

Adapting to climate change: is there scope for ecological management in the face of a global threat?

PHILIP E. HULME

NERC Centre for Ecology and Hydrology, Banchory, Kincardineshire AB31 4BW, UK

Summary

1. Climate change is recognized as a major threat to the survival of species and integrity of ecosystems world-wide. Although considerable research has focused on climate impacts, relatively little work to date has been conducted on the practical application of strategies for adapting to climate change. Adaptation strategies should aim to increase the flexibility in management of vulnerable ecosystems, enhance the inherent adaptability of species and ecosystem processes, and reduce trends in environmental and social pressures that increase vulnerability to climate variability.

2. Knowledge of the specific attributes of climate change likely to impact on species or habitats is central to any adaptive management strategy. Temperature is not the only climate variable likely to change as a result of anthropogenic increases in greenhouse gases. In some regions changes in precipitation, relative humidity, radiation, wind speed and/or potential evapotranspiration may be more marked than for temperature.

3. Uncertainty exists in the response of species and ecosystems to a given climate scenario. While climate will have a direct impact on the performance of many species, for others impacts will be indirect and result from changes in the spatiotemporal availability of natural resources. In addition, mutualistic and antagonistic interactions among species will mediate both the indirect and direct effects of climate change.

4. Approaches to predict species' responses to climate change have tended to address either changes in abundance with time or in spatial distribution. While correlative models may provide a good indication of climate change impacts on abundance, greater understanding is generated by models incorporating aspects of life history, intra- and interspecific competition and predation. Models are especially sensitive to the uncertainty inherent in future climate predictions, the complexity of species' interactions and the difficulties in parameterizing dispersal functions. Model outputs that have not been appropriately validated with real data should be treated with caution.

5. *Synthesis and applications.* While climate impacts may be severe, they are often exacerbated by current management practices, such as the construction of sea defences, flood management and fire exclusion. In many cases adaptation approaches geared to safeguard economic interests run contrary to options for biodiversity conservation. Increased environmental variability implies lower sustainable harvest rates and increased risks of population collapse. Climate change may significantly reduce habitat suitability and may threaten species with limited dispersal ability. In these cases, well-planned species translocations may prove a better option than management attempts to increase landscape connectivity. Mathematical models, long-term population studies, natural experiments and the exploitation of natural environmental gradients provide a sound basis for further understanding the consequences of climate change.

Key-words: carbon sequestration, climate envelope, multi-trophic interactions

Journal of Applied Ecology (2005) **42**, 784–794

doi: 10.1111/j.1365-2664.2005.01082.x

Introduction

'Climate change is the most severe problem that we are facing today: more serious even than the threat of terrorism' (King 2004). With these words, Sir David King, the UK Chief Scientific Adviser to HM Government, emphasized the priority for policymakers to address the implications and consequences of environmental change. Subsequently, and as a result of the UK holding both the European Union (EU) and G8 presidency in 2005, climate change has been placed at the forefront of the international political agenda. It is therefore especially germane that the *Journal of Applied Ecology* has the pleasure to publish Sir David's British Ecology Society (BES) lecture entitled 'Climate Change: the Science and the Policy' (King 2005). The paper provides a succinct overview of the scientific understanding of climate change, an illustration of the range of impacts on biodiversity and examples of policy responses aiming to adapt or mitigate these impacts in the UK. Environmental management has an important role to play in mitigating climate change by maximizing carbon sequestration within ecosystems such as forests (Pinard & Cropper 2000; Shan, Morris & Hendrick 2001) and peatlands (Komulainen *et al.* 1999; McNeil & Waddington 2003). However, a key message is that no matter how successful efforts may be to mitigate the consequences of climate change through lesser reliance on fossil fuels and the adoption of renewable energy sources, the considerable inertia in the earth's system will require the development of adaptation strategies directed at global warming impacts over the next 30–40 years (King 2005). Although considerable international research has focused on climate impacts, relatively little work to date has been conducted on the practical application of strategies for adapting to climate change (King 2004, 2005). This situation reflects that adaptation is primarily orientated to tackle localized impacts of climate change, while mitigation aims to address the impacts on the climate system. Furthermore, it is perceived that while adaptation has the potential to reduce adverse effects of climate change it will not prevent all damages. As a result, much of the debate regarding climate change has revolved around the pros and cons of different mitigation strategies and discussion has often been polarized by the entrenched views of different interest groups (King 2004). This ongoing debate will undoubtedly introduce time lags between adoption of mitigation goals and their achievement, increasing the need for adaptation strategies. Given that natural environment resources and biodiversity will be significantly impacted as a result of climate change, a move towards adaptive management of species and habitats is overdue.

Establishing effective climate adaptation strategies requires that scientists, managers and policymakers work together to:

1. identify climate-sensitive system components;
2. assess the likelihood and consequences of impacts;
3. identify and select options for adaptation.

Adaptation strategies should aim to increase the flexibility in management of vulnerable ecosystems, enhance the inherent adaptability of the species and ecosystem processes within vulnerable natural systems, and reduce trends in environmental and social pressures that increase vulnerability to climate variability. Underpinning this approach is the assumption that adapting to current climate risks is consistent with adapting to future changed conditions and thus current knowledge can be applied to address future risks (Houghton *et al.* 2001). This special profile brings together six papers relevant to adaptive management: two examine future trends in invertebrate pests (Gilbert *et al.* 2005; Goulson *et al.* 2005); a further two assess changes in plant communities along climatic gradients (Cocke, Fulé & Crouse 2005; de Bello, Leps & Sebastia 2005); while the final pair address the impact of flood and sea defences on biodiversity (Ratcliffe, Schmitt & Whiffin 2005; Wolters *et al.* 2005). These studies encompass a range of approaches examining the consequences of climate change on a diversity of species and habitats, and that illustrate different options and constraints for adaptive management. The wider context of adaptive management to climate change is largely drawn from the considerable body of pertinent work published in the *Journal of Applied Ecology* and illustrates the breadth of relevant coverage encompassed by this leading ecological journal.

Adaptation: to what, where and when?

Climate change is synonymous with global warming and the greenhouse effect. However, temperature is not the only climate variable likely to change as a result of anthropogenic increases in greenhouse gases. Indeed, in some regions changes in precipitation, radiation, wind speed and/or potential evapotranspiration may be more marked than for temperature. Knowledge of the specific attributes of climate change likely to impact on species or habitats is central to any adaptive management strategy. Low ambient temperatures are known to limit phytoplankton distribution (King 2005), plant biomass (Liang, Michalk & Millar 2002), tree growth and phenology (Hunter & Lechowicz 1992; Kramer 1994), the distribution of insects (Worner, Tatchell & Woiwod 1995; Fenton & Wall 1997; Lindblad & Solbreck 1998; Virtanen *et al.* 1998; Tenow *et al.* 1999), marine fish (Pinnegar *et al.* 2002) and cephalopods (Robin & Denis 1999), as well as the survival of amphibians (Beattie, Aston & Milner 1991). However, warming is not always good news. For example, the intrinsic rate of increase of certain freshwater snails is inversely related to water temperature (O'Keeffe 1985). Furthermore, high ambient temperatures have been proposed as a key factor in the local extinction of one species of terrestrial mollusc, suggesting that temperature tolerance in egg development can determine the distribution of a snail species and, in the case of climatic warming, cause its extinction (Baur & Baur 1993).

It appears that while ambient temperature may influence the demography of birds, impacts are strongly mediated via food availability (Benton *et al.* 2002; Stillman *et al.* 2003; Frederiksen *et al.* 2004). These examples support the hypothesis that, compared with endotherms, the dynamics, distribution and abundance of ectotherms may be more strongly correlated with variations in ambient temperature. However, such a generalization should take into account the opportunities for thermoregulatory behaviour in certain ectotherms.

Ambient temperatures are a function of net radiation, heat fluxes and the environmental capacity for heat storage. The ecological impact of changes in solar radiation is poorly understood, yet global dimming because of aerosols and pollutants has resulted in a reduction in sunlight over the past four decades (King 2005). Studies have shown that many adult and immature insects are able to maintain body temperature well above, and often independently of, ambient temperature in the presence of direct solar radiation (Bryant, Thomas & Bale 2002). They may do so directly by basking, or indirectly via microhabitat choice. The implications of changes in solar radiation and consequences for thermoregulatory behaviour are often ignored in models that serve to predict species' responses to climate change. Nevertheless, such behaviour can be especially important, and larval thermoregulation in two species of butterflies enables them to extend their northern range in the UK by up to 200 km (Bryant, Thomas & Bale 2002).

As might be expected, semi-arid ecosystems are especially sensitive to changes in rainfall. In these ecosystems, water availability strongly determines vegetation productivity (Mwalyosi 1992; O'Connor 1994; Robertson, Bacon & Heagney 2001) as well as plant survival (Fensham & Holman 1999), and consequently the population dynamics of a range of vertebrate herbivores, including feral pigs *Sus scrofa* (Dexter 2003), cattle (Fynn & O'Connor 2000), wildebeest *Connochaetus taurinus* (Pascual & Hilborn 1995), zebra *Equus burchelli* (Georgiadis, Hack & Turpin 2003), red kangaroos *Macropus rufus* (McCarthy 1996) and even magpie geese *Anseranus semipalmata* (Bayliss 1989). Rainfall also appears important in initiating pest outbreaks including rodents (Leirs *et al.* 1996; Brown & Singleton 1999) and locusts (Todd *et al.* 2002). The indirect impact of rainfall on herbivores, mediated by responses in primary productivity, often results in the abundance and dynamics of herbivores lagging behind interannual variations in rainfall. Even in temperate ecosystems changes in precipitation may have marked effects. Rainfall is the key climatic factor for growth of Norway spruce in Denmark (Munster-Swendsen 1987) as well as the composition of soil fauna. Long-term experiments designed to simulate wetter or drier summers in spruce forest highlight that different soil fauna communities develop as a result of the treatment applied (Lindberg, Engtsson & Persson 2002). A similar approach in farmland habitats revealed that the effects of spring

drought on the abundance of epigeic herbivores, mycophages, omnivores and predators were negative, while those of irrigation were positive (Frampton, van den Brink & Gould 2000). These results indicate that a drier climate may lead to the local extinction of some soil animal species and may ultimately affect the availability of arthropod prey for insectivorous wildlife. Increased rainfall may not always be good news for invertebrates. The physiological stress arising from the direct effects of drought on trees may facilitate outbreaks of forest pests (Munster-Swendsen 1987), and periods of intense rainfall can increase the mortality of surface-feeding insect herbivores (Norris, Memmott & Lovell 2002).

Temperature and rainfall cannot be viewed in isolation and for many animal species, ranging from butterflies to bighorn sheep *Ovis canadensis* (Picton 1984; Pollard 1988), the impacts of climate change will occur through the combined effects of both variables. For plants, temperature and water availability are integrated in measures of evapotranspiration that have been found useful in interpreting their distribution at both large (Collingham *et al.* 2000) and small spatial scales (Belsky *et al.* 1993). Rates of evapotranspiration can have considerable knock-on consequences for hydrological regimes (and soil moisture) in ecosystems ranging from semi-arid (Hatton, Pierce & Walker 1993) to arctic (Walker & Walker 1991). The rate of evapotranspiration is determined by wind speed and the gradient of vapour pressure between the ground surface and the atmosphere. Changes in wind speed may therefore strongly mediate the interactive effects of temperature and rainfall on evapotranspiration. Increased wind speeds are also likely to impact directly on ecosystems through damage to trees and forests (Wooldridge *et al.* 1996). The complexity of the climate has led some authors to use summaries derived from synoptic weather maps (e.g. Lamb daily weather types) rather than individual climate variables as more appropriate indices against which to assess species performance. Such indices have proven useful in predicting the autumn migration of the bird cherry aphid *Rhopalosiphum padi* (Masterman *et al.* 1996) as well as survivorship of ungulates (Picton 1984).

In addition to absorbing infra-red radiation and hence acting as a greenhouse gas, increases in atmospheric CO₂ will have a direct impact on photosynthesis. Carbon dioxide levels are now rising at a rate close to 2 p.p.m. per annum and in 2004 were 40% higher than pre-industrial levels (King 2005). The effects of elevated CO₂ on vegetation include an increase in photosynthesis rates and reduced stomatal conductance as well as reduced respiration, and as a result reduced foliar nitrogen leading to increased C:N ratios. These effects are species specific and elevated CO₂ is likely to alter the competitive balance in plant communities, resulting in changes to ecosystem structure (Clark *et al.* 1995). Legumes appear especially responsive and grasses less so, with C₄ plants expected to respond

Table 1. Confidence in predictions of levels of variables within general circulation models (after Hossell, Briggs & Hepburn 2000)

Variable	Effect	Confidence
Increased atmospheric CO ₂	Increased photosynthesis and reduced water use by plants; effects at ecosystem level are unclear	Very high
Sea-level rise	Loss of land or of coastal habitats if hard sea defences exist	Very high
Increased temperature	Accelerated growth; longer and earlier growing season; potential range expansion northwards and to higher altitudes; reduced frost and winter die-back; higher potential evapotranspiration	High
Change in precipitation patterns and amounts	Change in run-off and leaching, soil moisture levels, flooding risk, frequency of drought and intensity of rainfall events, and in the frequency of snow fall and duration of snow lie	Low
Increased storminess	Increased windthrow and soil erosion; reduced infiltration of rainfall	Very low

least to increases in availability of atmospheric CO₂. Elevated CO₂ may also indirectly influence invertebrate herbivores as a result of changes in the quality of plant material (Clark *et al.* 1997).

An uncertain future: positive and negative feedbacks on species' responses

The foregoing highlights that climate change will alter many of the environmental conditions that shape the distribution and abundance of species. Nevertheless, there is still uncertainty about the magnitude and direction of some elements of climate change (Table 1). Uncertainties in the assessment of climate change and its impacts result from a cascade of unknowns including: trends in future emissions of greenhouse gases; knowledge about the climate system (and hence in climate models); and the strength of causal links between observed changes to ecosystems and climate change. The natural variability of the climate makes it difficult to attach high levels of confidence to some of the predicted changes, particularly those associated with extreme events and/or where large natural variability is inherent. Furthermore, climate may exert its influence through intra-annual variation via seasonal changes in regional weather as well as longer interannual frequencies related to global climate systems (Robin & Denis 1999; Todd *et al.* 2002). Unfortunately, levels of confidence do not map onto potential impact and some of the potentially most severe changes to the global environment are the hardest to predict, e.g. major changes in the ocean circulation of the North Atlantic.

Uncertainty also occurs in the response of species and ecosystems to a given climate scenario. While climate variables will have a direct impact on the performance and demography of many species, for others the strongest impact will be indirect and will result from changes in the spatiotemporal availability of natural resources. In addition, mutualistic and antagonistic interactions among species will mediate both the indirect and indirect effects of climate change. For example, although drought is known to impact severely on trees in Australian savannas, spatial variation in dieback of

trees is not correlated with local rainfall patterns but with the density and composition of the trees, thus highlighting that competitive interactions influence the response (Fensham & Holman 1999). Grazers mediate the impact of rainfall on the vegetation structure of semi-arid shrublands, with annual species responding more strongly to rainfall while perennial vegetation and especially shrubs are proportionally more influenced by herbivory (O'Connor & Roux 1995). Temperature is a pervasive influence on frog development, particularly during the egg and larval stages. However, warm egg-rearing temperatures significantly decreased the likelihood that invertebrate predators would be able to capture tadpoles of the Australian frog *Limnodynastes peronii* (Broomhall 2004). In some cases, climate change and predators act synergistically and can significantly reduce the abundance of prey species. This is seen for two forest birds, capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix*, where breeding productivity is negatively related to June rainfall and predation on eggs by crows *Corvus corone* (Summers *et al.* 2004). As a consequence of low breeding success, both forest species are declining in the UK. Multi-trophic interactions within communities add another layer of complexity to species' interactions and present opportunities for both positive and negative feedbacks on climate change impacts. An increased occurrence of blue-green algal blooms as a result of global warming may be unrealized, at least in shallow unstratified lakes dominated by macrophytes (Moss *et al.* 2003). These ecosystems are complex, with many inherent stabilizers. In such communities predatory fish are associated with an abundance of grazing zooplankters. These, by feeding on the phytoplankton (including blue green algae), lead to conditions where the macrophyte community and its associated invertebrates can flourish at high diversity.

Assessing future risks: modelling species' responses to climate change

Approaches to predict species' responses to climate change have tended to address either changes in abundance

with time or in spatial distribution. Both approaches are limited by the availability of either sufficiently long temporal records or suitably extensive spatial data. The scarcity of repeat distribution censuses over time for many species has severely limited the integration of these two approaches (but for one such approach see Virtanen *et al.* 1998). Temporal analyses have proven valuable in detecting the correlates of abundance fluctuations assessed at one or a few samples sites (Picton 1984; Pollard 1988; Worner, Tatchell & Woiwod 1995; Lindblad & Solbreck 1998; Robin & Denis 1999; Goulson *et al.* 2005). For example, Goulson *et al.* (2005) used a 4-year data set of weekly calyprate fly catches from six sites in southern UK together with meteorological data. The first 3 years were used to develop predictive models, and these were then used to forecast fly populations in the fourth year. Of the weather variables included, temperature was the most powerful predictor, with a positive correlation between fly catch and temperature in the 3 preceding weeks. The predicted populations for the fourth year proved to be closely correlated with the observed fly populations. The statistical models were then parameterized using climate variables derived from climate change scenarios. The models predicted substantial increases in fly populations, up to 244% by 2080.

While these correlative models may provide a good indication of climate change impacts on abundance, greater understanding is generated by models incorporating aspects of life history, intra- and interspecific competition and predation. For example, using empirically derived relationships between temperature and development rate as well as detailed life tables, Fenton & Wall (1997) constructed a stochastic simulation model to predict the seasonal pattern of abundance of the sheep blowfly *Lucilia sericata*. This model highlighted that the dynamics were far more sensitive to adult mortality rates than temperature-dependent development. Georgiadis, Hack & Turpin (2003) developed a model of zebra population dynamics that was stage- and sex-structured and in which vital rates and age at first reproduction were adjusted annually, involving annual recalculation of carrying capacity as a function of rainfall. Models that included a rainfall-mediated density-dependent mechanism gave a better fit, yielded parameter settings that were meaningful ecologically, and better predicted the impact of a severe drought than when density dependence was not explicit in the model. Thus rainfall strongly influences the abundance of zebras by a mechanism involving adjustments in the strength of intraspecific density dependence.

Several attempts to predict the spatial response of species to climate change have relied on the 'climate envelope' approach (Kriticos *et al.* 2003), where the current distribution of a species is mapped in climate space and then used to predict the potential expansion under future climate scenarios. The wide availability of global and regional gridded climate data has facilitated

the use of climate envelopes. However, any variable that is spatially aggregated at one or more spatial scales can be described by a parsimonious set of minimum and maximum climate values. Yet a good statistical fit does not imply causation. Furthermore, even where climate plays a significant role in determining species' distribution, variables such as human population density, land use and geology can often be similarly, if not more, important (Collingham *et al.* 2000; Gilbert *et al.* 2005). While additional land-use data may improve the fit of observed data to environmental variables, a species is still likely to interact with natural enemies and competitors that potentially constrain its distribution. In addition, these distribution models are not equally reliable for all species, and range size can affect their performance. Models for species that have small ranges (and thus a small sample size) and/or that are rare (low prevalence) are prone to statistical artefacts that can confound comparative analyses of species' distributions (McPherson, Jetz & Rogers 2004). Given that climate envelope analyses have tended to focus on the fate of rare and declining native species or scarce but expanding non-native species, these statistical shortcomings may be especially relevant. An alternative approach to modelling species' distributions under future climates involves a more mechanistic perspective incorporating data on species' physiology. Pakeman & Marrs (1996) developed a mechanistic, physiological model describing the yearly growth cycle of bracken *Pteridium aquilinum* under mean climatic conditions. The model predicts that bracken biomass is limited by different environmental factors in different regions of Great Britain and that future climate change scenarios will result in a large increase in bracken biomass in the highlands of central Scotland but little change in England and Wales.

Whether mechanistic or phenomenological, distribution models will be judged on their ability to predict future changes in species' distributions. Therefore it is insufficient to predict where a species will be in the future without assessing how it will disperse to fill the new parameter space. Thus spatially explicit models play an important role in predicting the impacts of future environmental change (Wadsworth *et al.* 2000; Higgins, Richardson & Cowling 2001). Species differ widely in their dispersal ability, ranging from a few metres for the seeds of herbaceous plants (Coulson *et al.* 2001), tens of metres for damselflies (Purse *et al.* 2003), a couple of kilometres for willow ptarmigan *Lagopus lagopus* (Brøseth *et al.* 2005) to an astonishing 30 km in a single day for linyphiid spiders (Thomas, Brain & Jepson 2003). Appropriate parameterization of the dispersal function can be as important as correctly specifying the relationship with climate or land-use variables.

In this regard, the study by Gilbert *et al.* (2005) is especially instructive. The horse chestnut leafminer *Cameraria ohridella* is an invasive lepidopteran pest of uncertain origin that is currently spreading westwards in Europe from the Balkans. A spatially explicit model

was initially developed for Germany, subsequently validated for the distribution in France and finally used to predict the likely distribution in the UK, where the species has yet to establish significant populations. The models explored different dispersal kernels and highlighted that a stratified dispersal model accounting for human population density provided the strongest validation. Furthermore, the models did not include climate but indirectly modelled the distribution of the host-plant *Aesculus hippocastanum*, itself a non-native in Europe, that is widely planted in urban areas as a landscaping tree. The authors highlight that climate, especially rainfall, will probably influence the spread at the western margin of the range. However, in central Europe climate appears to play only a minor role in the initial spread of the species.

Robust models are pivotal to the prediction of future climate change impacts on biodiversity and ecosystems. However, models are especially sensitive to the uncertainty inherent in future climate predictions, the complexity of species' interactions and the difficulties in parameterizing dispersal functions. Model outputs that have not been appropriately validated with real data should be treated with considerable caution. If vulnerability to change is determined by the frequency and magnitude of extreme climate events and not on average events or changes in average events then prediction will become increasingly difficult.

Responding to future climate change: what are the options?

In most cases opportunities to prevent rising temperatures, manage rainfall and/or reduce CO₂ directly are limited. However, adapting to current climate risks should generally be consistent with adapting to future changed conditions. Thus current understanding of how species and ecosystems respond and can be managed in the light of climate drivers will be a key tool for future conservation strategies. Nevertheless, while climate impacts themselves may be severe, these problems are often exacerbated by current management practices often aimed to protect economic rather than ecological interests.

Sea level rise is an important indicator of climate change, with great relevance for flooding, coastal erosion and the loss of flat coastal regions. In the past hundred years global average sea level has risen by 0.1–0.2 m (Houghton *et al.* 2001). The adaptive management response has been through the enhancement of existing sea defences and managed retreat in areas of low-value land. Yet such solutions are difficult to implement when attempting to conserve coastal habitats such as saltmarshes that exist in a dynamic equilibrium with the sea. Saltmarshes not only provide a habitat for rare plants and migratory birds but are also important natural dissipaters of tidal currents and waves, thus protecting landward sea defences from scour and wave erosion (Wolters *et al.* 2005). There is considerable

debate regarding the extent to which the construction of coastal defences may lead to saltmarsh erosion and whether management to combat these effects is successful (Hughes & Paramor 2004; Morris *et al.* 2004). The prevailing hypothesis is that saltmarsh erosion is the result of coastal squeeze, where sea walls prevent a landward migration of saltmarsh in response to sea level rise. In a balanced assessment of the evidence, Wolters *et al.* (2005) highlight that the prevailing hypothesis has limited support. It appears that sediment availability is sufficient to enable saltmarsh growth to occur and thus accrete vertically in response to a moderate rise in sea level, in spite of the loss of pioneer plants. Where sea defences have an impact is where they increase lateral erosion of the seaward edge of saltmarshes and internal dissection as a result of extension and widening of the creeks. These latter processes may be instigated or accelerated by a rise in sea level and an increase in hydrological flow in a restricted area as a result of embankment. The effectiveness of deliberate rupturing of sea defences to facilitate re-establishment of saltmarsh (a process known as managed realignment) has been questioned as many sites have subsided considerably during their period of embankment and require high rates of sediment accretion in order to rise to levels at which saltmarsh vegetation can establish (Hughes & Paramor 2004). The evidence supports this view to some extent, with sites that have subsided significantly reverting to intertidal flats or standing water rather than saltmarsh after managed realignment. Adaptive management responses include increasing sediment budgets to raise the elevation and promote the establishment of pioneer plants, if necessary by increasing seed availability.

Flooding is the most common natural disaster in Europe (EEA 2004). The human and economic costs of floods is high and governments are under intense pressure to implement flood defences. Current approaches include dams and other flood protection constructions, and flood areas to which floodwaters are diverted. Both approaches have significant consequences for biodiversity. Reduced water-level fluctuations caused by the construction of dams and dykes lead to substantial changes in the spatial distribution of floodplain plant species and in species composition (Leyer 2005). However, spring floods may have significant impacts on the breeding productivity of birds nesting in riparian meadows (Ratcliffe, Schmitt & Whiffin 2005). By integrating population models with a range of management options, Ratcliffe, Schmitt & Whiffin (2005) highlight how adaptive habitat management can be used to conserve endangered populations of black-tailed godwits *Limosa limosa*. Floods caused breeding failure by forcing godwits to nest on nearby arable fields where nest and chick survival rates were low. Several management options were modelled, including reprofiling of the river, diverting high flows, constructing flood barriers and attenuating flows upstream using storage reservoirs. Some management options improved productivity, population growth and persistence likelihood, but the

chances of extirpation were still high and only where all measures were applied would populations be safeguarded. However, habitat creation outside the flood area was found to result in comparable productivity and population growth at a fraction of the cost. Thus provision of compensatory habitat is likely to be a more parsimonious means of conserving black-tailed godwits than flood mitigation.

Consistent with the perverse nature of climate change, while certain ecosystems and species are threatened by rising sea levels and more frequent floods, others will suffer an increased risk of drought and fire. Fire exclusion strategies aimed at reducing risks of combustion are widely practised in the conifer forests of North America (Freckleton 2004). In a unique study that integrates a long-term perspective on forest dynamics with current management practices, Cocke, Fulé & Crouse (2005) present further evidence that fire exclusion may be counterproductive in the long term when faced with climate change. Reconstructing the dynamics of forests on the San Francisco Peaks in Arizona highlighted dramatic changes in forest structure, composition and distribution along the altitudinal gradient since the late 19th century. These changes appear to have resulted from human interference: logging, grazing and especially fire exclusion. As a result, the distribution of mesic species has shifted downwards and occupied lower slopes that historically would have suffered frequent fires. This has increased the fuel load in lower altitude forests and altered the composition towards fire-sensitive species. Furthermore, as a result of climate change high-altitude forests, which usually retain higher moisture content, will become drier and more likely to burn. Current management practices have therefore exacerbated the situation and have substantially increased the risk of large-scale devastating fires in these ecosystems. Management needs to adapt to these new environmental circumstances, which could include prescribed burning to restore open forest and meadows at lower altitudes, thus reducing the risk at which high-intensity fires could enter higher altitudes.

The San Francisco Peaks study highlights the opportunities provided by altitudinal gradients for disentangling the impacts of climate and management on semi-natural ecosystems. An important goal in grazing ecology is to understand what traits make certain plant species more or less vulnerable to the impacts of grazing. Vesik, Neuvonen & Nikula (2004) identified that, in Australian pastures, the response of species to grazing was climate dependent. Plant species were more likely to decrease in response to grazing at lower rainfall than at higher rainfall, while forbs tended to increase under grazing at sites where wet seasons were cooler. de Bello, Leps & Sebastia (2005) extend this work to the Mediterranean and examine plant species' traits in relation to grazing pressure along a climatic gradient. Their results indicate that, in many cases, grazing and potential evapotranspiration (a measure of water loss) both select for similar plant traits, for example short-life

span, and reproduction by seed rather than rhizomes or stolons. However, contrasting effects were found for trees and shrubs with grazing selecting against this trait, while drought selected in favour of woodiness. The authors conclude that climate acts at a larger spatial scale, selecting out species with inappropriate traits from the species pool, while grazing acts as a successive filter at a more local scale. However, while selection by grazing may pre-adapt species for drought resistance where herbaceous vegetation is concerned, shrubs and trees may be vulnerable to conflicting selection pressures. Increasing aridity in the Mediterranean may therefore lead to a decline in pasture quality at lower altitudes as climate and grazing select for annual plant communities. Grazing and climate may interact to lead to a progressive reduction in water availability as grazing can also increase moisture loss from the soil (Landsberg *et al.* 2002). At higher altitudes, grazing may prevent the establishment of trees and shrubs. Stocking rates will need to be managed appropriately to ensure sustainability of pasture management in semi-arid ecosystems.

In semi-arid or highly seasonal ecosystems, demographic models of vertebrate game species (e.g. magpie geese, kangaroos, Saiga antelope, wildebeest and zebra) that incorporate density-dependent mortality related to climate variation can be powerful tools for adaptive management under future climate change. These models highlight that harvesting strategies will need to adapt to increasing variability in rainfall (Bayliss 1989; Milner-Gulland 1994; Pascual & Hilborn 1995; McCarthy 1996; Georgiadis, Hack & Turpin 2003). In general, sustainable harvesting rates will be overestimated if environmental stochasticity is ignored. The greater the variation in annual rainfall, the greater the proportion of time a population is likely to spend below carrying capacity. The risk of collapse of the unexploited population will be higher for more rainfall-dependent recruitment scenarios, and populations typically decline faster during dry phases than they can increase during wet phases (Georgiadis, Hack & Turpin 2003). If future climate scenarios predict increased rainfall variability in semi-arid ecosystems, consumptive management of non-protected game will need to adjust harvesting to ensure resources are not overexploited. A clear trade-off will exist between maximizing average harvest and minimizing the risk of population collapse. For magpie geese, sustainable harvest rates were found to be 25% less when variable rainfall was included in management models (Bayliss 1989). Constant harvest rate exploitation regimes can produce similar average harvests to constant quota regimes and at the same time significantly reduce the risk of collapse (Pascual & Hilborn 1995). Alternatively, harvest should be concentrated in good (wet) years, preferably targeting a higher proportion of males as this will facilitate population compensation (Milner-Gulland 1994). The robustness of these findings, across a wide range of taxa inhabiting different ecosystems,

indicates that general strategies can be developed to deal with the uncertainties in future climates.

Demographic models that incorporate density-dependent processes as well as climate drivers can be used to forecast pest outbreaks in semi-arid regions and to target control more effectively. For example, it is likely that rodent control measures applied only when densities are high will not have persistent effects, even at high mortality rates (Stenseth *et al.* 2001). Control measures reducing reproduction are likely to prevent outbreaks but will keep densities low over a long period only when the contraceptive effect is strong (> 75% reduction). Given that there are often lags between rainfall events and subsequent rodent outbreaks (Leirs *et al.* 1996; Brown & Singleton 1999), these models emphasize that there is scope to prevent or at least reduce the scale of outbreaks even if the amplitude and frequency of rainfall events become less predictable in the future.

The indirect consequences of species harvest on non-target species may require special attention where a common resource base is likely to alter under climate change. Under certain circumstances, current harvesting regimes may no longer be sustainable. The progressive warming of the seas around the UK has led to marked changes in the trophic composition and distribution of fish stocks (Pinnegar *et al.* 2002). Sandeel *Ammodytes marinus* recruitment is reduced in warm winters, and has a knock-on effect on the breeding success and survival of kittiwakes *Rissa tridactyla* (Fredriksen *et al.* 2004). Commercial harvesting of sandeels placed an increasing burden on the kittiwake food supply and further reduced breeding success and survival. Stochastic modelling indicated that the kittiwake population was unlikely to increase if the fishery was active or sea temperature increased, and that the population was almost certain to decrease if both occurred. Adaptive management for conservation of seabirds influenced the subsequent closure of the sandeel fishery and early results reveal a modest recovery of kittiwake populations. However, further increases in sea temperatures may result in kittiwake population collapse.

Climate envelope models suggest that for some species predicted changes in climate may significantly reduce the suitability of currently occupied habitats (Thomas *et al.* 2004). Such threats are likely to be most keenly felt by species with limited dispersal ability. Under these circumstances, two primary options exist: improve the connectivity of habitats to facilitate natural dispersal, or translocate species to appropriate habitats. A first step in either approach is to identify potentially suitable habitat, and this requires detailed understanding of relevant ecosystem and species characteristics to generate conservation strategy maps (Holloway, Griffiths & Richardson 2003; Hirzel *et al.* 2004). Facilitating dispersal by increasing landscape connectivity using habitat corridors is appealing in theory but its value is often species specific and may not always be appropriate (Andreassen, Halle & Ims 1996;

Major *et al.* 1999; Holl & Crone 2004; Kramer-Schadt *et al.* 2004). Thus management should not necessarily focus excessively on wildlife corridors at the expense of appropriate management of large areas of native habitat. As the latter option may be especially difficult to implement in human-modified landscapes, translocation is often seen as a more robust alternative. Species translocations have proved a successful means of re-establishing a wide range of taxa and, as long as habitat suitability is adequately assessed, potential deleterious impacts addressed and public opinion is supportive, it can present an important conservation tool (Hodder & Bullock 1997). Success can be improved by ensuring the size of the introduction is sufficiently large to compensate for possible Allee effects (Gascoigne & Lipcius 2004), wild-caught individuals are used and acclimated to the sites before release (Bright & Morris 1994), and proximate provenances are identified as source material (Krauss & Koch 2004).

These examples illustrate the range of options available for adaptive strategies in relation to the impact of climate change on natural resources. Current management practices may not be sustainable under future climates and ecologists must attempt to go beyond describing the potential impacts of climate change and begin addressing possible solutions. A move must be made away from individualistic assessments of single species and towards the implications of interacting species and ecosystems. Vulnerability to change will be determined by the frequency and magnitude of extreme events and not necessarily on average events or changes in average events. The capacity to adapt will vary with the specific ecosystem, region and through time. Unfortunately, policymakers in the past have tended to muddle through rather than use forward planning to deal with the consequences of climate change, and have often required an environmental catastrophe to catalyse action (Glantz 1988). Therefore there is a need to ensure that environmental and conservation policies not only address climate change but are sufficiently flexible to respond to rapid ecosystem alteration. Awareness among policymakers is increasing and hopefully catastrophes will not be required to further catalyse global efforts (King 2005). Clearly, future environmental change poses considerable challenges for biodiversity and conservation but inaction should not be an option. This special profile illustrates how mathematical models, long-term population studies, natural experiments and the exploitation of natural environmental gradients provide a sound basis for further understanding the consequences of climate change and the opportunity for adaptive management.

References

- Andreassen, H.P., Halle, S. & Ims, R.A. (1996) Optimal width of movement corridors for root voles: not too narrow and not too wide. *Journal of Applied Ecology*, **33**, 63–70.
- Baur, B. & Baur, A. (1993) Climatic warming due to thermal radiation from an urban area as possible cause for the local

- extinction of a land snail. *Journal of Applied Ecology*, **30**, 333–340.
- Bayliss, P. (1989) Population-dynamics of magpie geese in relation to rainfall and density: implications for harvest models in a fluctuating environment. *Journal of Applied Ecology*, **26**, 913–924.
- Beattie, R.C., Aston, R.J. & Milner, A.G.P. (1991) A field-study of fertilization and embryonic-development in the common frog (*Rana temporaria*) with particular reference to acidity and temperature. *Journal of Applied Ecology*, **28**, 346–357.
- de Bello, F., Leps, J. & Sebastia, M.T. (2005) Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology*, **42**, 824–833.
- Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M. & Ali, A.R. (1993) Comparative effects of isolated trees on their undercanopy environments in high-rainfall and low-rainfall savannas. *Journal of Applied Ecology*, **30**, 143–155.
- Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673–687.
- Bright, P.W. & Morris, P.A. (1994) Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. *Journal of Applied Ecology*, **31**, 699–708.
- Broomhall, S.D. (2004) Egg temperature modifies predator avoidance and the effects of the insecticide endosulfan on tadpoles of an Australian frog. *Journal of Applied Ecology*, **41**, 105–113.
- Brosseth, H., Tufto, J., Pedersen, H.C., Steen, H. & Kastdalen, L. (2005) Dispersal patterns in a harvested willow ptarmigan population. *Journal of Applied Ecology*, **42**, 453–459.
- Brown, P.R. & Singleton, G.R. (1999) Rate of increase as a function of rainfall for house mouse *Mus domesticus* populations in a cereal-growing region in southern Australia. *Journal of Applied Ecology*, **36**, 484–493.
- Bryant, S.R., Thomas, C.D. & Bale, J.S. (2002) The influence of thermal ecology on the distribution of three nymphalid butterflies. *Journal of Applied Ecology*, **39**, 43–55.
- Clark, H., Newton, P.C.D., Bell, C.C. & Glasgow, E.M. (1995) The influence of elevated CO₂ and simulated seasonal changes in temperature on tissue turnover in pasture turves dominated by perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*). *Journal of Applied Ecology*, **32**, 128–136.
- Clark, H., Newton, P.C.D., Bell, C.C. & Glasgow, E.M. (1997) Dry matter yield, leaf growth and population dynamics in *Lolium perenne* *Trifolium repens*-dominated pasture turves exposed to two levels of elevated CO₂. *Journal of Applied Ecology*, **34**, 304–316.
- Cocke, A.E., Fulé, P.Z. & Crouse, J.E. (2005) Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, USA. *Journal of Applied Ecology*, **42**, 814–823.
- Collingham, Y.C., Wadsworth, R.A., Willis, S.G., Huntley, B. & Hulme, P.E. (2000) Predicting the spatial distribution of alien riparian species: issues of spatial scale and extent. *Journal of Applied Ecology*, **37** (Supplement 1), 13–27.
- Coulson, S.J., Bullock, J.M., Stevenson, M.J. & Pywell, R.F. (2001) Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *Journal of Applied Ecology*, **38**, 204–216.
- Dexter, N. (2003) Stochastic models of foot and mouth disease in feral pigs in the Australian semi-arid rangelands. *Journal of Applied Ecology*, **40**, 293–306.
- EEA (2004) *Impacts of Europe's Changing Climate: An Indicator-Based Assessment*. EEA, Copenhagen, Denmark.
- Fensham, R.J. & Holman, J.E. (1999) Temporal and spatial patterns in drought-related tree dieback in Australian savanna. *Journal of Applied Ecology*, **36**, 1035–1050.
- Fenton, A. & Wall, R. (1997) Sensitivity analysis of a stochastic model for the sheep blowfly *Lucilia sericata*. *Journal of Applied Ecology*, **34**, 1023–1031.
- Frampton, G.K., van den Brink, P.J. & Gould, P.J.L. (2000) Effects of spring drought and irrigation on farmland arthropods in southern Britain. *Journal of Applied Ecology*, **37**, 865–883.
- Freckleton, R.P. (2004) The problem of prediction and scale in applied ecology: the example of fire as a management tool. *Journal of Applied Ecology*, **41**, 599–603.
- Frederiksen, M., Wanless, S., Rothery, P. & Wilson, L.J. (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology*, **41**, 1129–1139.
- Fynn, R.W.S. & O'Connor, T.G. (2000) Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology*, **37**, 491–507.
- Gascoigne, J.C. & Lipcius, R.N. (2004) Allee effects driven by predation. *Journal of Applied Ecology*, **41**, 801–810.
- Georgiadis, N., Hack, M. & Turpin, K. (2003) The influence of rainfall on zebra population dynamics: implications for management. *Journal of Applied Ecology*, **40**, 125–136.
- Gilbert, M., Guichard, S., Freise, J., Gregoire, J.-C., Heitland, W., Straw, N., Tilbury, C. & Augustin, S. (2005) Forecasting *Cameraria ohridella* invasion dynamics in recently invaded countries: from validation to prediction. *Journal of Applied Ecology*, **42**, 805–813.
- Glantz, M. (1988) *Societal Responses to Climate Change: Forecasting by Analogy*. Westview Press, Boulder, CO.
- Goulson, D., Derwent, L.C., Hanley, M.E., Dunn, D.W. & Abolins, S.R. (2005) Predicting calyptrate fly populations from the weather, and likely consequences of climate change. *Journal of Applied Ecology*, **42**, 795–804.
- Hatton, T.J., Pierce, L.L. & Walker, J. (1993) Ecohydrological changes in the Murray-Darling basin. II. Development and tests of a water-balance model. *Journal of Applied Ecology*, **30**, 274–282.
- Higgins, S.I., Richardson, D.M. & Cowling, R.M. (2001) Validation of a spatial simulation model of a spreading alien plant population. *Journal of Applied Ecology*, **38**, 571–584.
- Hirzel, A.H., Posse, B., Oggier, P.A., Crettenand, Y., Glenz, C. & Arlettaz, R. (2004) Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *Journal of Applied Ecology*, **41**, 1103–1116.
- Hodder, K.H. & Bullock, J.M. (1997) Translocations of native species in the UK: implications for biodiversity. *Journal of Applied Ecology*, **34**, 547–565.
- Holl, K.D. & Crone, E.E. (2004) Applicability of landscape and island biogeography theory to restoration of riparian understorey plants. *Journal of Applied Ecology*, **41**, 922–933.
- Holloway, G.J., Griffiths, G.H. & Richardson, P. (2003) Conservation strategy maps: a tool to facilitate biodiversity action planning illustrated using the heath fritillary butterfly. *Journal of Applied Ecology*, **40**, 413–421.
- Hossell, J., Briggs, B. & Hepburn, I.R. (2000) *Climate Change and Nature Conservation: A Review of the Impact of Climate Change on UK Species and Habitat Conservation Policy*. DETR, London, UK.
- Houghton, J.E.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (2001) *Climate Change 2001. The Scientific Basis*. Cambridge University Press, Cambridge, UK.
- Hughes, R.G. & Paramor, O.A.L. (2004) On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, **41**, 440–448.
- Hunter, A.F. & Lechowicz, M.J. (1992) Predicting the timing of budburst in temperate trees. *Journal of Applied Ecology*, **29**, 597–604.

- King, D.A. (2004) Climate change science: adapt, mitigate, or ignore? *Science*, **303**, 176–177.
- King, D.A. (2005) Climate change: the science and the policy. *Journal of Applied Ecology*, **42**, 779–783.
- Komulainen, V.-M., Tuittila, E.-S., Vasander, H. & Laine, J. (1999) Restoration of drained peatlands in southern Finland: initial effects on vegetation change and CO₂ balance. *Journal of Applied Ecology*, **36**, 634–648.
- Kramer, K. (1994) Selecting a model to predict the onset of growth of *Fagus sylvatica*. *Journal of Applied Ecology*, **31**, 172–181.
- Kramer-Schadt, S., Revilla, E., Wiegand, T. & Breitenmoser, U. (2004) Fragmented landscapes, road mortality and patch connectivity. *Journal of Applied Ecology*, **41**, 711–723.
- Krauss, S.L. & Koch, J.M. (2004) Rapid genetic delineation of provenance for plant community restoration. *Journal of Applied Ecology*, **41**, 1162–1173.
- Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.W. & Maywald, G.F. (2003) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *Journal of Applied Ecology*, **40**, 111–124.
- Landsberg, J., James, C.D., Maconochie, J., Nicholls, A.O., Stol, J. & Tynan, R. (2002) Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia. *Journal of Applied Ecology*, **39**, 427–444.
- Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. & Mbise, T. (1996) Forecasting rodent outbreaks in Africa: an ecological basis for *Mastomys* control in Tanzania. *Journal of Applied Ecology*, **33**, 937–943.
- Leyer, I. (2005) Predicting plant species' responses to river regulation: the role of water level fluctuations. *Journal of Applied Ecology*, **42**, 239–250.
- Liang, C., Michalk, D.L. & Millar, G.D. (2002) The ecology and growth patterns of *Cleistogenes* species in degraded grasslands of eastern Inner Mongolia, China. *Journal of Applied Ecology*, **39**, 584–594.
- Lindberg, N., Engtsson, J.B. & Persson, T. (2002) Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *Journal of Applied Ecology*, **39**, 924–936.
- Lindblad, M. & Solbreck, C. (1998) Predicting *Oscinella frit* population densities from suction trap catches and weather data. *Journal of Applied Ecology*, **35**, 871–881.
- McCarthy, M.A. (1996) Red kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology*, **33**, 45–53.
- McNeil, P. & Waddington, J.M. (2003) Moisture controls on *Sphagnum* growth and CO₂ exchange on a cutover bog. *Journal of Applied Ecology*, **40**, 354–367.
- McPherson, J.M., Jetz, W. & Rogers, D.J. (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology*, **41**, 811–823.
- Major, R.E., Christie, F.J., Gowing, G. & Ivison, T.J. (1999) Age structure and density of red-capped robin populations vary with habitat size and shape. *Journal of Applied Ecology*, **36**, 901–908.
- Masterman, A.J., Foster, G.N., Holmes, S.J. & Harrington, R. (1996) The use of the Lamb daily weather types and the indices of progressiveness, southerliness and cyclonicity to investigate the autumn migration of *Rhopalosiphum padi*. *Journal of Applied Ecology*, **33**, 23–30.
- Milner-Gulland, E.J. (1994) A population model for the management of the Saiga antelope. *Journal of Applied Ecology*, **31**, 25–39.
- Morris, R.K.A., Reach, I.S., Duffy, M.J., Collins, T.S. & Leafe, R.N. (2004) On the loss of saltmarshes in south-east England and the relationship with *Nereis diversicolor*. *Journal of Applied Ecology*, **41**, 787–791.
- Moss, B., McKee, D., Atkinson, D., Collings, S.E., Eaton, J.W., Gill, A.B., Harvey, I., Hatton, K., Heyes, T. & Wilson, D. (2003) How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms. *Journal of Applied Ecology*, **40**, 782–792.
- Munster-Swendsen, M. (1987) The effect of precipitation on radial increment in Norway spruce (*Picea abies* Karst) and on the dynamics of a lepidopteran pest insect. *Journal of Applied Ecology*, **24**, 563–571.
- Mwalyosi, R.B.B. (1992) Influence of livestock grazing on range condition in south-west Masailand, Northern Tanzania. *Journal of Applied Ecology*, **29**, 581–588.
- Norris, R.J., Memmott, J. & Lovell, D.J. (2002) The effect of rainfall on the survivorship and establishment of a biocontrol agent. *Journal of Applied Ecology*, **39**, 226–234.
- O'Connor, T.G. (1994) Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology*, **31**, 155–171.
- O'Connor, T.G. & Roux, P.W. (1995) Vegetation changes (1949–71) in a semiarid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology*, **32**, 612–626.
- O'Keefe, J.H. (1985) Population biology of the fresh-water snail *Bulinus globosus* on the Kenya coast. I. Population fluctuations in relation to climate. *Journal of Applied Ecology*, **22**, 73–84.
- Pakeman, R.J. & Marrs, R.H. (1996) Modelling the effects of climate change on the growth of bracken (*Pteridium aquilinum*) in Britain. *Journal of Applied Ecology*, **33**, 561–575.
- Pascual, M.A. & Hilborn, R. (1995) Conservation of harvested populations in fluctuating environments: the case of the Serengeti wildebeest. *Journal of Applied Ecology*, **32**, 468–480.
- Picton, H.D. (1984) Climate and the prediction of reproduction of three ungulate species. *Journal of Applied Ecology*, **21**, 869–879.
- Pinard, M.A. & Cropper, W.P. (2000) Simulated effects of logging on carbon storage in dipterocarp forest. *Journal of Applied Ecology*, **37**, 267–283.
- Pinnegar, J.K., Jennings, S., O'Brien, C.M. & Polunin, N.V.C. (2002) Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology*, **39**, 377–390.
- Pollard, E. (1988) Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*, **25**, 819–828.
- Purse, B.V., Hopkins, G.W., Day, K.J. & Thompson, D.J. (2003) Dispersal characteristics and management of a rare damselfly. *Journal of Applied Ecology*, **42**, 716–728.
- Ratcliffe, N., Schmitt, S. & Whiffin, M. (2005) Sink or swim? Viability of a black-tailed godwit population in relation to flooding. *Journal of Applied Ecology*, **42**, 834–843.
- Robertson, A.I., Bacon, P. & Heagney, G. (2001) The responses of floodplain primary production to flood frequency and timing. *Journal of Applied Ecology*, **38**, 126–136.
- Robin, J.P. & Denis, V. (1999) Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. *Journal of Applied Ecology*, **36**, 101–110.
- Shan, J., Morris, L.A. & Hendrick, R.L. (2001) The effects of management on soil and plant carbon sequestration in slash pine plantations. *Journal of Applied Ecology*, **38**, 932–941.
- Stenseth, N.C., Leirs, H., Mercelis, S. & Mwanjabe, P. (2001) Comparing strategies for controlling an African pest rodent: an empirically based theoretical study. *Journal of Applied Ecology*, **38**, 1020–1031.
- Stillman, R.A., West, A.D., Goss-Custard, J.D., Caldwell, R.W.G., McGrorty, S., Durell, S.E.A.L.D., Yates, M.G., Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J. & Mander, M. (2003) An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. *Journal of Applied Ecology*, **40**, 1090–1101.

- Summers, R.W., Green, R.E., Proctor, R., Dugan, D., Lambie, D., Moncrieff, R., Moss, R. & Baines, D. (2004) An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *Journal of Applied Ecology*, **41**, 513–525.
- Tenow, O., Nilssen, A.C., Holmgren, B. & Elverum, F. (1999) An insect (*Argyresthia retinella*, Lep., Yponomeutidae) outbreak in northern birch forests, released by climatic changes? *Journal of Applied Ecology*, **36**, 111–122.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., 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. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thomas, C.F.G., Brain, P. & Jepson, P.C. (2003) Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. *Journal of Applied Ecology*, **40**, 912–927.
- Todd, M.C., Washington, R., Cheke, R.A. & Kniveton, D. (2002) Brown locust outbreaks and climate variability in southern Africa. *Journal of Applied Ecology*, **39**, 31–42.
- Vesk, P.A., Leishman, M.R. & Westoby, M. (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology*, **41**, 22–31.
- Virtanen, T., Neuvonen, S. & Nikula, A. (1998) Modelling topoclimatic patterns of egg mortality of *Epirrita autumnata* (Lepidoptera: Geometridae) with a geographical information system: predictions for current climate and warmer climate scenarios. *Journal of Applied Ecology*, **35**, 311–322.
- Wadsworth, R.A., Collingham, Y.C., Willis, S.G., Huntley, B. & Hulme, P.E. (2000) Simulating the spread and management of alien riparian weeds: are they out of control? *Journal of Applied Ecology*, **37** (Supplement 1), 28–38.
- Walker, D.A. & Walker, M.D. (1991) History and pattern of disturbance in Alaskan Arctic terrestrial ecosystems: a hierarchical approach to analysing landscape change. *Journal of Applied Ecology*, **28**, 244–276.
- Wolters, M., Bakker, J.P., Bertness, M.D., Jefferies, R.L. & Möller, I. (2005) Salt-marsh erosion and restoration in south-east England: squeezing the evidence requires realignment. *Journal of Applied Ecology*, **42**, 844–851.
- Wooldridge, G.L., Musselman, R.C., Sommerfeld, R.A., Fox, D.G. & Connell, B.H. (1996) Mean wind patterns and snow depths in an alpine–subalpine ecosystem as measured by damage to coniferous trees. *Journal of Applied Ecology*, **33**, 100–108.
- Worner, S.P., Tatchell, G.M. & Woiwod, I.P. (1995) Predicting spring migration of the damson-hop aphid *Phorodon humuli* (Homoptera, Aphididae) from historical records of host-plant flowering phenology and weather. *Journal of Applied Ecology*, **32**, 17–28.

Received 22 June 2005; final copy received 23 June 2005