the rise in atmospheric CO_2 and global warming are recent concerns," and "earthworms are known to play a role in aggregate formation and soil organic matter (SOM) protection." However, they say, "it is still unclear at what scale and how quickly earthworms manage to protect SOM." They conducted a pair of experiments to address that question.

In the first experiment, Bossuyt *et al*. measured soil aggregate size distribution and total C and ^{13}C in three treatments—control soil, soil + ^{13}C-labeled sorghum leaf residue, and soil + ^{13}C-labeled residue + earthworms—after 20 days of incubation, where earthworms were added after the eighth day. In the second experiment, they determined the protected C and ^{13}C pools inside the newly formed casts and macro- and micro-soil-aggregates. They found the proportion of large water-stable macroaggregates was on average 3.6 times greater in the soil-residue samples that contained earthworms than in those that lacked earthworms, and the macroaggregates in the earthworm treatment contained approximately three times more sequestered carbon.

Bossuyt *et al*. state, "earthworms were found to form a significant pool of protected C in micro-aggregates within large macroaggregates after 12 days of incubation," thereby demonstrating the rapidity with which earthworms perform their vital function of sequestering carbon in soils when plant residues become available to them.

Don *et al*. (2008) studied the effects of anecic earthworms—which generally inhabit a single vertical burrow throughout their entire lives that can be as much as five meters in depth but is generally in the range of one to two meters—on soil carbon stocks and turnover at two extensively managed grassland sites in Thuringia, Germany. Analyzing enzyme activity, stable isotopes, nuclear magnetic resonance spectroscopy, and the ^{14}C age of the earthworm burrow linings, the seven German scientists found "the carbon distribution in soils is changed by anecic earthworms' activity with more carbon stored in the subsoil where earthworms slightly increase the carbon stocks." They also state "the translocation of carbon from [the] organic layer to the subsoil will decrease the carbon vulnerability to mineralization," because "carbon in the organic layer and the surface soil is much more prone to disturbances with rapid carbon loss than subsoil carbon."

Don *et al*. note "earthworms are present in almost all ecosystems around the globe with particularly high abundances in grasslands, where they increase productivity (Partsch *et al*., 2006)" and where "100–800 burrows per square meter have been reported by Lavelle (1988)." The presence and activity of earthworms play important roles in helping Earth's soils store and preserve carbon—and thereby mitigate the rate of rise of the atmosphere's CO_2 concentration.

Yeates *et al*. (2003) report a number of results they obtained from a season-long FACE study of a 30-year-old New Zealand pasture, where three experimental plots were maintained at the ambient atmospheric CO_2 concentration of 360 ppm and three others at a concentration of 475 ppm (a CO_2 enhancement of only 32%) for a period of four to five years. The pasture contained about 20 species of plants, including C_3 and C_4 grasses, legumes, and forbs, but the scientists' attention was focused more on what happened to the microfauna inhabiting the soil in which the plants grew.

Nematode populations increased significantly in response to the 32% increase in the air's CO_2 concentration. Of the various feeding groups studied, Yeates *et al*. report the relative increase "was lowest in bacterial-feeders (27%), slightly higher in plant (root) feeders (32%), while those with delicate stylets (or narrow lumens; plant-associated, fungal-feeding) increased more (52% and 57%, respectively)." The greatest nematode increases were recorded among omnivores (97%) and predators (105%). Most dramatic, root-feeding populations of the *Longidorus* nematode taxon rose by 330%. Also increasing in abundance were earthworms: *Aporrectodea caliginosa* by 25% and *Lumbricus rubellus* by 58%. Enchytraeids decreased in abundance, by approximately 30%.

Yeates *et al*. note the introduction of lumbricids has been demonstrated to improve soil conditions in New Zealand pastures (Stockdill, 1982), which helps pasture plants grow. Hence, the CO_2-induced increase in earthworm numbers observed in Yeates *et al*.'s study would be expected to do more of the same, and the reduced abundance of enchytraeids they documented in the CO_2-enriched pasture would lead to less carbon being released to the air from the soil, as per the known ability of enchytraeids to promote carbon loss from British peat lands under current temperatures.

Larsen and Clarke (2002) fed diets with and without coenzyme Q to wild-type nematodes (*Caenorhabditis elegans*) and several mutants during the adult phases of their lives, recording the lengths of time they survived. They found "withdrawal of coenzyme Q (Q) from the diet of wild-type nematodes extends adult life-span by ~60%." They also report the lifespans of the four mutants they studied were extended by a Q-less diet. More detailed analyses of their results led them to conclude the lifespan extensions were due to reduced generation and increased scavenging of reactive oxygen species.

The results and conclusions of this study are similar to those of Melov *et al*. (2000), who also studied *C. elegans*, testing the theory reactive oxygen species cause aging by examining the effects of two superoxide dismutase-/catalase-like mimetics (EUK–8 and EUK–134) on the lifespans of normal and mutant *C. elegans* worms that ingested various amounts of the mimetics. In every experiment, treatment of normal worms with the antioxidant mimetics significantly increased both mean and maximum lifespan. Treatment of normal worms with but 0.05 mM EUK–134, for example, increased their mean lifespan by fully 54%; in mutant worms whose normal lifespan was genetically shortened by 37%, treatment with 0.5 mM EUK–134 restored their lifespan to normal by increasing their mutation-reduced lifespan by 67%. They also determined these effects were not caused by a reduction in worm metabolism, which could have reduced the production of oxygen radicals, but "by augmenting natural antioxidant defenses without having any overt effects on other traits."

Melov *et al*. say their results "suggest that endogenous oxidative stress is a major determinant of the rate of aging." The significance of this statement resides in the fact that antioxidants tend to reduce such stresses in animals, and in the observation atmospheric CO_2 enrichment has been shown to significantly enhance the concentrations of many of these plant constituents (see Antioxidants, Section 7.3.1) as well as the concentrations of several substances that have been proven effective in fighting cancers, viral infections, and other animal maladies (see Health Effects of CO_2, Section 7.3).

It appears earthworms and soil nematodes respond to increases in the air's CO_2 content, via a number of plant-mediated phenomena, in ways that further enhance the positive effects of atmospheric CO_2 enrichment on plant growth and development, while helping to sequester more carbon more securely in the soil and thereby reducing the potential for CO_2-induced global warming.

References

Bertsch, P.M., Peters, R.A., Luce, H.D., and Claude, D. 1988. Comparison of earthworm activity in long-term no-tillage and conventionally tilled corn systems. *Agronomy Abstracts* **80**: 271.

Bossuyt, H., Six, J., and Hendrix, P.F. 2005. Protection of soil carbon by microaggregates within earthworm casts. *Soil Biology & Biochemistry* **37**: 251–258.

Cole, L., Bardgett, R.D., and Ineson, P. 2000. Enchytraeid worms (Oligochaeta) enhance mineralization of carbon in organic upland soils. *European Journal of Soil Science* **51**: 185–192.

Cole, L., Bardgett, R.D., Ineson, P., and Hobbs, P.J. 2002. Enchytraeid worm (Oligochaeta) influences on microbial community structure, nutrient dynamics and plant growth in blanket peat subjected to warming. *Soil Biology & Biochemistry* **34**: 83–92.

Cragg, J.B. 1961. Some aspects of the ecology of moorland animals. *Journal of Ecology* **49**: 477.

Cragg, R.G. and Bardgett, R.D. 2001. How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. *Soil Biology and Biochemistry* **33**: 2073–2081.

De Vleesschauwer, D. and Lal, R. 1981. Properties of worm casts under secondary tropical forest regrowth. *Soil Science* **132**: 175–181.

Don, A., Steinberg, B., Schoning, I., Pritsch, K., Joschko, M., Gleixner, G., and Schulze, E.-D. 2008. Organic carbon sequestration in earthworm burrows. *Soil Biology & Biochemistry* **40**: 1803–1812.

Edwards, C.A. 1988. Earthworms and agriculture. *Agronomy Abstracts* **80**: 274.

Guggenberger, G., Thomas, R.J., and Zech, W. 1996. Soil organic matter within earthworm casts of an anecic-endogeic tropical pasture community, Columbia. *Applied Soil Ecology* **3**: 263–274.

Hall, R.B. and Dudas, M.J. 1988. Effects of chromium loading on earthworms in an amended soil. *Agronomy Abstracts* **80**: 275.

Haynes, R.J. and Fraser, P.M. 1998. A comparison of aggregate stability and biological activity in earthworm casts and uningested soil as affected by amendment with wheat and lucerne straw. *European Journal of Soil Science* **49**: 629–636.

Hendrix, P.F., Mueller, B.R., van Vliet, P., Bruce, R.R., and Langdale, G.W. 1988. Earthworm abundance and distribution in agricultural landscapes of the Georgia piedmont. *Agronomy Abstracts* **80**: 276.

Jegou, D., Cluzeau, D., Balesdent, J., and Trehen, P. 1998. Effects of four ecological categories of earthworms on carbon transfer in soil. *Applied Soil Ecology* **9**: 249–255.

Jongmans, A.G., Pulleman, M.M., Balabane, M., van Oort, F., and Marinissen, J.C.Y. 2003. Soil structure and characteristics of organic matter in two orchards differing in earthworm activity. *Applied Soil Ecology* **24**: 219–232.

Kemper, W.D. 1988. Earthworm burrowing and effects on soil structure and transmissivity. *Agronomy Abstracts* **80**: 278.

Kladivko, E.J. 1988. Soil management effects on earthworm populations and activity. *Agronomy Abstracts* **80**: 278.

Laakso, J. and Setala, H. 1999. Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos* **87**: 58–64.

Larsen, P.L. and Clarke C.F. 2002. Extension of life-span in *Caenorhabditis elegans* by a diet lacking coenzyme Q. *Science* **295**: 120–123.

Lavelle, P. 1988. Earthworm activities and the soil system. *Biology and Fertility of Soils* **6**: 237–251.

Logsdon, S.D. and Linden, D.L. 1988. Earthworm effects on root growth and function, and on crop growth. *Agronomy Abstracts* **80**: 280.

Maraldo, K., Krogh, P.H., van der Linden, L., Christensen, B., Mikkelsen, T.N., Beier, C., and Holmstrup, M. 2010. The counteracting effects of atmospheric CO_2 concentrations and drought episodes: studies of enchytraeid communities in a dry heathland. *Soil Biology & Biochemistry* **42**: 1958–1966.

Marinissen, J.C.Y. and Hillenaar, S.I. 1996. Earthworm induced distribution of organic matter in macro-aggregates from differently managed arable fields. *Soil Biology & Biochemistry* **29**: 391–395.

Martin, A. 1991. Short- and long-term effects of the endogenic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas on soil organic matter. *Biology and Fertility of Soils* **11**: 234–238.

Martin, A. and Marinissen, J.C.Y. 1993. Biological and physico-chemical processes in excrements of soil animals. *Geoderma* **56**: 331–347.

McCabe, D., Protz, R., and Tomlin, A.D. 1988. Earthworm influence on soil quality in native sites of southern Ontario. *Agronomy Abstracts* **80**: 281.

McKenzie, B.M. and Dexter, A.R. 1987. Physical properties of casts of the earthworm *Aporrectodea rosea*. *Biology and Fertility of Soils* **5**: 328–332.

Melov, S., Ravenscroft, J., Malik, S., Gill, M.S., Walker, D.W., Clayton, P.E., Wallace, D.C., Malfroy, B., Doctrow, S.R., and Lithgow, G.J. 2000. Extension of life-span with superoxide dismutase/catalase mimetics. *Science* **289**: 1567–1569.

Parmelee, R., Beare, M.H., Cheng, W., Hendrix, P.F., Rider, S.J., Crossley, D.A., and Coleman, D.C. 1990. Earthworms and enchytraeids in conventional and no-tillage agroecosystems. A biocide approach to assess their role in organic matter breakdown. *Biology and Fertility of Soils* **10**: 1–10.

Partsch, S., Milcu, A., and Scheu, S. 2006. Decomposers (Lumbricadae, Collembola) affect plant performance in model grasslands of different diversity. *Ecology* **87**: 2548–2558.

Scullion, J. and Malik, A. 2000. Earthworm activity affecting organic matter, aggregation and microbial activity in soils restored after open cast mining for coal. *Soil Biology & Biochemistry* **32**: 119–126.

Sharpley, A.N., Syers, J.K., and Springett, J. 1988. Earthworm effects on the cycling of organic matter and nutrients. *Agronomy Abstracts* **80**: 285.

Stockdill, S.M.J. 1982. Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia* **24**: 29–35.

Swift, M.J., Andren, O., Brussaard, L., Briones, M., Couteaux, M.M., Ekschmitt, K., Kjoller, A., Loiseau, P., and Smith, P. 1998. Global change, soil biodiversity, and nitrogen cycling in terrestrial ecosystems—three case studies. *Global Change Biology* **4**: 729–743.

van Rhee, J.A. 1977. A study of the effect of earthworms on orchard productivity. *Pedobiologia* **17**: 107–114.

Yeates, G.W., Newton, P.C.D., and Ross, D.J. 2003. Significant changes in soil microfauna in grazed pasture under elevated carbon dioxide. *Biology and Fertility of Soils* **38**: 319–326.

Zachmann, J.E. and Molina, J.A. 1988. Earthworm-microbe interactions in soil. *Agronomy Abstracts* **80**: 289.

Zaller, J.G. and Arnone III, J.A. 1997. Activity of surface-casting earthworms in a calcareous grassland under elevated atmospheric CO_2. *Oecologia* **111**: 249–254.

Zaller, J.G. and Arnone III, J.A. 1999. Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO_2. *Ecology* **80**: 873–881.