6

Terrestrial Animals

6. Terrestrial Animals

Introduction

According to the Intergovernmental Panel on Climate Change (IPCC), "new evidence suggests that climate-driven extinctions and range retractions are already widespread" and the "projected impacts on biodiversity are significant and of key relevance, since global losses in biodiversity are irreversible (very high confidence)" (IPCC-II, 2007, p. 213). The IPCC claims that "globally about 20% to 30% of species (global uncertainty range from 10% to 40%, but varying among regional biota from as low as 1% to as high as 80%) will be at increasingly high risk of extinction, possibly by 2100, as global mean temperatures exceed 2 to 3°C above pre-industrial levels" (ibid.).

The Nongovernmental International Panel on Climate Change (NIPCC) disagreed. According to Idso and Singer (2009), "These claims and predictions are not based on what is known about the phenomenon of extinction or on real-world data about how species have endured the warming of the twentieth century, which the IPCC claims was unprecedented in the past two millennia" (p. 579).

The basis of the IPCC's forecasts is an assumption that the increase in temperature predicted to result from the ongoing rise in the atmosphere's CO_2 concentration will be so fast and of such great magnitude that many animal species will not be able to migrate poleward in latitude or upward in elevation rapidly enough to avoid extinction. In this chapter we review new research that contradicts this assumption as well as extensive observational data that contradict the claim of impending species extinctions.

References

Idso, C.D. and Singer, S.F. 2009. *Climate Change Reconsidered: 2009 Report of the Nongovernmental International Panel on Climate Change (NIPCC)*. Chicago, IL: The Heartland Institute.

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*. M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.D. Hanson. (Eds.) Cambridge University Press, Cambridge, UK.

6.1. Problems with Model-based Predictions of Extinctions

Thomas et al. (2004) 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 that were promoted by the Intergovernmental Panel on Climate Change (IPCC, 2007). Their ominous projections (the annihilation of more than a million unique 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, and they were typically portrayed as well-founded scientific predictions of what was bound to occur.

The 19 scientist-authors of the paper began their analysis by determining the "climate envelopes" of 1,103 species. Each of these envelopes represented the current climatic conditions under which a given species was found in nature. Then, after seeing how the habitat area of each of the studied species would be expected to change 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, this procedure seems reasonable enough, all else being equal. But "all else" is almost always not equal when something changes in the real world. An entirely different analysis of the available data was provided by Stockwell (2004), who noted, for example, that 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 described 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 continued, "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 noted, "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 the study of Bakkenes et al. (2002), for example, Stockwell wrote, "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 continued, "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 ecological models are so unreliable for reasons cited by Stockwell, the common-sense response should be to attempt to verify model-based projects with independent data. However, in the words of Stockwell, "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 concluded, "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's final thoughts on the matter, therefore, were, "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*'."

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. In doing so, 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 concluded, "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.

Nogues-Bravo (2009) noted climate envelope models—which are often employed to predict species responses to global warming—"are sensitive to theoretical assumptions, to model classes and to projections in non-analogous climates, among other issues." Against this backdrop, the researcher 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.

In the researcher's own words, "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 palaeoclimatic 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%)."

According to Nogues-Bravo, "ignoring the theoretical assumptions behind niche modeling and using inadequate methods for hindcasting" may well 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."

In conclusion, it is clear that model-based projections of extinctions are riddled with assumptions and limitations that make them an unreliable guide to the actual impact of climate change on species. As Dormann (2007) concluded, the shortcomings associated with analyses of the impact of climate on distributions of species "are so numerous and fundamental that common ecological sense should caution us against putting much faith in relying on their findings for further extrapolations."

References

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.

Botkin, D.B., Saxe, H., Araújo, 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.

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

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

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.* Edited by M.L. Parry, et al. Cambridge, UK: Cambridge University Press.

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.

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

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

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

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. and Peterson, A.T. 2002a. Controlling bias during predictive modeling with museum data. In *Predicting Species Occurrences: Issues of Scale and Accuracy*. Edited by J.M. Scott et al. 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.

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.

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.

6.2. Comparing Model Projections with Observations

Model-based projections of CO_2 and warming-induced extinctions suffer a major loss of credibility when tested against real-world data. Animal life flourished during past epochs of planetary warmth, and warming of the magnitude experienced during the twentieth and early twenty-first centuries has occurred many times in the past and typically has benefitted terrestrial animals. In the subsections that follow, we highlight studies that focus on seven types of animals, beginning with amphibians.

6.2.1. Amphibians

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 totally went extinct locally, or were extirpated—had occurred over the prior two decades, a period described by the IPCC as having experienced unprecedented warming. Holmes (1999), in a popular science article describing the mystery’s putative solution, wrote that the authors of the two reports made “a convincing case blaming global climate change for these ecological events.”

Then, however, came the study of Lawton et al. (2001), which presented “an alternative mechanism—upwind deforestation of lowlands—that may increase convective and orographic cloud bases even more than changes in sea surface temperature do.”

The four scientists began 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. They 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.

At this point 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). The matter was resolved by Lawton et al. 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 that 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 that 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, while 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 after that—in a study that 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. (2006) 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, in the researchers' words, that 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 suggested "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." These findings clearly relieved anthropogenic CO_2 emissions of blame for the decreases in frog and toad populations that had been experienced in the highland forests of Monteverde, Costa Rica, instead placing that blame squarely on the shoulders of those responsible for the felling of the adjacent lowland forests.

As additional cases of amphibian mass mortality were reported throughout the world, Parmesan (2006) and Pounds et al. (2006) pointed accusing fingers at 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 within the Penalara Natural Park in the Sierra de Guadarrama of Central Spain, Bosch et al. (2007) looked for relationships between 20 different 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, as they described it, "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. noted "associations between climate and disease do not necessarily imply causation." They also stated, "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 said it would 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." Consequently, and in light of the many complexities they listed, it was clear the last word on the subject was yet to be written—and, in fact, several additional studies appeared in print the following year.

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."

In discussing their findings, Lips et al. said they revealed "a classical pattern of disease spread across native populations, at odds with the CLEH proposed by Pounds et al. (2006)." Emphasizing that the latter's "analyses and re-analyses of data related to the CLEH all fail to support that hypothesis," Lips et al. went on to conclude their own analyses supported "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 made it clear disease dynamics are indeed "affected by micro- and macro-climatic variables," and "such synergistic effects likely act on *Bd* and amphibians," their work clearly showed 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 amphibian 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 extinctions." This he did "using 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, in Laurance's words, provided "little direct support for the warm-year hypothesis of Pounds et al." Instead, he "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."

In further discussing his findings, Laurance stated 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 noted, 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 continued, "it stretches plausibility to argue that the chytrid pathogen is simply an opportunistic, endemic microparasite 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." After completing their research, the five scientists reported "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 note, "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*."

The next year, Alford et al. (2009)—no longer feeling any need to address the repudiated climate-linked epidemic hypothesis—quantified four movement characteristics of three groups of radio-tracked cane toads (*Bufo marinus*) at three places in Australia: (1) a location where the toads had been established for some 50 years at the time of their sampling, (2) a location where the first toads arrived about six months before sampling began in 1992 and 1993, and (3) a location where sampling occurred for a period of 13 months, starting at the time of the toads' initial arrival in 2005. The results of this exercise revealed that 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." As for why this is so, 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 of the fact that "invasion-front toads in 1992 were more dispersive than origin-population toads in the same year, but that 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."

In discussing their findings, Alford et al. write that 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 implication to which they refer is that 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.

In further exploration of the issue, Bustamante et al. (2010) exposed groups of Panamanian golden frogs (*Atelopus zeteki*) to varying dosages of zoospores of *Batrachochytrium dendrobatidis* (*Bd*) as well as to different temperatures and hydric environments, in order to ascertain whether the frogs were susceptible to the pathogen and, if so, how environmental factors might affect the frogs' survival. Results of these several operations indicated (1) "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," (2) "exposed frogs housed at 23°C survived significantly longer than those that were housed at 17°C," and (3) "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.

The most recent work to be devoted to the struggles of amphibians comes from Anchukaitis and Evans (2010). They write, "widespread amphibian extinctions in the mountains of the American tropics have been blamed on the interaction of anthropogenic climate change and a lethal pathogen." In this regard, 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," questioning once again the original contention that modern global warming was the primary culprit in the demise of the Monteverde golden toad (*Bufo periglenes*).

In an attempt to shed significant new light on the subject, 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, in the words of the two researchers, that "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, in this regard, "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, while indicating, "ENSO anomalies in the most recent decades are not beyond the range of natural variability during the instrumental period (Rajagopalan et al., 1997)."

In conclusion, Anchukaitis and Evans state 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 that provide any support for the contention that global warming is, or ever will be, responsible for driving them to extinction. In fact, there are examples of just the opposite occurring.

Writing that "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 metapopulation of pool frogs (*Rana lessonae*) in Central Sweden. This they did by exposing larvae from three closely located populations to two temperatures (20 and 25°C) in the laboratory and then documenting their growth and development responses at the two different temperatures. According to the two Swedish researchers, the results of their experiment indicated (1) "in general, larvae exposed to warmer temperature experienced higher survival and metamorphosed faster," (2) there "were differences among the populations in both trait mean values and in the plastic responses," and (3) "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."

Based on these observations, Orizaola and Laurila found "strong population differentiation at a microgeographic scale in life-history characteristics and temperature-induced plasticity in [the] isolated amphibian metapopulation," and that in spite of "the near absence of molecular genetic variation within [the] metapopulation, [their] 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," which phenomenon may be preparing them for still further temperature increases by providing them "ample phenotypic variation" to deal with a potentially warming environment.

In additional studies showing real-world data refute the contention that global warming is driving amphibians to extinction, Berger et al. (2004) found *lower* temperatures enhanced the development of chytridiomycosis in a study of eastern Australian frogs, while Seimon et al. (2007) determined glacial recession in the Peruvian Andes has been creating new amphibian habitats at recently deglaciated sites. McCaffery and Maxell (2010) documented an increase in survival and breeding probability in the Columbia spotted frog of the Bitterroot Mountains of Montana (USA) as the severity of winter decreased, leading them to conclude "a warming climate with less severe winters is likely to promote population viability in this montane frog population."

Woodhams et al. (2010) recently noted "amphibian skin peptides are one important defense against chytridiomycosis," while examining "the population-level variation in this innate immune defense to understand its relationship with disease dynamics." Briggs et al. (2010) have noted 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.

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.

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.

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.

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.

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

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

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

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., 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.

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.

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.

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.

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. *NewScientist* **2790** (10 December) http://www.newscientist.com/article/mg20827903.500-fungus-out-the-frog-resistance-is-here.html.

6.2.2. Birds

The IPCC characterizes global warming as detrimental for most of the planet's animals, including birds, even suggesting rising temperatures could drive many of them to extinction. When contemplating the special abilities of these winged creatures—such as the ability to fly—one would think highly mobile species such as birds could overcome whatever degree of stress a temperature increase might impose upon them, merely by moving to more-hospitable habitat, of course, or to take advantage of whatever new opportunities global warming might present for them.

In what follows, we review several studies that indicate birds do indeed respond in such a manner. The studies also show birds are able to tolerate much greater heat stress than previously thought.

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. In doing so, 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 shifted, in the mean, not at all. British birds have expanded their ranges in the face of global warming, clearly a positive response that makes extinction much less a possibility than it was before the warming.

Simultaneously, Brown et al. (1999) had been studying a natural 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 the 29-year period of their study, they determined the date of first nest construction occurred 10.8 days earlier, while the date of first clutch in the population came 10.1 days earlier. These changes were associated with significant upward trends in monthly minimum temperature in the study area, of which they said that 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 and earlier over their study period, they suggested this climatic trend could be producing an earlier abundance of such food, which would help explain the increasingly earlier egg-laying date.

The three 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 suggested 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." And once again, 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.

Five years later in Europe, 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 1974–79 and one covering the period 1986–89, in an attempt 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). This exercise revealed southern species experienced a mean poleward advancement of their northern range boundaries of 18.8 km over the 12-year period. However, 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 species (primarily butterflies) elsewhere (Parmesan, 1996; Parmesan et al., 1999), Brommer concluded "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 that the ranges of birds (and possibly other animals) in a warming world will likely increase in size, 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.

Also working in Europe, and using data from the *Breeding Bird Atlas* of Lake Constance, which borders Germany, Switzerland, and Austria, Lemoine et al. (2007) analyzed 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. This work revealed, in their words, "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," while "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." This is a very important finding because the warming has tremendously benefited European birds and helped to buffer them against extinction.

Contemporaneously, 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 finding they describe as being "consistent with the results of Thomas and Lennon (1999) from Great Britain." Also in agreement with the observations about 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," a finding that is being replicated around the world.

Halupka et al. (2008) documented various breeding parameters of reed warblers (long-lived passerine birds that spend their winters in Africa but breed in the reed beds of marshlands in the Palaearctic, with some of them nesting in fishponds of southwest Poland) during 12 breeding seasons (1970–73, 1980–83, 1994, 2003, and 2005–06) that encompassed the period 1970–2006. They compared trends in what they measured with concomitant trends in mean monthly temperatures. This work revealed that mean breeding season (April–August) temperature 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. They found that in 2005 and 2006, egg-laying started three weeks earlier 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 in time 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 concluded, "the studied population of reed warblers benefits from climate warming."

Another case in point was described by Jensen et al. (2008), who wrote, "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 contentions of 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 then used the most parsimonious of these models to "predict their distribution under a warmer climate scenario," based upon "mean May temperature, the number of frost-free months and the proportion of moist and wet moss-dominated vegetation in the area," the latter of which is "an indicator of suitable feeding conditions."

The results of this exercise indicated, in the words of the six scientists, that 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 noted this result does not even consider the likelihood that glaciers will decrease in size and expose still more potential nest sites. Thus they concluded their paper by stating increased temperatures could release the population of pink-footed geese from the "present density-dependent regulation during the nesting period," and "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."

In another relevant study, based on bird-ringing records covering a time span of 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," after which they compared their results with the climatic history of the region over the same time period. They thus determined temperatures in May significantly increased over the period of their study, and they state, "in line with this increasing May temperature" there was "a 3– to 4–day shift towards earlier breeding." This pattern, in their words, "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." And of this latter finding 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."

About the same time, Seoane and Carrascal (2008) wrote, "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," while noting "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, in their words, that "one-half of the study species showed significant increasing recent trends despite the public concern that bird populations are generally decreasing," while "only one-tenth showed a significant decrease."

In discussing their findings, 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 come to this conclusion. They noted, 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 explained "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 indicated "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."

Commenting further on their findings, Seoane and Carrascal state that in their study, "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 the thinking of 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, 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 should be abundantly clear from these several observations that 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."

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 surveillance 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." In addition, they report 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." In fact, the productivity of the double-brooded females was approximately 75 percent greater than that of the single-brooded females. And in summarizing their findings in the concluding paragraph of their paper, Monroe et al. write, "in general, late summer and fall nesting among North American birds is underappreciated and may be increasing due to global warming," citing the work of Koenig and Stahl (2007).

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) remind us that "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)." To shed more light on the subject, they 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. More specifically, "using data on the European distribution of 100 bird species, [they] generated 99 synthetic distribution patterns for each species," and "for each of the 100 species, [they] fitted climate envelope models to both the true distribution and the 99 simulated distributions by using standard climate variables." They then 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."

In a rather surprising result, 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 conclude, "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 bottom line with respect to our stewardship of the Earth is thus well described by their conclusion: "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," as is also evident from the results of the many other studies reviewed in this brief analysis of the subject.

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." This work revealed, in their words, "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." What is more, 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."

In light of these findings, the six scientists concluded, "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 the work of Thompson (2006). These conclusions are of course very different from the "end of the world" scenarios painted by the IPCC.

In much the same vein, Brommer (2008) wrote that a "population-level change expected under a climate-warming scenario is a poleward shift in the distribution of organisms," and he stated it is thus believed by many that 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 he noted "the trend slope describing the change in their abundance for the period 1983–2005 was calculated for 53 species by Vaisanen (2006)." This, he noted, 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." Therefore, to complete the behavioral picture of the latter 53 species, Brommer (2008) determined the concomitant changes in their northern range margins.

The Finnish bird specialist found "species foraging in wet habitats had experienced strong range margin shifts as compared with other feeding ecologies." But he said 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 stated 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."

In another revealing study, 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 different 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.

This work revealed, in the words of the seven scientists, that "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." In fact, they found, "at warmer sites, there was no palpable relationship between changes in bird numbers and changes in temperature." They concluded, "range expansions rather than shifts are occurring" as the planet warms.

In discussing the significance of their findings, the members of the international research team state 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."

In further discussing their important finding, Maclean et al. 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 the work of Connell (1983) and Begon et al. (2005). They concluded 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."

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 a remarkable 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).

The two researchers thus concluded, "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 the work of Visser et al. (2002) and Sanz (2003).

Moving from Europe to Asia, 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 they then analyzed for their relationships to 13 different environmental variables. In the words of the authors, "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." More specifically, they determined that four of the 13 variables they tested explained 45.3 percent of the total species richness variance, with 21.2 percent being accounted for by NDVI, 12.5 percent by elevation range, and 11.6 percent by annual potential evapotranspiration and mean annual temperature together. In addition, 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."

These findings make a good deal of sense, for 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. As such, it should be abundantly clear that greater plant productivity—both terrestrial and aquatic—leads to greater populations of plants and the animals that feed upon them, which should therefore lead to greater ecosystem biodiversity, because each species of plant and animal must maintain a certain "critical biomass" to sustain its unique identity and ensure its long-term viability. And that's where atmospheric CO_2 enrichment enters the picture: It increases plant productivity, which supports more animal life, which leads to greater animal biodiversity, which is good for the planet and good for mankind, the stewards and beneficiaries of all life upon it.

Moving on from Asia to Africa, 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." However, they state "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 bar 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."

In discussing their findings, 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."

Also in 2009, but farther south in the Southern Hemisphere, Huang et al. (2009) evaluated 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 also evident in the data from about 4,700 to 2,400 BP, which corresponds closely to a substantially warmer period at this site. While this is interesting in and of itself, the authors document four other studies (all of the studies conducted to date) 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. Studies of elephant seals (Hall, 2006) show they, too, were found closer to the South Pole during past warmer periods. And since all data currently available point to penguins having been most abundant during the warmest period of the Holocene several thousand years ago, it would seem reasonable to presume that penguins would respond positively, not negatively as the IPCC contends, to any future warming that may occur.

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 she 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."

In another study exploring bird responses to past periods of climate change, 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, however, 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, therefore, regions were delineated in which many of the identified species coexisted, and if it was found the same sets of species share the same common ranges today, it was concluded that 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 the species 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 indeed 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, 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.

In light of these and other findings, 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."

Another concern about the effects of potential global warming on birds is that various links of certain food chains may not respond in a compatible manner in terms of the temporal development of the different stages of their life cycles, leading to a serious mismatch among the unique needs of different ecosystem trophic levels that could well spell disaster for some species. This concept has been said by Visser and Both (2005) to constitute an "insufficient adjustment" to climate change.

In a study designed to explore this phenomenon for certain elements of an important ecosystem of Central Europe, Bauer et al. (2010) examined the responses to 47 years of warming (1961–2007) of (1) the time of leafing-out of dominant English oak (*Quercus robur*) trees at four different research sites in the Czech Republic that are located in full-grown, multi-aged floodplain forests that had been under no forestry management; (2) 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 (3) 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," which was 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," while "the mean laying date has advanced by 6.4 to 8.0 days." Likewise, they found 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."

With respect to the importance of their findings, Bauer et al. state that because "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," it is readily apparent that 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." Hence, there is reason to believe other food chains also may not be as seriously disrupted by global warming as many have postulated they could be. Of course, much more work of this nature is needed before any generalities are warranted.

In a contemporaneous study, 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 further explore the issue. Specifically, they studied 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 that is broadly representative of bird communities in the Appalachian region of eastern North America. At this location, (1) 35 mist nets were operated five to six days per week during spring and autumn migrations, (2) a reduced number of nets was used during summer, and (3) 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 that "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, as they describe it, that "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.

Popy et al. (2010) employed data from two bird atlas surveys performed on a 1 km by 1 km grid (the first in 1992–94 and the second in 2003–05) in an alpine valley in the Italian Piedmont to see if there was any 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. Their results indicated "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 indicate, "at the European scale, no overall expansion or contraction of the distributions of the studied species was detected." In light of their findings, as well as those of others they cite, Popy et al. thus 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."

In one final study to be considered here, Thomas et al. (2010) write, "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.” Many people worry, in this regard, that global warming may upset such biological synchronizations, leading to downward trends in the populations of many species of birds and other animals.

Thomas et al. studied this situation using “confirmatory path analysis and data on laying date” for two populations of blue tits in northern Corsica (Muro and Pirio) in order to determine “how laying date is related to spring temperatures and vegetation phenology”—as these two factors figure highly in determining the peak period of blue tit food abundance (in this case caterpillars)—in order to provide “critical information on how passerine birds may adjust breeding in the face of directional climate change [such as regional warming] by identifying the causal paths that link laying date and environmental cues.” The French and Canadian researchers discovered, in their words, “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 (interannual) 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.”

In discussing their findings, Thomas et al. acknowledge that “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.”

References

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

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

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.

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.

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.

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.

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

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

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

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

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.

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

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.

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.

Hall, B.L., Hoelzel, A.R., Baroni, C., Denton, G.H., Le Boeuf, B.J., Overturf, B., and Topf, A.L. 2006. Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea. *Proceedings of the National Academy of Sciences, USA* **103**: 10,213–10,217.

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

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

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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.

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 *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Working Group II Contribution to the 4th Assessment Report of the Intergovernmental Panel on Climate Change, edited by M. Parry, et al. 79–131. Cambridge, UK: Cambridge University Press.

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.

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.

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

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.

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

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.

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.

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., 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.

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.

6.2.3. Butterflies

The butterfly is another animal species the IPCC claims to be at risk of extinction due to global warming. In this section, we analyze how butterflies respond to rising air temperatures and CO_2 concentrations.

Over the prior century of global warming, Parmesan et al. (1999) examined the distributional changes of non-migratory butterfly species whose northern boundaries were in northern Europe (52 species) and whose southern boundaries were in southern Europe or northern Africa (40 species). This work revealed the northern boundaries shifted northward for 65 percent of of the first group, remained stable for 34 percent, and shifted southward for 2 percent. The southern boundaries shifted northward for 22 percent of of the second group , remained stable for 72 percent, and shifted southward for 5 percent. Thus "nearly all northward shifts," according to Parmesan et al., "involved extensions at the northern boundary with the southern boundary remaining stable."

This behavior is precisely what we would expect to see if the butterflies were responding to shifts in the ranges of the plants upon which they depend for their sustenance, because increases in atmospheric CO_2 concentration tend to ameliorate the effects of heat stress in plants and induce an upward shift in the temperature at which they function optimally. These phenomena tend to cancel the impetus for poleward migration at the warm edge of a plant's territorial range, yet they continue to provide the opportunity for poleward expansion at the cold edge of its range. Hence it is possible the observed changes in butterfly ranges over the past century of warming and rising atmospheric CO_2 concentration are related to matching changes in the ranges of the plants upon which they feed. Alternatively, this similarity could be a result of some more complex phenomenon, possibly even some direct physiological effect of temperature and atmospheric CO_2 concentration on the butterflies themselves. In any event, and in the face of the 0.8°C of warming that occurred in Europe over the twentieth century, the consequences for European butterflies were primarily beneficial.

Across the Atlantic in the United States, Fleishman et al. (2001) 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)." In discussing their results, the three researchers noted "during the Middle Holocene, approximately 8000–5000 years ago, temperatures in the Great Basin were several degrees warmer than today." They note "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."

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) remarked that 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."

Three years later, Crozier (2004) noted "*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. Thus intrigued, and 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."

This work revealed, in Crozier's words, "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 indicated "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, which should enable it to move further back from the "brink of extinction" that some advocates associate with rapid global warming.

Davies et al. (2006) introduced their study of the silver-spotted skipper butterfly (*Hesperia comma*) by noting that 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. But that was not the end of the matter, for then came the warming claimed by some to have been unprecedented over the past two millennia, which could ultimately drive the already decimated species to extinction.

The four researchers analyzed population density data, 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, as well as the effects of ambient and oviposition site temperatures on egg-laying, and the effects of sward composition on egg location. This multifaceted work of Davies et al. (2006) revealed, in their words, that "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."

In discussing their findings, 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 suggest "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, they state "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, they argue "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, they note "higher temperatures may directly increase flight (dispersal) capacity, and the greater fecundity of immigrants may improve the likelihood of successful population establishment." Consequently, 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 they suggest "warmer winter temperatures could also allow survival in a wider range of microhabitats."

In a concurrent study, Menendez et al. (2006) provided what they called "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." By these means 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 were able to determine that 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."

Also working in Britain, 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 of this exercise were then 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." This work indicated the empirical data the researchers gathered "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. In addition, the researchers indicate "increased dispersal ability was evident in populations from areas colonized >30 years previously."

In discussing their findings, 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 that 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." Put another way, it would appear global warming is proving not to be an insurmountable problem for the speckled wood butterfly, which is evolving physical characteristics that allow it to keep up with the poleward migration of its current environmental niche, whereas direct destructive assaults of humanity upon its natural habitat could still end up driving it to extinction.

Analyzing data pertaining to 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," Dennis and Sparks (2007) reported, "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 the work of 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." All of 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.

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," such that "the average species richness of communities has increased." They also found species abundances following colonization likewise increased, due to "climate-related increases in the [land's] carrying capacity."

In comparing their results with those of 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 that to their knowledge, "this is the broadest scale, longest term dataset yet assembled to quantify global change impacts on patterns of species richness."

The two researchers discovered 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."

In another study conducted in Canada, Westwood and Blair (2010) measured the responses of 19 common butterfly species of the boreal forests of Manitoba 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 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." In addition, 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)," while indicating "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)." These results confirm the observations of White and Kerr and contradict the negative prognostications about climate impacts from warming.

One additional means by which butterflies can cope with high 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.

In discussing their findings, Karl et al. state their observation that "HSP70 expression increased substantially at the higher rearing temperature in low-altitude butterflies ... might represent an adaptation to occasionally occurring heat spells," which further suggests this response should serve these organisms well in the days and years to come, especially if the dramatic warming and increase in heat spells predicted by the IPCC should come to pass.

Most recently, Forister et al. (2010) analyzed 35 years of butterfly presence-absence data collected by a single observer at ten 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 (1) both maximum and minimum temperatures rose, (2) low-altitude habitat was negatively affected by encroaching land development, and (3) there was no systematic variation in precipitation. This effort revealed, in the words of the eight researchers, that over this period, species richness "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 actually increased, and "in addition to an increase in richness, abundance has also generally increased at the highest-elevation site."

References

Beirne, B.P. 1955. Natural fluctuations in abundance of British Lepidoptera. *Entomologist's Gazette* **6**: 21–52.

Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* **85**: 231–241.

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.

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.

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.

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.

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.

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, heterogeniety, and the potential consequences of climate change. *Conservation Ecology* **5**: 10.

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.

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.

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.

Sorensen, J.G., Kristensen, T.N., and Loeschcke, V. 2003. The evolutionary and ecological role of heat shock proteins. *Ecology Letters* **6**: 1025–1037.

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.

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.

Williams, C.B. 1965. *Insect Migration*. London, UK: Collins.

6.2.4. Other Insects

Hickling et al. (2005) 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 1960–70 and 1985–95. 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."

In prefacing their study of the subject, 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 will likely play a major role in determining future geographic distributions of insects in a warming world.

Against this backdrop 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, one-week-long acclimation responses of each species' critical minimum and maximum temperature ($CT_{\mathbf{min}}$ and $CT_{\mathbf{max}}$) to exposure to temperatures of 20, 25, and 30°C were investigated, as well as their interactions with short-term sub-lethal temperature exposures to the same conditions as arrived at via different rates of warming.

In discussing their findings, the two authors report, "generally, increasing the acclimation temperature significantly increased $CT_{\mathbf{max}}$, whereas decreasing the acclimation temperature significantly lowered $CT_{\mathbf{min}}$." In addition, they found "slower ramping rates significantly increase $CT_{\mathbf{max}}$ 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)."

In light of their observations, 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," additionally citing Chown and Nicolson (2004) in this regard.

This phenomenon is not restricted to flies. The two researchers indicate, for example, that 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 the work of Lee et al. (1987), Kelty and Lee (2001), Shreve et al. (2004), and Powell and Bale (2006), while further indicating 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.

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, in this regard, "a suite of invasive weevils has become established in the northern hardwood forests of North America," noting that how these insects will respond to continued increases in the air's CO_2 content is "unknown."

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."

In light of their findings and the continued upward trend in the air's CO_2 content, 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.

In one final study focusing on the future effects of rising atmospheric CO_2, as opposed to temperature, Rao et al. (2009) determined what foliage-mediated effects atmospheric CO_2 enrichment might have on another pernicious insect pest. As background for their study, they explain that 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," during which periods castor oil yields can be reduced "by 30-50% by the semilooper alone," and the tobacco caterpillar "can cause yield losses of 25-40%."

In conducting their study, 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 indicated, "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 that 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.

References

Chown, S.L. and Nicolson, S.W. 2004. *Insect Physiological Ecology: Mechanisms and Patterns*. Oxford, UK: Oxford University Press.

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.

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.

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.

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.

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.

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.

Lee, R.E., Chen, C.P., and Denlinger, D.L. 1987. A rapid cold-hardening process in insects. *Science* **238**: 1415–1417.

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.

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.

Overgaard, J. and Sorensen, J.G. 2008. Rapid thermal adaptation during field temperature variations in *Drosophila melanogaster*. *Cryobiology* **56**: 159–162.

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.

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.

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.

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.

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.

West-Eberhard, M.J. 2003. *Developmental Plasticity and Evolution*. New York, NY: Oxford University Press.

Whitman, D.W. 2009. Acclimation. In *Phenotypic Plasticity of Insects. Mechanisms and Consequences*, edited by D.W. Whitman and T.N. Ananthakrishnan, 675–739. Enfield, NH: Science Publishers.

6.2.5. Lizards

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 scattered 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. More specifically, from 1984 to 2001 they monitored several life-history traits of the subpopulations, 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 stated, "it might be concluded that the common lizard has been advantaged by the shift in temperature." This finding, in their words, 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 concluded, "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."

In providing some background for their study of montane rainforest lizards, Bell et al. (2010) note tropical species long have been considered 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." NASA's James Hansen expressed this concept much more bluntly on 21 November 2006—when accepting the World Wildlife Fund's Duke of Edinburgh Conservation Medal at St. James Palace in London—by declaring, "species living on the biologically diverse slopes leading to mountains will be pushed off the planet" as the planet warms, opining—as we have already noted he also did before the U.S. House of Representatives—that there will simply be no place else for them to go.

In an empirical test of this idea, Bell et al. 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," by combining "spatial modeling of potential distributions under representative palaeoclimates, multi-locus phylogeography and analyses of phenotypic variation." This work revealed, in the words of the seven scientists, that "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 indicate 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, they write, "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."

References

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.

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.

Fjeldsa, J. and Lovett, J.C. 1997. Biodiversity and environmental stability. *Biodiversity and Conservation* **6**: 315–323.

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.

Hoskin, C.J. 2004. Australian microhylid frogs (*Cophixalus and Austrochaperina*): phylogeny, taxonomy, calls, distributions and breeding biology. *Australian Journal of Zoology* **52**: 237–269.

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.

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.

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.

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.

6.2.6. Mammals

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. Over this time period, red squirrel, moose, porcupine, river otter, and beaver were found to have established themselves in the area, significantly increasing its biodiversity. The three researchers stated these primarily northward range expansions could be explained by "a recent warming trend at the northern treeline during the 1970s and 1980s." Alternatively, they noted the influx of new species may have been due to "increasing populations in more southerly areas." But in either case, we have a situation where several types of mammals appear to have fared quite well in the face of increasing temperatures in this forest-tundra landscape.

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. Given the latter characteristic, it is not surprising that 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." In fact, 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 the course of 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.

In reporting their findings, the two U.S. Forest Service researchers state, "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 1827 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 may also be better able to cope with various aspects of climate change than we have been led to believe possible.

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," the logic being that "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 the work of Schwartz and Renecker (1998).

The authors thus "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. state they "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 they state "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, which they analyzed in ways that allowed them to obtain the following results.

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; and now 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." Thus, they go on to state that, to their knowledge, "this is the first report of hybrid zone formation following a range expansion induced by contemporary climate change." These unique findings indicate yet another way in which living organisms can both physically (by shifting their ranges) and genetically (by hybridization) successfully confront the challenges that may be presented to them by global warming.

Pockley (2001) reported the results of a survey of the plants and animals on Australia's Heard Island, a small island located 4,000 kilometers southwest of Perth. Over the prior 50 years, this sub-Antarctic island had experienced a local warming of approximately 1°C that had resulted in a modest (12 percent) retreat of its glaciers. For the first time in a decade, scientists were attempting to document what this warming and melting had done to the ecology of the island.

Pockley began by stating the scientists' work had unearthed "dramatic evidence of global warming's ecological impact," which obviously consisted of "rapid increases in flora and fauna." He quoted Dana Bergstrom, an ecologist at the University of Queensland in Brisbane, as stating that areas once poorly vegetated had become "lush with large expanses of plants." And he added that populations of birds, fur seals, and insects also had expanded rapidly. One of the real winners in this regard was the king penguin, which, according to Pockley, had "exploded from only three breeding pairs in 1947 to 25,000."

Eric Woehler of Australia's environment department was listed as a source of other equally remarkable information, such as the Heard Island cormorant's comeback from "vulnerable" status to a substantial 1,200 pairs, and fur seals' emergence from "near extinction" to a population of 28,000 adults and 1,000 pups. Given such findings, it can be concluded the regional warming experienced at Heard Island actually rescued these threatened animal populations from the jaws of extinction.

References

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.

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.

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.

Howell, A.H. 1924. *Revision of the American Pikas.* North American Fauna No. 47. Washington, DC: USDA Bureau of Biological Survey.

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.

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.

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.

Schwartz, C.C. and Renecker, L.A. 1998. Nutrition and energetics. In *Ecology and Management of the North American Moose*, edited by A.W. Franzmann and C.C. Schwartz, C.C., 441–478. Washington, DC: Smithsonian Institution.

Sumner, L. and Dixon, J.S. 1953. *Birds and Mammals of the Sierra Nevada.* Berkeley, Ca: University of California Press.

6.2.7. Worms

Small oligochaete worms known as enchytraeids, according to Maraldo et al. (2010), “are widely distributed from the Arctic to tropical areas, and typically inhabit the organic horizon in soils,” where they “contribute to the decomposition processes and nutrient mineralization.” These 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 these authors describe it, “by consuming large amounts of organic matter,” and indirectly “by their feeding activity and modifications of soil structure.” And they note, in this regard, “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 the work of Cragg (1961) and Swift et al. (1998).

Working on a hilly nutrient-poor sandy soil with a dry heath/grassland cover at Brandbjerg, Denmark, the seven scientists conducted an experiment beginning October 2005 and extending through 2007. They studied the individual and combined effects of (1) soil warming: a mean daily temperature increase of 0.3°C in winter and 0.7°C in summer at a depth of 5 cm, provided by 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; (2) drought: peak soil water content reductions of 11 percent and 13 percent compared to control plots in 2006 and 2007, provided by waterproof curtains that were automatically pulled over the vegetation during rain events; and (3) atmospheric CO_2 enrichment: a CO_2 concentration increase from 382 to 481 ppm, provided by a free-air CO_2 enrichment (FACE) system.

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. On the other hand, the extra 99 ppm of CO_2 stimulated enchytraeid biomass by 40 percent. They remark that at certain times this latter phenomenon was “especially positive,” as in the summer of 2007, when they state “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.”

References

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.

Laakso, J. and Setala, H. 1999. Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos* **87**: 58–64.

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.

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.

6.2.8. Other Studies

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 contemporary Earth, all in a search 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 indicates “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 he adds “such a model suggests that we should expect greatest marine diversity during globally warm intervals,” as is typically also found to be the case 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 the IPCC with respect to 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 badly for Earth’s 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.”

In further explanation of 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.” Indeed, he states “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’s parting comment in this regard is his statement, “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.”

Whatever the details may be, two generalizations clearly can be made: warmth typically begets speciation, whereas cold tends to lead to species extinctions.

Independent support for this thesis was provided in two 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 that at that time, carbon dioxide rose rapidly 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 also able to identify various plant species that existed during this period. In spite of the high temperatures and possibly less-moist conditions, it was found the number of drought-tolerant plants did not increase, nor were moisture-requiring plants shown to decrease during the PETM. These facts led the authors to speculate that either rainfall or water use efficiency increased because of higher levels of atmospheric carbon dioxide, which would have compensated for the higher temperatures.

It was also noted the PETM brought a radical increase in diversity, measured in both absolute terms (number of species/taxa) and in terms of 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 that tropical forests of today are currently growing in climates near the maximum temperature the plants can tolerate (~27.5 °C), and that future global warming in tropical zones may stress plants and cause a reduction in forest growth, perhaps leading some species to extinction. However, as shown by Jaramillo et al., 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.

In the study by Willis et al. (2010), past historical periods were identified in which 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 real-world periods were examined to see if any real-world climate-related extinctions had occurred.

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. There is evidence from many sites for 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." On the other hand, 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.

The study by Willis et al. also makes use of recent historical data, as in the case of 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 of the periods they studied, with either very warm temperatures or very rapid warming, there were no detectable extinctions.

Taking a slightly different approach to the subject were D'Odorico et al. (2008), who 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. In light of this exercise, it would appear what the IPCC looks upon as unfavorable may be just what is needed to (1) increase the diversity and resilience of myriads of terrestrial and aquatic ecosystems and (2) propel them to higher levels of activity in the brave new world of our CO_2-enriched future.

Finally, 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) write 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 "typically ignores the potential physiological capacity of animals to respond to climate change," and they go on to 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 begin by noting 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." In the latter instance, 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). And in the first case, they state phenotypic plasticity "is likely to represent the first response of individual organisms," and 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 the work of 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)." And they state "other adaptations also ensue, including plasma volume expansion and decreased electrolyte content of sweat," such that "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)," which "phenotypic adaptation (in this case, heat acclimatization) can alter physiological tolerance (the risk of heat illness)."

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." And 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," whereby cooling 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 they add "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, much of Earth's animal life is well-endowed with inherent abilities to cope, either through behavior or otherwise, 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.

6.3. Diseases

Another animal-related concern with respect to global warming is that rising temperatures will increase the prevalence of parasitic and vector-borne diseases, resulting in increasing mortality rates. To date, very little research has been published on this concern. Here, however, we cite two papers that have provided some understanding of the subject.

Writing in *Trends in Parasitology*, Morgan and Wall (2009) state “global climate change predictions suggest that far-ranging effects might occur in population dynamics and distributions of livestock parasites, provoking fears of widespread increases in disease incidence and production loss.” However, they indicate, “just as development rates of many parasites of veterinary importance increase with temperature, so [too] do their mortality rates [increase].” They further note “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 that, in the end, “the net effect of climate change could be complex and far from easily predicted.”

In perusing the subject in greater detail, as they elucidate some of the many complexities involved, the two U.K. researchers indicate “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.” However, 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,” as they characterize the situation, 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.” It likely will be some time before the temperature-related parasitic disease relationship for animals is resolved.

Turning to a well-known vector-borne disease, 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 and others to contend the BTV vector had expanded its range northward "because of rising temperatures," as suggested by the work of Mellor (2004), Purse et al. (2005), and Mellor et al. (2008). However, a careful examination of *Culicoides* population data in Italy prior to 2000 was made by Goffredo et al. (2003). They 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 to make the case for a warming-induced northward expansion of the BTV vector, because it may already have 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 the year 2000, where 70,000 light-trap collections were made at about 3,800 different sites. Using the first year of data obtained from this program, Conte et al. defined the spatial distributions of three different *C. imicola* infection zones: zone I (endemicity), zone II (transition), and zone III (absence). Then, 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 state their results indicated "no detectable range expansion of *C. imicola* population in Italy over the past six years." In fact, 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 due to a modification of the interaction between the virus, the vector and the environment, as may also have been the case in northern Europe." As for the future, they write, their results indicate "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 demonstrates once again that it is easy to blame global warming for the poleward expansion of a vector-spread disease, but it is quite another thing to prove the case.

References

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.

Goffredo, M., Conte, A., Cocciolito, R., and Meiswinkel, R. 2003. Distribution and abundance of *Culicoides imicola* in Italy. *Veterinaria Italiana* **47**: 22–32.

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.

Morgan, E.R. and Wall, R. 2009. Climate change and parasitic disease: farmer mitigation? *Trends in Parasitology* **25**: 308–313.

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.