6

Managing biodiversity in the light of climate change: current biological effects and future impacts

Terry L. Root, Diana Liverman and Chris Newman

Now there is one outstandingly important fact regarding Spaceship Earth, and that is that no instruction book came with it.

(R. Buckminster Fuller (1895–1983), *Operating Manual for Spaceship Earth,* 1963.)

Introduction

Climate is one of the primary controls on species diversity and distribution globally, and past climate changes have surely modified biodiversity. Thus, predicted changes in global and regional climates as a result of increasing atmospheric carbon dioxide have tremendous implications for species and habitat conservation. As carbon dioxide increases are associated with human activities, principally the burning of fossil fuels and through deforestation, climate change poses a challenge to development, international environmental policy and resource consumption. This is particularly so in the developed world where, per capita, emissions of carbon dioxide are highest. Climate change must become an integral consideration in conservation, linking those concerned with non-human life on the planet with the polluting activities of its human inhabitants.

Many earlier predictions of global warming are becoming a reality as glaciers melt, hotter summers become more frequent, and in many places the distributions of species begin to shift. Britain's Chief Scientist, David King, sounded a dramatic warning when, in 2004, he identified climate change as a greater risk to society than terrorism (King 2004). At the Kyoto Climate Summit in 1997, dozens of eminent scientists issued a World Scientists' Call of Action. They stated, 'Climate change will accelerate the appalling pace at which species are now being extirpated, especially in vulnerable ecosystems. One-fourth of the known species of mammals are threatened, and half of these may be gone within a decade. Possibly one-third of all species may be lost before the end of the next century'. The recent Millennium Ecosystem Assessment Synthesis Report agreed that 'the balance of scientific evidence suggests that there will be a significant net harmful impact on ecosystem services worldwide if global mean surface temperature increases more than 2°C above preindustrial levels or at rates greater than 0.2°C per decade'. It concludes that 'by the end of the century, climate change and its impacts may be the dominant direct drivers of biodiversity loss and the change in ecosystem services globally' (Millennium Ecosystem Assessment, 2005, p. 126). Consequently, plans for the next several centuries of biodiversity conservation must already take into account that the emissions of greenhouse gases due to the human activities will continue to increase the global temperature.

Lessons from patterns of palaeoclimatic change

This is far from the first time that global temperatures have changed – indeed, they have done so often, and radically, throughout geological history, thereby affecting the distribution of fauna and flora. For example, dramatic climatic events are implicated in mass extinctions at the conclusion of both the Palaeozoic and Mesozoic, 245 and 65 million years ago, respectively. During the Pleistocene Epoch, since the Olduvai–Matuyama boundary about 1.8 million years ago, there have been 32 cycles of cooling and warming, with annual mean global air temperature dipping to 5°C cooler than today's average of 14°C, bringing ice to much of the Northern Hemisphere. Intriguingly, early in the Pleistocene, mammal numbers and diversity stayed fairly stable. However, of more than 150 genera of megafauna (>44 kg) known to be alive 50,000 years ago, 97 were extinct by 11,000 years ago when the last glacial period concluded (Stuart, 1991). Theory has it that the knock-out punch to megafaunal biodiversity in the closing part of the Pleistocene Epoch was the combination of this climate change with the escalating pressures (in the forms of hunting and habitat change) brought about by growing populations of early humans. The contemporary parallels are obvious, with hunting, land-use change and other human activities making ecosystems more vulnerable to climatic change.

So if climate changes happen naturally, why all the fuss? First, this time it is changing much faster—an order of magnitude faster—than during most of the Pleistocene. Second, the resulting pressures are having an impact on ecosystems already clearly stressed by an ever-growing human footprint (as evidenced in diverse ways by every other essay in this book). Third, at least parts of society at large have committed to protecting biodiversity for reasons spanning economics to philosophy. Climate change is one of the most profound changes that humanity has brought to the planet and to its non-human inhabitants and some find this ethically uncomfortable.

The magnitude and nature of climate change

GREENHOUSE GAS EMISSIONS AND PREDICTED CLIMATE CHANGE

The role of 'greenhouse' gases is critically important for understanding the mechanisms underlying accelerated climate change. These gases, such as carbon dioxide (CO_2), methane (CH_4), nitrous oxide (NO) and water vapour, are normal atmospheric components essential for life. They trap solar energy, which warms the surface of the Earth from what would otherwise be around −18°C. Thus, the concern is not that the greenhouse effect exists (without it life would be in trouble), but that it is enhanced by human activities which result in the trapping of more solar energy causing the planet to warm further. Nobody seriously disputes that fossil fuel combustion has increased the concentration of atmospheric greenhouse gases, principally CO_2. According to the report on emission scenarios by the Intergovernmental Panel for Climate Change (IPCC 2001a), pre-industrial levels of carbon dioxide were in the region of 280 parts per million by volume (ppmv), whereas current levels are around 370 ppmv. This is the highest level of CO_2 in the past 400,000 years, which is as far back as accurate estimates can be made, and probably it is the highest level in the past 20 million years. By the end of the twenty-first century the IPCC anticipates CO_2 concentrations to be anywhere from 490 to 1250 ppmv, depending on economic development paths, population and technology. Projections of future CO_2 concentrations under various emission scenarios are used to drive complex atmospheric general circulation models (GCMs), which are used to predict global climate. The scientific consensus (IPCC, 2001a) suggests an increase in globally averaged surface temperatures of 1.4 to 5.8°C by 2100. An increase above 2°C, which equates to levels greater than 450 ppmv, will cause serious economic and possibly disastrous ecological impacts (Mastrandrea & Schneider, 2004). Models are, of course, only models (see Chapter 9), but the observational evidence to suggest that these models are right is growing.

OBSERVED TEMPERATURE CHANGES

Since the late nineteenth century average global surface temperatures have increased about 0.6°C, with two-thirds of the increase in the past 25 years (Fig. 6.1). A longer term record (Fig. 6.2) has been called the 'hockey stick' plot because it shows a dramatic hook-like increase after 1975 following almost 1000 years

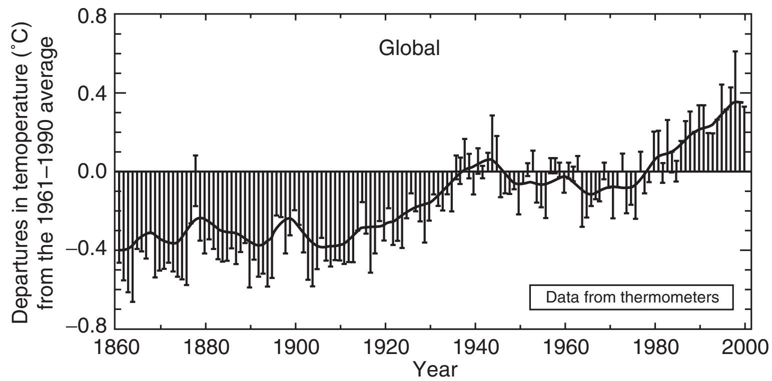


Fig. 6.1 Temperature deviations (°C) from the average temperatures between 1961 and 1990. These data are collected from thermometers around the globe.

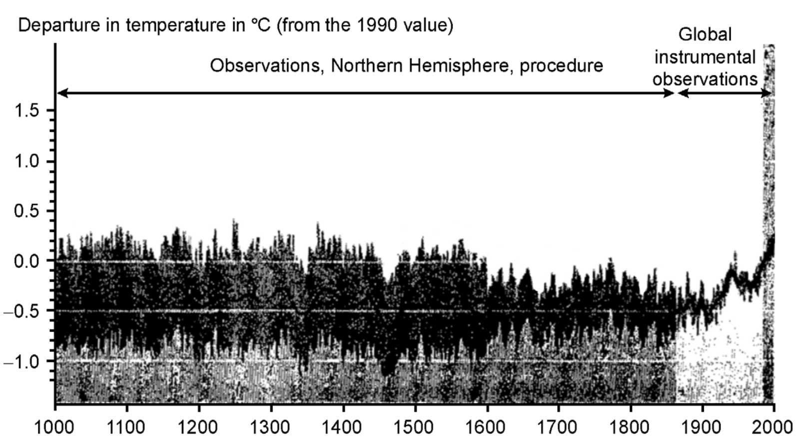


Fig. 6.2 Temperature deviations (°C) from the average global temperatures in 1990. These data are collected from proxies, such as tree rings and ice cores, and from thermometers placed around the globe.

Macdonald/Key Topics in Conservation Biology 1405122498_4_006 Final Proof page 88 6.5.2006 2:49am

of fluctuations around a level or slightly decreasing trend (IPCC, 2001a; Mann et al. 1998).

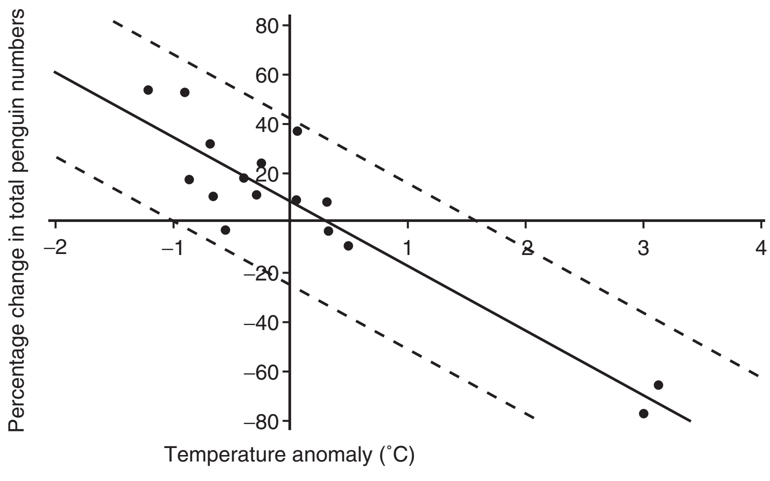
All rigorous investigations of the average global air temperatures indicate significant increases in recent decades. As we go to press, the warmest year globally on record was 1998, closely followed in sequence by the ominously recent series: 2002 and 2003, then 2001, 1997,

Box 6.1 El Niño and climate change

During an El Niño event, the Equatorial undercurrent weakens, the surface water warms, macronutrients are reduced, primary production decreases (Chavez et al. 1999) and fish numbers diminish. In recent decades, however, the periodicity and magnitude of El Niño events have changed. El Niño events now occur two to seven times more frequently than they did 7000–15,000 years ago (Riedinger et al. 2002). Recent climate models show an increased El Niño pulse in the past three decades (Trenberth & Hoar 1996). The 1982–83 and 1997–98 El Niño events were the strongest recorded in the past 100 years and had severe biological impacts. Sea-surface temperatures and precipitation between 1965 and 1999 indicate that 1983 and 1998 were the hottest and wettest years on record for the Galapagos Islands.

Vargas et al. (2005, 2006) examined the impacts of El Niño activity on the population of Galapagos Penguins (*Spheniscus mendiculus*). Between 1965 and 2003, nine El Niño events were recorded of which two were strong (1982–83 and 1997–98); both were followed by crashes of 77% and 65% of the penguin population, respectively. Furthermore, increased frequency of weak El Niño events limits population recovery (Box Fig. 6.1).

In 2003 the penguin population was estimated to be at less than 50% of that prior to the strong 1982–83 El Niño event. Three causal mechanisms were identified: (i) shortage of food, (ii) unbalanced sex ratio and (iii) flooding of nests. For example, data from commercial fisheries indicated that the catch of mullets from the Galapagos during the 1997–1998 El Niño event was half that of the commercial catch in 1999 (Nicolaides & Murillo 2001) when there was no El Niño. Similarly, the catch of sardines along the coast of mainland Ecuador during the 1998 El Niño year was the lowest of the past two decades (Jácome & Ospina 1999). The Galapagos penguin has evolved in the presence of the environmental fluctuations caused by El Niño, and the associated negative effects probably have always affected their populations. However, the impacts of global warming will increase the frequency and intensity of these fluctuations, which will pose serious challenges for penguin conservation.



Box Fig. 6.1 Percentage change in penguin numbers in relation to the mean normalized sea-surface temperature (SST) anomalies for the period December–April that preceded each penguin count. We calculated changes in the penguin population for counts that were not more than 3 years apart ($n = 17$) ($F_{1,15} = 71.1$, pL 0.001, $b_{(adj)} = 0.81$). We also tested the relationship without the two strong El Niño events in 1983 and 1998 to determine that the relationship remained significant without these extreme values ($F_{1,13} = 10.2$, $p = 0.007$, $b_{(adj)} = 0.40$). Dotted lines are 95% confidence limits.

1995, 1990, 1999, 1991 and 2000. The warmth of 1997 and 1998 was exacerbated by a strong El Niño pattern of ocean heating in the South Pacific that had impacts around the world (see Box 6.1).

The temperature has not warmed uniformly around the globe. Some areas have been below the global average (e.g. south-eastern USA). The most pronounced warming has been in temperate and Arctic areas of Eurasia and North America between 40° and 70°N. Interestingly, urbanized and industrialized regions seem to have warmed less than expected owing to the countervailing role of air pollution. The particles can filter solar energy reaching the surface, producing a global 'dimming' effect, which may hide the true magnitude of temperature increases (Stanhill & Cohen, 2001).

OBSERVED ICE CHANGES

The 'fingerprints' of global warming – flowers blooming earlier in spring, sea-ice thinning and the like – are in substantial agreement with more direct measures from thermometers and satellites. One indirect measure of temperature is the melting of glaciers, which, for example, in Glacier National Park in Montana, USA are retreating so rapidly that they are projected to disappear by 2030 (Hall & Fagre, 2003). Those on Kilimanjaro and several Andean peaks are amongst the many rapidly following (Thompson et al. 2002). Glaciers have trapped information on the Earth's atmosphere for eons, so melting them is as irreparable (one might say sacrilegious) as the burning of the library at Alexandria. They are also critical water resources for the landscapes below them.

The poles are more sensitive to climate change than is the Equator. Arctic sea ice has decreased by 20% since 1988, and 87% of the Antarctic marine glaciers have retreated in the past 60 years (Stone et al. 2004; Cook et al. 2005). As melting continental glaciers flow into the sea, ocean levels rise, and much more so because the warming water expands, reminiscent of mercury rising in a thermometer. Mean global sea level has been rising at a rate of 1–2 mm yr^{-1} over the past 100 years, significantly faster than the rate averaged over the past several thousand years. Indeed, the Greenland ice sheet has been melting at a rate equivalent to a 0.13 mm yr^{-1} increase in global sea level. Projected increases by 2100 range from 90 to 880 mm. At the higher end of this projection many densely populated areas, such as Bangladesh, would be submerged, and expanses of inland fresh water turned brackish, probably spurring mass migrations of people and terrestrial species. Warmer seas and sea-level rise will also affect the conservation of corals, mangroves and diverse marine and coastal ecosystems.

Although fraught with uncertainty, and depending on the model used, precipitation is also projected to increase with considerable regional variation, including increased rainfall in high and northern mid-latitudes in winter and decreases in winter rainfall in Australia, Central America and southern Africa. Although highly variable, land precipitation since 1900 has increased 2% on average. In most of the northern mid- to high latitudes precipitation has been rising at the rate of 0.5–1.0% per decade. Simultaneously, a decrease of 0.3% per decade has been observed in subtropical latitudes, although this appears to be a weakening trend. The extent of annual snow cover in the Northern Hemisphere has remained consistently below average since 1987, having decreased by 10% since 1966, mostly from a decline in spring and summer (IPCC, 2001a).

EVIDENCE OF ANTHROPOGENIC CLIMATE CHANGE.

Species are able to detect changes in temperatures and often adjust to them (Parmesan & Yohe, 2003; Root et al. 2003), but what is causing the temperature change to occur? Using wild animals and plants as temperature proxies, Root et al. (2005) found that warming on a local scale, which is the scale that is important to species, can be attributed to human emissions. They compared the timings of life-histories (so-called phenological data) from species around the globe to temperatures modelled by a GCM. When natural forces alone, such as volcanoes or solar variations, are included as drivers in global GCMs over the past 100 years the predicted and observed temperatures do not match (Fig. 6.3a). When only anthropogenic sources, such as increased atmospheric dust particles, CO_2 and methane are considered, the modelled and actual values show a better match (Fig. 6.3b), but the best and most statistically significant match occurs when both natural and anthropogenic forces are included in the models (Fig. 6.3c). This strongly suggests that human activities are contributing significantly to the global warming of the atmosphere. This means that humans are indeed changing the temperatures at the local level. Plants and animals can detect this warming in our back gardens, and the warming can be attributed to humans using fossil fuels and burning tropical forests.

Uncertainty and the sceptics

Considering the weight of the foregoing evidence, it may seem surprising that so much airtime is given to the views of the small number of so-called contrarian 'scientists' disputing the interpretation of the evidence (McIntyre & McKitrick 2005). Some sceptics question the validity of the models and dismiss predictions of extinctions and other serious impacts as alarmist (e.g. www.marshall.org). Some maintain that there is no evidence of significant climate changes, whereas others acknowledge the changes but conclude they are not anthro-

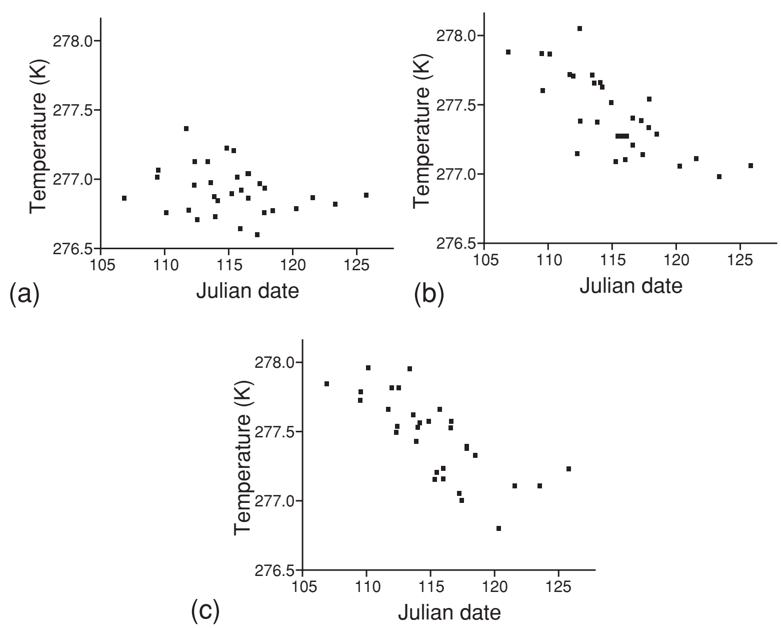


Fig. 6.3 For each year, the occurrence dates (Julian) of spring phenological traits are averaged over all Northern Hemisphere species exhibiting statistically significant changes in those traits ($n = 130$). These averages are plotted against: (a) the average modelled spring (March, April, May) temperatures including only natural forcings at each study location ($r = 0.22$, $p < 0.23$); (b) the same as (a) except including only anthropogenic forcings ($r = -0.71$, $p < 0.001$); (c) a combination of natural and anthropogenic forcings ($r = -0.72$, $p \leq 0.001$) (Root et al. 2005).

pogenic. Others, acknowledging the changes are unnatural, conclude that they are good for plant productivity and may beneficially 'green' the planet. Yet others look for an explanation in solar irradiance. The solar irradiance gambit rests on the observation that solar output varies cyclically, and may therefore theoretically contribute to temperature change. It is rebutted because irradiance on the Earth's surface is estimated to account for only 0.09 W m^{-2}, compared with 0.4 W m^{-2} warming from the insulation of greenhouse gases (IPCC, 2001a). The Earth's position and orientation relative to the Sun follow predictable cycles over long time periods (called Milankovitch cycles). Variations in the cycles are believed to be responsible for the Earth's ice-ages or glacial periods (Hays et al. 1976), when they bring a paucity of summer irradiance at northern latitudes during the summer months, allowing snow and ice to persist year round over an ever larger area. Milankovitch cycles, however, cannot explain the extent or rate of change in temperature over the past few decades. Additionally, if the Sun itself causes the warming, then the different vertical levels of the atmosphere would all show warming. They do not. The lower atmosphere is warming while the top atmosphere is cooling, which is exactly what you would expect if the warming is due to greenhouse gases.

One contrarian view is exemplified by the reconstruction of Northern Hemisphere temperatures for the past 1000 years using records of past climate captured in tree rings, corals and other proxies by Mann et al. (1999). This study produced the aforementioned 'hockey stick' curve that shows relatively stable temperatures until a significant rise in the twentieth century. Critics suggest that the increase is an artefact of the statistical techniques used and that the reconstructed curve is so unreliable that it fails to show past events that are well documented, such as the Little Ice Age – a period of cooling lasting from the mid-fourteenth to the mid-nineteenth centuries (McIntyre & McKitrick, 2003). Mann et al. (1999) rebuts this with the argument that the hockey-stick curve is robust under alternative methodologies and, in any case, events such as the Little Ice Age and Medieval warming were regional and so not well reflected in global data sets (see www.realclimate.org).

Worst case scenarios and surprises: rapid climate change

In 1989 the National Science Foundation funded the Greenland Ice Sheet Project II (GISP2) to drill an ice core through the 2-mile depth of the Greenland ice sheet at a cost of $25 million. Simultaneously, a separate European project (GRIP) 20 miles away, drilled an independent, but corroborating core. By 1993, the two cores, detailing 110,000 years of climate history were ready to reveal their secrets, astonishing researchers with the apparent rapidity at which climate changes had occurred in the past. Warming and cooling of 8°C were evidenced frequently through the ice-core record, often flipping from extremes in as little as 10 years. This is what apparently occurred at the conclusion of the most recent ice-age, 11,600 years ago, with vast increases in snowfall leading to a doubling of accumulation within 3 years. Simultaneously, lake and ocean sediment data from Venezuela to Antarctica corroborate these rapid and extreme global temperature fluctuations. These data indicate at least 20 abrupt climate changes over the past 110,000 years.

The most dramatic scenarios for the near term are associated with the possibility of changes in the Atlantic thermohaline circulation associated with arctic melting and an influx of freshwater into the north Atlantic. At present currents in the Atlantic bring warm water north, warming the ocean and land areas such as north-west Europe by at least 5°C. The movement of the water is partially driven by a contrast in salinity between the less saline Southern Ocean, which receives freshwater from melting glaciers, and the more saline and denser waters of the northern Atlantic. A large change in the amount of freshwater from a melting Arctic can slow this circulation, causing much cooler temperatures in the north Atlantic. A sudden shutdown of the circulation pattern could cause a rapid cooling, similar to that shown in the ice-core records. Rahmstorf (1995) modelled the circulation pattern and concluded that this could happen with global average temperature changes from 2 to 5°C.

Changes in carbon and other biogeochemical cycles associated with warming could also trigger a reduction in the take up of carbon by oceans and terrestrial systems, or result in the large-scale release of methane, further increasing warming and creating positive feedbacks that could accelerate change (IPCC 2001a and www.stabilisation2005.com). Even without sudden and rapid changes, extreme events are likely to increase because a warmer atmosphere can hold more water and intensify the hydrological cycle. The IPCC reports an increase in the frequency and intensity of the extreme events associated with El Niño – the periodic warming of Pacific currents off the coast of Peru that produces droughts in the Andes and northeast Brazil, floods along the coast of western South America and declining marine productivity as warm waters replace colder nutrient-rich ones. Storms with heavy rain are becoming more frequent and intense in the Northern Hemisphere, yet as higher temperatures drive up evaporation the likelihood of drought and water shortages also increases (IPCC, 2001b).

The impacts of climate change on flora and fauna

Flora and fauna are responding fairly consistently with large-scale warming: flowers are blooming earlier, migrating birds are changing their arrival schedules, and some plant and animals are shifting their ranges northward (IPCC 2001b). For certain species, the consequences are quite dramatic. The yellow-bellied marmot (*Marmota flaviventris*), a small mammal that lives in the alpine zone of North American mountains, is literally at risk of being 'squeezed' off the top of the mountain as temperatures increase and alpine habitat disappears (McDonald & Brown 1992), the same fate which Hersteinsson & Macdonald (1992) correctly predicted for arctic foxes (*Alopex lagopus*). In this case, however, the mechanism illustrates the sort of domino effect that should not surprise those familiar with the complexity of ecological communities: the northern limit of the red fox's (*Vulpes vulpes*) geographical range is determined by resource availability (and thus ultimately by climate), whereas the southern limit of the arctic fox's range is determined through interspecific competition with the red fox. If warming allows the red fox to thrive further north, or at higher altitude, and thus out-compete the arctic fox over more of its range, the arctic fox's distribution will become squeezed, paradoxically, in the face of ameliorating conditions. Pounds & Puschendorf (2004) suggest that 15–37% of a sample of 1103 land animals and plants could become extinct by 2050 as a result of climate change. For some there simply will be nowhere left with a suitable climatic regime, others will not be able to reach places where the climate remains suitable as warmer weather patterns shift polewards.

The different responses of species to climatic changes include:

1. shifts in the densities of species and their ranges, either poleward or upwards in altitude;
2. changes in the timing of events (phenology), such as when trees come into leaf or migrants arrive;
3. change (primarily loss) in genetic diversity;
4. morphological changes, such as longer wing length or larger egg sizes in birds;
5. behavioural changes such as relocation of bird nests;
6. extirpation or extinction (Parmesan & Yohe 2003; Root et al. 2003).

The most common or threatening of these changes are discussed below.

Density and range shifts

One of the most serious problems to face species around the globe is the combined or synergistic effect of climate change and habitat fragmentation (caused by urbanization, industrialization and agricultural development) (Root & Schneider 1993). Optimal conditions for the existence of a species can be defined as its 'fundamental range' (*sensu* Hutchinson, 1958), a major component of which is an appropriate bioclimatic envelope. As the climate warms many plants and animals will need to shift their ranges to remain within this envelope (e.g. by moving poleward, or ascending in altitude) – this is what happened during Pleistocene warm stages. Today such dispersals are much more difficult because, in most cases, individuals would face the generally impossible challenge of travelling across severely fragmented habitat. For instance, the quino checkerspot butterfly (*Euphydryas editha quino*), a resident of northern Baja California in Mexico, is being squeezed by temperature northwards from the southern boundary of its range, but urbanization in the area around San Diego, California is blocking its retreat. Such poleward range changes are widespread in temperate latitudes; in a sample of 35 non-migratory European butterflies, 63% have ranges that have shifted to the north by 35–240 km during the past 100 years, whereas only 3% have shifted to the south (Parmesan & Yohe 2003).

The responses of bird species to climate change are also likely to be highly variable (Harrison et al. 2003a,b). Some, such as the capercaillie (*Tetrao urogallus*) and red-throated diver (*Gavia stellata*), could decline with losses of suitable habitat, whereas others, such as turtle dove (*Streptopelia turtur*), yellow wagtail (*Motacilla flava*) and reed warbler (*Acrocephalus scirpaceus*), may expand their viable ranges. Several bird species, including willow tit (*Parus montanus*), nightingale (*Luscinia megarhynchos*) and nuthatch (*Sitta europaea*), respond well to moderate climate change but not to severe climate change, owing to their distributions in southern England either contracting significantly or becoming more fragmented.

The suggestion that birds might shuffle poleward and up in elevation will offer no solace to those striving to conserve species already at the poleward end of a continent, such as species in southern South Africa, or at the top of mountains. As climate change causes some species to redistribute polewards and upwards, the prospects are poor for those that already inhabit high latitudes or mountains. For example, denizens of what are called the 'Sky Islands' mountain ranges in the deserts of the southwestern USA survive only because they can thrive in the cooler and wetter climates at higher altitudes. The Sky Island complex contains 90 mammal species, 265 bird species, 75 reptile species and over 2000 plant species. Many species inhabiting the Sky Island range are also endemic, including six mammal subspecies and 60 snail species, nearly a third of all those found in the region. If these isolated mountain habitats disappear as a result of warming, the species that are unable to migrate, that is, the most unique and rare residents, will disappear.

The risk of 'falling off' the end of a continent is facing the numerous species in the highly speciose Fynbos in southern Africa, a region so rich in plant diversity that it qualifies as both a Biodiversity Hotspot (Myres et al. 2000) and a distinct floristic kingdom despite encompassing only 500,000 ha. Southward dispersal into the ocean is an unpromising option for its 7000 plus endemic species. Researchers at South Africa's National Botanical Institute predict a loss of Fynbos biome area of between 51% and 65% by 2050 (Midgley et al. 2002). At a chillier extreme, polar bears (*Ursus maritimus*) require sea ice on which to hunt seals all winter, thereby becoming sufficiently corpulent to fast through a relatively foodless Arctic summer. An adult female weighing 175 kg after weaning her cubs needs to gain at least 200 kg to have a successful pregnancy. If the sea ice forms later and melts earlier, the window of opportunity for hunting may be too brief for the bears to accumulate enough fat to breed, raise young, or even to survive themselves (Derocher et al. 2004).

No species exists in isolation. If species' distributions shuffle across the globe in response to climate change, there is a risk of tearing apart contemporary natural communities, and most importantly, uncoupling the predatory, competitive or beneficially coevolved relationships between species (Root & Schneider 1993). Faced with the same environmental change, species react differently, so the consequences of climate change may cascade. A disturbing example comes from the Monteverde Cloud Forest in Costa Rica, where Pounds (2002) found that submontane species are moving up to higher altitudes. This results in new encounters between species. The resplendent quetzal (*Pharomachrus mocinno*), for example, is a bird that nests in tree cavities. Until 1995, this species was not affected by the keel-billed toucan (*Ramphastos sulfuratus*). Coincident with increasing temperature, declining diurnal temperature range, and fewer days of montane mist, the toucans, formerly restricted to lowlands, have ascended the mountain to live alongside the quetzals in the cloud forest (Pounds et al. 1999). This situation proves problematic for the quetzal owing to the toucan's proclivity for predatorily poking its long bill into quetzal nests.

Climate change and phenology

Phenology – the study of the timing of such ecological events as when flowers bloom or when migrants arrive – has already revealed numerous shifts seemingly associated with climate change (see references cited in Appendix to Root et al. 2003). Changes have been observed in the timing of events such as maximum zooplankton biomass in the North Pacific (Mackas et al. 1998), peak insect abundance in Europe (Sparks & Yates 1997) and New Zealand (White & Sedcole 1991), calling by frogs (which reflects timing of breeding) in North America (Gibbs & Breisch 2001), migration arrival and departure of birds in Europe (Bezzel & Jetz, 1995; Visser et al. 1998) and North America (Ball 1983; Bradley et al. 1999), breeding of birds in the UK (Thompson et al. 1986; Crick et al. 1997), Germany (Ludwichowski 1997) and North America (Brown et al. 1999; Dunn & Winkler 1999), and bud burst and blooming by trees in North America (Beaubien & Freeland 2000) and Asia (Kai et al. 1996).

The first calls of frogs and toads are a familiar harbinger of spring for many people in temperate parts of the world. Some amphibian species brave still-ice-crusted ponds at the first spring warming to begin courtship and the laying of eggs. Spring chorusing behaviour, which is associated with breeding activity, is closely linked to temperature (Busby & Brecheisen, 1997). Constituting one of the longest-running records of species' natural history, a study in England recorded the timing of first frog and toad croaks each year from 1736 to 1947 (Sparks & Carey, 1995). The date of spring calling for these amphibians occurred earlier over time, and was positively correlated with the annual mean spring temperature. For example, from 1980 and 1998, researchers found that the time of arrival of sexually mature common toads (*Bufo bufo*) at breeding ponds was highly correlated with the mean temperatures in the 40 days preceding their arrival (Reading, 1998). Similarly, two frog species, at their northern range limit in the UK, spawned 2 to 3 weeks earlier in 1994 than in 1978 (Beebee, 1995). Three species of newt similarly arrived 5 to 7 weeks earlier at breeding ponds.

Studies of migratory species such as birds are more complex. There is considerable documentation of changes in the spring arrival or breeding of birds in Europe (e.g. Berthold et al. 1995; Crick et al. 1997; Winkel & Hudde 1997; McCleery & Perrins 1998; Penuelas et al. 2002; Huppop & Huppop 2003) and more limited research in North America (e.g. Oglesby & Smith 1995; Bradley et al. 1999; Strode 2003). Although these studies used a combination of the biological observations, climate correlations and life-history information as described above, it is often difficult to determine which climate variables to associate with the observations of a species at one location. For instance, if a migrant species from Africa arrives earlier in the UK, has this been prompted by the conditions in Africa or along the migratory route?

Many aspects of breeding in some birds seem to be associated with temperatures. In southern Germany, the number of reed warblers (*Acrocephalus scirpaceus*) fledging early in the season increased significantly between 1976 and 1997, probably due to long-term increases in spring temperatures (Bergmann 1999). The spring arrival of this warbler was earlier in warm years. Also in Germany, Winkel & Hudde (1996) documented significant advances in hatching dates of nuthatches (*Sitta europea*) over the period 1970–1995. These advances correlated with a general warming trend. Migratory patterns of birds in Africa are also changing (Gatter 1992).

Differential shifts in the phenology of interacting species could easily disrupt the populations of all species involved. For instance, if each species in an obligatory mutualistic relationship responds differentially to climatic change, then the resulting asynchrony may be damaging, and perhaps catastrophic, to both. Even in non-obligatory relationships, such as between pollinators and plants, differential responses of species due to climate change, may lead to population declines.

If a scenario like that for the great tits and moth larva (see Box 6.2) occurs for species that control insect pests in an agriculture setting, there could be a boom in insect populations, resulting in a need for more pesticide control. In pasture and grassland ecosystems, for example, birds are important predators of grasshoppers. Models estimate that a single pair of savannah sparrows (*Passerculus sandwichensis*) raising their young consume approximately 149,000 grasshoppers over a breeding season. Considering typical bird densities, roughly 218,000 grasshoppers per hectare are consumed each season (Kirk et al. 1996). In many of these areas, the economic threshold for spraying insecticides occurs as densities reach approximately 50,000 grasshoppers per hectare (McEwen 1987). The birds are thus thought to keep current grasshopper populations at levels below which spraying would otherwise be required.

Management and policy implications

We have already hinted at some of the implications of climate change for conservation management – and climate change is a difficult challenge for policy making. If we wish to prevent our climate from changing we must find ways to reduce carbon emissions or to recapture carbon and other greenhouse gases from the atmosphere. If we unable or unwilling to reduce our dependence on greenhouse gases we will have to find ways to adapt to a warmer world and either accept the loss and change of ecosystems or manage them closely in the context of climatic change.

Carbon mitigation and the new carbon economy

The most direct way to prevent serious climate-change impacts on biodiversity is to slow or reverse the rate of global warming by either reducing greenhouse gas emissions or finding ways to recapture carbon from the atmosphere. Both options are being addressed internationally by the Framework Convention on Climate Change, most immediately through the Kyoto protocol that commits developed countries that adopt it to reducing their carbon dioxide emissions to 1990 levels by 2012. The Kyoto protocol sits at the centre of international debates about who should do what about climate change and when. For example, the current USA Government has been unwilling to ratify Kyoto because it does not require emissions

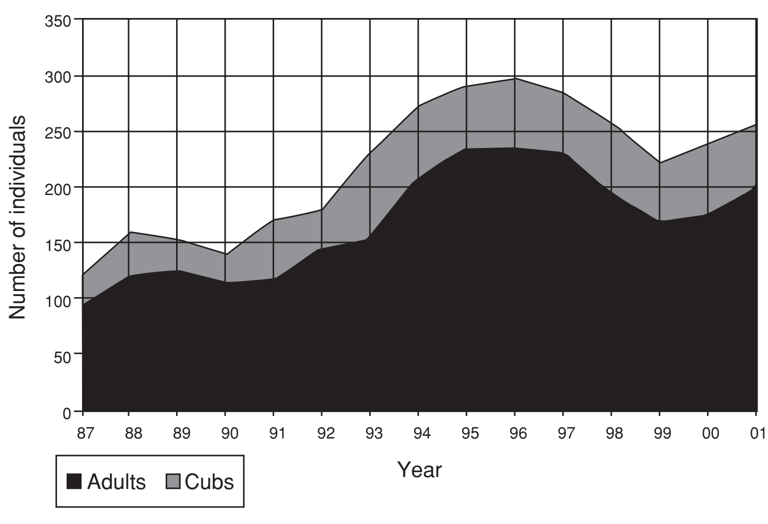
Box 6.2 Studies from Wytham Woods: from great tits to badgers

Oxford University's Wytham Estate embraces ancient woodland, plantation, grassland and mixed farmland. A microcosm of the countryside of lowland England, it has been used for ecological research for over 60 years, and two of these long-term data sets have revealed important effects of climate change (although, as is generally the way with the huge value of long-term data, this topic was not even in mind when the original data were gathered).

Long-term studies by the Edward Grey Institute of Ornithology have revealed that climatic change may be causing mismatching in the timing between the breeding of great tits (*Parus major*) in the UK and the hatching of caterpillars (Vannoordwijk et al. 1995; Visser et al. 1998). The tits do not seem to be shifting their clutch laying dates effectively. Because caterpillars are only abundant for a short period of time in the spring, females are under great pressure to lay early enough to take advantage of the richest flush of caterpillars, especially, the winter moth larva *Operophtera brumata*. The earliest breeders are generally much more successful, in terms of clutch size and survival. Late broods have to fledge and learn to feed while caterpillar abundance is rapidly diminishing (Haywood & Perrins, 1992). Simultaneously, laying early poses females with the problem of finding sufficient food to form their eggs a month before peak caterpillar abundance (Perrins, 1996); which seems to be so difficult that many birds breed later than they 'should'. Also, both sexes have to develop their reproductive systems from a regressed winter state in order to breed, which is another energetically expensive process. There is, however, a considerable advantage to the birds to breed as early as they can, because the earliest breeders tend to produce the most surviving offspring.

From 1970 onwards, tit laying-dates occurred earlier (Perrins & McCleery 1989), as caterpillar hatching dates, triggered by temperature, occurred earlier. With continued warming, the date of peak caterpillar abundance will probably continue to shift earlier, so much earlier that the tits may struggle to build nests, lay eggs and have the eggs hatch in time to take advantage of the caterpillars. Not least, earlier in the year nights are longer and colder, putting the tits under severe feeding constraints. The lack of the caterpillar availability could negatively affect the population size of this bird, and could greatly increase the population of caterpillars. In turn, greater caterpillar numbers could be detrimental to the trees.

The Wildlife Conservation Research Unit has also undertaken long-term ecological studies at Wytham, looking at the population dynamics of the Eurasian badger, *Meles meles*. The badger makes a good model species for testing the impacts of climate change owing to its wide geographical distribution, variable social system and, where available, favoured diet of earthworms (*Lumbricus terrestris*). Macdonald & Newman (2002) report that badger numbers at Wytham more than doubled between 1987 and 2001, with no change in population range, peaking in 1996 at 235 adults and 62 cubs (Box Fig. 6.2)



Box Fig. 6.2 Minimum number alive retrospective estimate for badger adult and cub numbers, 1987–2001.

Cub survival had a very significant affect on population size. In warmer, drier years cub survival was low (minimum 48.15%). In wetter years, and years with more wet days (both climatic factors influence earthworm availability), cub survival was much higher (maximum 94.74%), owing to a greater availability of earthworms under damp conditions.

Adult survival was not effected by annual temperature or absolute rainfall values, although the number of wet days showed a predictive trend, benefiting survival.

Developing this hydrological theme, volumetric soil water content (VSWC), although not a significant predictor of cub survival over the entire year, was strongly linked to cub survival in key spring months. Both lactating sows and their dependent offspring were very sensitive to food supply through the early part of the year. Badger cubs, weaned in May, start searching for food independently and thus effectively increase the number of foraging badgers in the population by up to one-third over a short time period.

Badgers preferentially eat earthworms. Of especial interest is the suggestion by the IPCC (2001a) that warming in annual mean temperature has occurred particularly as a result of night-time rather than day-time increases, thereby reducing the diurnal temperature range (DTR). This increases the availability of earthworms to nocturnal foraging badgers, as worms surface under mild, damp microclimatic conditions, and only in the absence of frost.

Warmer winters have been a particular feature of global warming (Brunetti et al. 2000). Northern Hemisphere annual snow-cover extent has consistently remained below average since 1987, and has decreased by about 10% since 1966 (IPCC, 2001a). Inspecting the relationship between winter temperatures, adult body-mass and subsequent cub productivity revealed a more insidious effect of climate change. In mild Januarys, both male and female badgers weighed up to 1 kg (c.10%+) more than in cold years. This weight gain cycle evolved precisely so that badgers can lay down a body-fat reserve should winter conditions turn harsh. In milder, wetter conditions, without ground frost or continuous snow cover (see Sagarin & Micheli 2001), badgers were able to continue to successfully forage for earthworms (and other food sources). A similar correlation between badgers' body-condition in January and the prediction of consequent offspring sex ratio was reported by Dugdale et al. (2003), as male cubs were favoured in milder years when adult females were heavier.

Adult female body mass in January was also a predictor of cub productivity and survival in the following spring. Badgers exhibit delayed implantation and while they mate post-partum in February–March, day-length (winter solstice) mediated by body condition (Woodroffe 1995) dictates implantation date. Gestation occurs through the winter; thus fat reserves are critical to embryonic and subsequent neonatal survival (Cheeseman et al. 1987). Warming trends in Fennoscandia (Carter 1998), affecting badger abundance and distribution (Bevanger &Lindstrom 1995), have allowed badgers to extend their distribution 100 km northwards in Finland since the mid-1940s, now as far north as the Arctic circle, with numbers in southern Finland doubling (Kauhala 1995a,b).

A climatic paradox appears to be developing. Mild, wet winters provide badgers with good earthworm foraging during a time of year when typically frozen ground forces them to live off their fat reserves. These conditions allow badgers to maintain better winter masses and lead to larger cub cohorts. Trends towards spring droughts, however, may not be so advantageous. The IPCC predicts that winters classified as 'cold' will become much rarer by 2020 and almost disappear by 2080. Simultaneously, hot dry summers will become much more frequent. These are scenarios in which the adult badger population likely could survive well, but could fail to produce enough surviving cubs to sustain their populations.

reductions in developing countries, including those that compete economically with the USA, such as China, and because many Americans think that the costs of carbon cuts will outweigh the benefits. Underlying such beliefs are cost-benefit analyses that place low or no value on biodiversity and that assume there are minimal economic opportunities in a lower carbon economy. Developing countries argue that they should not have to slow the growth of their economies by switching from coal and oil, given that the developed world has already based their economic success on the use of cheap fossil fuels. Again, this assumes that economic growth is only possible with fossil fuels rather than alternatives.

As a result of Russia's decision to ratify Kyoto, the treaty (which required 55 countries producing at least 55% of the emissions to sign) went into force in 2005, but without the participation of major emitters including the USA and Australia.

Unfortunately the Kyoto protocol as currently implemented only achieves a modest (2–5.2%) reduction in emissions, whereas to stabilize the climate at, for example, twice the pre-industrial levels of greenhouse gases, would require a 60% reduction in worldwide emissions. Even with such dramatic reductions, the planet would still experience some warming with associated impacts on ecosystems. The scale of mitigation requires not only aggressive reductions by the USA, but also the participation of major developing countries such as China, India and Brazil, whose current development paths will produce significant emissions over the next 50 years. The developing world is reluctant to reduce its energy use and development when they perceive the profligate per capita consumption of developed countries (see Chapter 18). One widely accepted proposal is to stabilize emissions at 450 ppmv through a process of 'contraction and convergence', permitting the developing world to grow economies and emissions while the developed world reduces emissions so that the two converge at a roughly equal per capita allocation by 2050 or 2100, perhaps as a result of trading in carbon permits. But given the wide range in current per capita emissions, from less than 1 ton per capita in most of Africa to more than 20 in the USA (2002 data from http://cdiac.esd. ornl.gov/home.html), such convergence will prove hard to achieve in a world with such vast differences in consumption and lifestyles.

Kyoto provides an option for countries to meet their commitments by investing in energy efficiency or carbon sequestration (through reforestation) in the developing world through the UN Clean Development Mechanism (CDM) and in Eastern Europe through Joint Implementation (JI) options. Thus, countries and corporations can offset domestic emissions by a development project that plants forests or increases the efficiency of a power station (effectively allowing them to continue to burn fossil fuels by investing in carbon reduction more cheaply elsewhere). Carbon trading has provided a new investment opportunity as companies arrange for carbon reductions and sell the credit. One of the challenges to mitigation is to derive accurate estimates of the carbon savings and to ensure that the price of carbon reflects the costs of potential damages rather than speculation in a highly uncertain market. On its own reforestation or other land uses that sequester carbon to reduce emissions cannot balance the consumption of fossil fuels, and, often have serious implications for biodiversity. For example, sequestration through large-scale plantations is likely to reduce species diversity and require conversion of natural forests and grasslands to intensive carbon management.

So far, the international commitment to mitigation does not hold out much hope for preventing climate change because Kyoto will produce such a modest reduction by 2012. Some countries are already struggling to meet their Kyoto commitments and the USA and the developing countries currently outside the regime are likely to continue to increase emissions. Major investments are now being made in carbon capture options that might re-inject carbon into deep wells or oceans, but these are unlikely to move beyond pilot projects over the next decade. And policies to move energy use away from fossil fuels towards renewables or nuclear are already controversial, with wind power, for example, opposed by some ecologists and conservationists because of risks to species and landscape aesthetics and nuclear risks and waste management unacceptable to the public in many countries.

Researchers at Princeton University (Socolow et al. 2004) have offered a set of seven 'stabilization wedges' that they suggest produce a reduction of 200 billion tons of carbon between 2004 and 2054. This would be achieved through expansion and investments in: (i) energy conservation (especially transport fuel efficiency, and building construction); (ii) renewable energy, especially wind and solar; (iii) renewable fuels such as biofuels; (iv) enhanced natural sinks to capture carbon, such as well managed forests and soils; (v) nuclear energy; (vi) substitution of gas for other fossil fuels; and (vii) carbon capture within geological storage. Although these 'wedges' might reduce emissions and climate change, several of them, such as biofuels and nuclear, might have other implications for ecosystems and biodiversity (Chapter 18 concludes that such unhappy trades-off are facing the future of biodiversity conservation at every turn).

Adaptation

Adapting to climate change might seem the easier option, especially for natural systems that have coped with variations in climate over the millennia. But on a planet where humans are everywhere modifying and managing ecosystems, and given the rapidity of anthropogenic climate change, conservation for climate change adaptation is a complex technical, ethical and economic challenge.

The World Wildlife Fund has produced several reports proposing conservation strategies for climate change (e.g. WWF 2003), which is now accepted by most ecologists and conservation organizations – not least through the Millennium Ecosystem Assessment (2005) – as a major threat to biodiversity. The major proposals include:

1. Establishing protected areas that provide a margin for adaptation to climate change through, for example, north–south transects securing space for species to shift northwards or upwards as they adapt, conservation corridors that facilitate migration, or buffer zones that allow adjustment of range within the protected area. The World Wildlife Fund suggests that protected area creation and management could focus on potential refuges that might be more resilient to climate changes because they are in the core rather than the margins of climatic zones. Alternatively conservation might focus on the critical margins between climatic zones where there will be competition between species moving poleward at a faster rate than slower ones and where larger protected areas might thus be needed.
2. Reducing the non-climatic stresses on key species and ecosystems including land-use change, simplification, pollution, introduction of exotics, and hunting pressures in order to reduce vulnerability and maximize flexibility to cope with climate change. A reduction in ecosystem fragmentation is particularly important for adaptations in terms of the protected areas noted above, where continuous areas are needed for movement across the landscape.
3. Employing adaptive management strategies that can adjust to the onset of climatic changes and directly intervene to reduce its impacts and facilitate adaptation through, for example, assisted migration, species reintroduction, prescribed burning and control of invasive species.

Some of these strategies pose great challenges and unprecedented costs to conservation managers. For example, the management of species range and density is very complex. For species that need to move upslope on mountains to escape warmer temperatures lower down, one solution is to plan for reserves that include both lower and upper elevations, but this poses the conundrum faced by the competition of quetzals encountering toucans in the Costa Rica case, mentioned above. Wildlife managers are in a challenging situation: to increase the quetzal's chance of survival, do they begin to kill toucans? Such intertwined ethical and ecological dilemmas will continue to arise as historically unprecedented environmental changes such as these unfold.

The solution to northward movement of suitable habitats by setting up interconnected nature reserves that run north–south, or along altitudinal gradients, is also complicated. Unfortunately the human footprint of large swaths of agricultural and urban lands and private ownership of property in many regions means that contiguous reserves may not be possible without land purchase or appropriation. Routes for fauna to cross over or under highways may be needed to facilitate dispersal, similar to what was done for caribou (*Rangifer tarandus*) in the Arctic when the Alaskan pipeline was built (Smith & Cameron 1985). Costa Rica has established conservation corridors that join several protected areas including part of the Paseo Pantera (Panther Path) that would provide migration routes for the panther through Central America.

Such a programme would be costly and it is hard to protect large enough areas to make a difference. Many migratory birds use a series of staging areas along their north–south migration routes, meaning an appropriate reserve system would need to consider much of a hemisphere. Conversely, a small sedentary amphibian might spend its entire life in a small pond and have no means to migrate to the next wetland without assistance, even over short distances. And for some species, such as polar bears and many migratory geese, who rely on the presence of Arctic ice and large areas of tundra vegetation, it is hard to envisage a solution that would adequately protect their habitat from the serious changes projected for Arctic ecosystems.

Another outcome would be for the remnants of relatively immobile wildlife and plant communities to remain in existing isolated reserves and parks. Such 'habitat islands' probably would require management and manipulation, and examples of metapopulation management are already surfacing (see Chapter 5), as are those of small, isolated populations (Chapter 4). The resulting difficult distinctions along the spectrum from zoo to wilderness are raised in Chapter 18. Biodiverse and more complete communities are sometimes less vulnerable to the impacts of climate change than impoverished ones that lack keystone species (Power et al. 1996; Naem & Li 1997; Wilmers et al. 2002).

As in cases with range shifts, species experiencing discordant phenological shifts face peril. The opportunities for conservation and mitigation are more daunting – because they are so limited. The need for interventions seems likely to increase, perhaps 'helping' a species bypass an obstacle to reach new, more suitable habitat, or intervening to, for example, protect prey from predators – the morass of awkward judgments is unappealing. The reality is that spring plants and insects cannot be convinced to 'wait' for later migrants. The early bird gets the worm, so to speak! Migrants that do adapt their arrival times will be at a competitive advantage to later arrivals, claiming nesting sites and taking advantage of the optimal food sources. Unsurprisingly, most conservation legislation can cope poorly with change, and does so all the worse across national boundaries. Thus, even as dramatic and dangerous as climatic-induced range shifts are projected to be, phenological shifts, although difficult to anticipate and observe, have the potential to be an equal or greater conservation risk to many species.

Conclusion

Climatic change is an environmental challenge unprecedented in historical times because of its global scope and far-reaching implications for biodiversity and human society. Furthermore, the social responses to these challenges step out of the scientific realm and into decisions that must be made in the swirling waters of ethics, politics and theoretical uncertainty.

Projected future rapid climate change (Mastrandrea & Schneider 2004) could soon become a more looming concern, especially when occurring in concert with other already well-established stressors, particularly habitat fragmentation. Attention must be focused not only on each of these stressors by themselves, but the interactions between them. Change can best be managed, even ameliorated, if it is anticipated, and that necessitates understanding its causes and thereby predicting its scope and tenor. The study of climate change, and its interaction with numerous other complex factors that together impact biodiversity, is an immense, daunting, but urgent challenge for the twenty-first century.

Acknowledgements

We wish to acknowledge partial support for this work for TLR from the US Environmental Protection Agency and the Winslow Foundation. CN gratefully acknowledges support from the Peoples Trust for Endangered Species and the Earthwatch Institute. Thanks to Stephen Schneider, Dena MacMynowski and Christina Buesching for many helpful comments on early drafts of this paper.

Facts do not cease to exist because they are ignored.

(Aldous Huxley, *Proper Studies*, 1927.)

References

Ball, T. (1983) The migration of geese as an indicator of climate change in the southern Hudson Bay region between 1715 and 1851. *Climatic Change* **5**: 85–93.

Beaubien, E.G. & Freeland, H.J. (2000) Spring phenology trends in Alberta, Canada: links to ocean temperature. *International Journal of Biometeorology* **44**: 53–9.

Beebee, T.J.C. (1995) Amphibian breeding and climate. Nature **374**: 219–20.

Bergmann, F. (1999) Long-term increase in numbers of early-fledged Reed Warblers (*Acrocephalus scirpaceus*) at Lake Constance (Southern Germany). *Journal Fuer Ornithologie* **140**: 81–6.

Berthold, P., Nowack, E. & Querner, U. (1995) Satellite tracking of migratory birds from Central Europe to South African winter quarters – a case-report of the white stork. *Journal für Ornithologie* **136**: 73–6.

Bevanger, K. & Lindstöm, E.K. (1995) Distributional history of the European badger *Meles meles* in Scandinavia during the 20th century. *Annales Zoologicae Fennici* **32**: 5–9.

Bezzel, E. & Jetz, W. (1995) Delay of the autumn migratory period in the blackcap (*Sylvia atricappila*) 1966–1993: a reaction to global warming? *Journal Fuer Ornithologie* **136**: 83–7.

Bradley, N.L., Leopold, A.C., Ross, J. & Huffaker, W. (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America* **96**: 9701–4.

Brown, J.L., Li, S.-H. & Bhagabati, N. (1999) Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proceedings of the National Academy of Sciences of the United States of America* **96**: 5565–9.

Brunetti, M., Maugeri, M. & Nanni, T. (2000) Variations of temperature and precipitation in Italy from 1866 to 1995. *Theoretical and Applied Climatology* **65**: 165–74.

Busby, W.H. & Brecheisen, W.R. (1997) Chorusing phenology and habitat associations of the crawfish frog, *Rana areolata* (Anura: Ranidae), in Kansas. *Southwestern Naturalist* **42**: 210–17.

Carter, T.R. (1998) Changes in the thermal growing season in Nordic countries during the past century and prospects for the future. *Agricultural and Food Science in Finland* **7**: 161–79.

Chavez, F.P., Ryan, J., Luch-Cota S.E. & Niquen, M. (1999) Biological and chemical response of the equatorial Pacific Ocean to the 1997–98 El Niño. *Science* **286**: 2126–31.

Cheeseman, C.L., Wilesmith, J.W., Ryan, J. & Mallinson, P.J. (1987). Badger population dynamics in a high-density area. *Symposia of the Zoological Society of London* **58**: 279–94.

Cook, A.J. Fox, A.J., Vaughan, D.G. & J.G. Ferrigno, J.G. (2005) Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science* **22**: 541–544.

Crick, H.Q., Dudley, C., Glue, D.E. & Thomson, D.L. (1997) UK birds are laying eggs earlier. *Nature* **388**: 526.

Derocher, A.E., Lunn, N.J. & Stirling, I. (2004) Polar bears in a warming climate. *Integrative and Comparative Biology* **44**: 163–76.

Dugdale, H.L., Macdonald, D.W. & Newman, C. (2003) Offspring sex ratio variation in the European badger, *Meles meles*. *Ecology* **84**(1): 40–5.

Dunn, P.O. & Winkler, D.W. (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London Series B – Biological Sciences* **266**: 2487–90.

Gatter, W. (1992) Timing and patterns of visible autumn migration: can effects of global warming be detected? *Journal Fuer Ornithologie* **133**: 427–36.

Gibbs, J.P. & Breisch, A.R. (2001) Climate warming and calling phenology of frogs near Ithaca, New York, 1900–1999. *Conservation Biology* **15**: 1175–8.

Hall, M.H. & Fagre, D.B. (2003) Modeled climate-induced glacier change in Glacier National Park, 1850–2100. *BioScience* **53**: 131–40.

Harrison, D., Vanhinsbergh, P., Fuller, R.J. & Berry, P.M. (2003a) Modelling climate change impacts on the distribution of breeding birds in Britain and Ireland. *Journal for Nature Conservation* **11**: 31–42.

Harrison, P.A., Berry, P.M. & Dawson, T.P. (2003b) Modelling natural resource responses to climate change (the MONARCH project): an introduction. *Journal for Nature Conservation* **11**: 1–4.

Hays, J.D., Imbric, J. & Shackleton, N.J. (1976) Variations in the Earth's orbit: pacemaker of the ice ages. *Science* **194**: 1121–32.

Haywood, S. & Perrins, C.M. (1992) Is clutch size in birds affected by environmental conditions during growth? *Proceedings of the Royal Society of London* **249**: 196–197.

Hersteinsson, P. & Macdonald, D.W. (1992) Interspecific competition and geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**: 505–515.

Huppop, O. & Huppop, K. (2003) North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London* **270**: 233–40.

Hutchinson, G.E. (1958) Concluding remarks. *Cold Spring Harbor Symposium for. Quantitative. Biology* **22**: 415–27.

Intergovernmental Panel on Climate Change (IPCC) (2001a) *Climate Change 2001: the Science of Climate Change*. Cambridge University Press, New York.

Intergovernmental Panel on Climate Change (IPCC) (2001b) *Climate Change 2001: Impacts, Adaptations and Vulnerabilities*. Cambridge University Press, New York.

Jácome, R. & Ospina, P. (1999) La Reserva Marina de Galápagos. Un año difícil. In *Informe Galápagos 1998–1999* (Eds P. Ospina & E. Muñoz,), pp. 35–42. Fundación Natura-WWWF, Quito.

Kai, K., Kainuma, M. & Murakoshi, N. (1996) Effects of global warming on the phenological observation in Japan. In *Climate Change and Plants in East Asia* (Eds K. Omasa, K. Kai, H. Taoda & Z. Uchijima), pp. 164–73. Springer-Verlag, New York, NY.

Kauhala, K. (1995a) Mayran levinneisyys ja runsaus Suomessa. *Suomen Riista* **41**: 85–94.

Kauhala, K. (1995b) Distributional history of the European badger *Meles meles* in Scandinavia during the 20th century. *Annales Zoologicae Fennici* **32**: 183–91.

King, D. (2004) Climate change science: adapt, mitigate, or ignore? *Science* **303**: 176–7.

Kirk, D.A., Evenden, M.D. & Mineau, P. (1996) Past and current attempts to evaluate the role of birds as predators of insect pests in temperate agriculture. *Current Ornithology* **13**: 175–269.

Ludwichowski, I. (1997) Long-term changes of wing-length, body mass and breeding parameters in first-time breeding females of goldeneyes (*Bucephala clangula clangula*) in northern Germany. *Vogelwarte* **39**: 103–16.

Macdonald, D.W. & Newman, C. (2002) Badger *(Meles meles*) population dynamics in Oxfordshire, UK. Numbers, density and cohort life histories, and a possible role of climate change in population growth. *Journal of Zoology* **256**: 121–38.

Mackas, D.L., Goldblatt, R. & Lewis, A.G. (1998) Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacfic. *Canadian Journal of Fisheries and Aquatic Science* **55**: 1858–93.

Mann, M.E., Bradley, R.S. & Hughes, M.K. (1998) Global-scale temperature patterns and climate forcing over the past six centuries. *Nature* **392**: 779–87.

Mann, M.E., Bradley, R.S. & Hughes, M.K. (1999) Northern Hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. *Geophysical Research Letters* **26**: 759–62.

Mastrandrea, M.D. & Schneider, S.H. (2004) Probabilistic integrated assessment of dangerous climate change. *Science* **304**: 571–5.

McCleery, R.H. & Perrins, C.M. (1998) Temperature and egg laying dates. *Nature* **391**: 30–1.

McDonald, K.A. & Brown, J.H. (1992)Using montane mammals to model extinctions due to global change. *Conservation Biology* **6**(3): 409–15.

McEwen, L.C. (1987) Function of insectivorous birds in a shortgrass IPM system. In *Integrated Pest Management on Rangeland: a Shortgrass Prairie Perspective* (Ed. J.L. Capinera), pp. 389–402. Westview Press, Jackson, TN.

McIntyre, S. & McKitrick, R. (2003) Corrections to the Mann et al. (1998) Proxy data base and Northern Hemispheric average temperature series. *Energy and Environment* **14**(6): 751–71.

McIntyre, S. & McKitrick, R. (2005) Hockey sticks, principal components and spurious significance. *Geophysical Research Letters* **32**(3): 12 February, LO 3710.

Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C. & Powrie, L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography* **11**(6): 445–51.

Millennium Ecosystem Assessment (2005) *Synthesis Report*. http: //www.millenniumassessment.org [Last accessed on 1 August 2005]

Myres, N.R., Mittermeier, A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–8.

Naem, S. & Li. S.B. (1997). Biodiversity enhances ecosystem reliability. *Nature* **390**: 507–9.

Nicolaides, F. & Murillo, J. C. (2001). Efectos de El Niño 1997–1998 y Post Niño 1990 en la pesca del bacalao (*Mycteroperca olfax*) y la lisa rabo negro (*Mugil cephalus*) de las Islas Galápagos. In *Informe Galápagos 2000 –2001* (Eds C. Falconí, R. E. Ruiz & C. Valle), pp. 104–9. Fundación Natura and WWF, Quito.

Oglesby, T.T. & Smith, C.R. (1995) Climate change in the northeast. In *Living Resources: a Report to the Nation on the Distribution, Abundance and Health of U.S. Plant, Animals and Ecosystems* (Eds E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran & M.J. Mac), pp 38–56. Department of the Interior, National Biological Service, Washington, DC.

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

Penuelas, J., Filella, I. & Comas, P. (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* **8**: 531–44.

Perrins, C.M. (1996) Eggs, egg formation and the timing of breeding. *Ibis* **138**: 2–15.

Perrins, C.M. & McCleery, R.H. (1989) Laying dates and clutch size in the great tit. *Wilson Bulletin* **101**: 234–53.

Pounds, J.A. (2002) Impacts of climate change on birds, amphibians and reptiles in a tropical montane cloud forest reserve. In *Impacts of Climate Change on Wildlife* (Eds R.E. Green, M. Harley, M. Spalding & C. Zöckler), pp. 30–32. Royal Society for the Protection of Birds, Sandy.

Pounds, J.A. & Puschendorf, R. (2004) Feeling the heat: climate change and biodiversity loss (editorial). *Nature* **427**: 107–9.

Pounds, J.A., Fogden, M.P.L. & Campbell, J.H. (1999). Biological response to climate change on a tropical mountain. *Nature* **398**: 611–5.

Power, M.E., Tilman, D., Estes, J.A., et al. (1996). Challenges in the quest for keystones. *BioScience* **46**: 609–20.

Press, F. & Siever, R. (1982) *Earth*, 3rd edn. W.H. Freeman and Co, New York.

Rahmstorf, S. (1995) Bifurcations of the Atlantic thermohaline circulation in response to changes in the hydrological cycle. *Nature* **378**: 145–9.

Reading, C.J. (1998) The effect of winter temperatures on the timing of breeding activity in the common toad *Bufo bufo*. *Oecologia* **117**: 469–75.

Riedinger M.A., Steinitz-Kannan M., Last W.M. & Brenner M. (2002.) A similar 6100 C–^{14}C yr record of El Niño activity from the Galapagos Islands. *Journal of Paleolimnology* **27**: 1–7.

Root, T.L. & Schneider, S.H. (1993) Can large-scale climatic models be linked with multi-scaled ecological studies? *Conservation Biology* **7**: 256–70.

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

Root, T.L, MacMynowski, D.P., Mastrandrea, M.D. & Schneider, S.H. (2005) Human-modified temperatures induce species changes: joint attribution. *Proceedings of the National Academy of Sciences* **102**: 7465–9.

Sagarin, R. & Micheli, F. (2001) Climate change in nontraditional data sets. *Nature* **294**: 811.

Smith, W.T. &. Cameron, R.D. (1985) Reactions of large groups of caribou to a pipeline corridor on the arctic coastal plain of Alaska. *Arctic* **38**: 53–7.

Socolow, R., Hotinski, R., Greenblatt, J.B. & Pacala, S. (2004) Solving the climate problem: technologies available to curb CO_2 emissions. *Environment* **46**: 8–19.

Sparks, T.H. & Carey, P.D. (1995) The responses of species to climate over two centuries: An analysis of the Marsham phenological record. *Journal of Ecology* **83**: 321–9.

Sparks, T.H. & Yates, T.J. (1997) The effect of spring temperature on the appearance dates of British butterflies 1883–1993. *Ecography* **20**: 368–74.

Stanhill, G. & Cohen, S. (2001) Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. *Agricultural and Forest Meteorology* **107**: 255–78.

Stone, R.S., Belchansky, G., Drobot, S. & Douglas, D.C. (2004) Diminishing sea ice in the western Arctic Ocean. In *State of the Climate in 2003* (Eds D.H. Levinson & A.M. Waple). *Bulletin of the American Meteorological Society* **85**: S32–S33.

Strode, P.K. (2003) Implications of climate change for North American wood warblers (Parulidae). *Global Change Biology* **9**: 1137–44.

Stuart, A.J. (1991) Mammalian extinctions in the Late Pleistocene of northern Eurasia and North America. *Biological Review of the Cambridge Philosophical Society* **66**: 453–62.

Thompson, D.B.A., Thompson, P.S. & Nethersole-Thompson, D. (1986) Timing of breeding and breeding performance in a population of greenshank. *Journal of Animal Ecology* **55**: 181–99.

Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Lin, P.-N., Henderson, K. & Mashiotta, T.A. (2002) Tropical glacier and ice core evidence of climate change on annual to millennial time scales. *Climatic Change* **59**: 137–155.

Trenberth, K.E. & Hoar, T.J. (1996) The 1990–1995 El Nino Southern Oscillation event: longest on record. *Geophysical Research Letters* **23**: 57–60.

Vannoordwijk, A.J., McCleery, R.H. & Perrins, C.M. (1995) Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology* **64**: 451–458.

Vargas, H., Lougheed, C. & Snell, H. (2005) Population size and trends of the Galapagos Penguin *Spheniscus mendiculus. Ibis* **147**: 367–74.

Vargas, H., Harrison, S., Rea, S. & Macdonald, D.W. (2006) Biological effects of El Niño on the Galapagos Penguin. *Biological Conservation* **127**:107–14

Visser, M.E., Vannoordwijk, A.J., Tinbergen, J.M. & Lessells, C.M. (1998) Warmer springs lead to mistimed reproduction in Great Tits (*Parus major*). *Proceedings of the Royal Society of London Series B – Biological Sciences* **265**: 1867–70.

White, E.G. & Sedcole, J.R. (1991) A 20–year record of alpine grasshopper abundance, with interpretations for climate change. *New Zealand Journal of Ecology* **15**: 139–52.

Wilmers, C.C., Sinha, S. & Brede, M. (2002) Examining the effects of species richness on community stability: an assembly model approach. *Oikos* **99**: 363.

Winkel, W. & Hudde, H. (1996) Long-term changes of breeding parameters of Nuthatches *Sitta europaea* in two study areas of northern Germany. *Journal Fuer Ornithologie* **137**: 193–202.

Winkel, W. & Hudde, H. (1997) Long-term trends in reproductive traits of tits (*P.arus major*, *P. caeruleus*) and pied flycatchers (*Ficedula hypoleuca)*. *Journal of Avian Biology* **28**: 187–90.

Woodroffe, R. (1995) Body condition effects implantation date in the European badger, *Meles meles. Journal of Zoology* **236**: 183–8.

WWF (2003) *Annual Report*. World Wide Fund for Nature, Gland, Switzerland.