



The complexity of predicting climate-induced ecological impacts

Karen Mustin^{1,*}, William J. Sutherland², Jennifer A. Gill^{3,4}

¹School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

²Department of Zoology, Cambridge University, Downing Street, Cambridge CB2 3EJ, UK

³School of Biological Sciences, and ⁴Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

ABSTRACT: The anticipated future increases in global surface temperatures are likely to have major impacts on the distribution of species. Predicting future species' distributions is a key area of importance in research, which is largely being addressed through the use of climate envelope models. While climate envelope models may indicate the broad direction of likely changes in distribution, they fail to incorporate the non-climatic factors that are important determinants of species' distributions within their current range, which may mean that the observed response will differ greatly from these predictions. When considering specific species, these ecological details are likely to be extremely important, but their inclusion in predictive models is difficult. We illustrate the complexities of unravelling climate impacts on species distribution and population size using migratory shorebirds as an example.

KEY WORDS: Distribution · Range size · Population processes · Migration · Shorebirds

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1. INTRODUCTION

In the last 100 yr, global surface temperatures have risen by 0.76°C (IPCC 2007). The most recent IPCC climate projections, under a range of different scenarios, suggest further increases of 1.8 to 4°C by 2099 (IPCC 2007). An inevitable consequence of this will be changes in the location of suitable climatic conditions for individual species, with predicted changes typically being polewards or to higher elevations. One key question is whether species will track these changes in climate distributions. Predicting future distributions of species is perceived as a priority by many organisations involved in biodiversity conservation (Sutherland et al. 2006), and developing methods capable of making these predictions is an area of ongoing interest (Carey 1996, Sykes et al. 1996, Hill et al. 2002, Thuiller 2003, Araújo et al. 2005, Sutherland 2006). An open question in this field of research is how much detail needs to be incorporated in order to accurately predict the dynamic responses of species to changing climate.

The current 'state of the art' approach for predicting such distributional changes is climate envelope modelling (Berry et al. 2002, Pearson et al. 2002, Pearson & Dawson 2003, Huntley et al. 2004). These models correlate existing data on current species' distributions with various climatic variables, and then use the inferred relationships to project potential distributions to future climate scenarios based on the output of global climate models. This approach is limited because climate change is likely to have an impact on a wide range of aspects of the species' ecology, and the issue remains as to whether species are capable of shifting to occupy new ranges (for reviews see Hampe 2004, Guisan & Thuiller 2005, Heikkinen et al. 2006, Ibanez et al. 2006). Recent work has begun to address the importance of spatial variation in the landscape in determining species' responses to climate change (Best et al. 2007, McInerny et al. 2007, K. Mustin et al. unpubl. data), and further work is required to establish the role of a wide range of ecological interactions in governing these responses.

*Email: karen_mustin@abdn.ac.uk

Predicting responses to climatic changes is particularly challenging for migratory species, as population size, and so, ultimately, local abundance and dispersal patterns, depend upon the interaction between conditions in the breeding, staging and wintering areas. In each of these stages, the impact of climate change may operate in different manners, extents and even directions (for review see Gordo 2007, this issue). The future biogeographical range of migratory species will therefore depend upon how they respond to changing climate in each of these 3 stages. The area and condition of the habitat can be impacted through a wide range of mechanisms, affecting the number of surviving

migrants, breeding output and, ultimately, population size (Fig. 1). The conditions and density at one stage will often impact the performance at the next stage; for example, larger offspring leaving earlier are more likely to survive, and, to an extent, adults arriving earlier and in better condition are often more likely to breed successfully.

To illustrate how these complexities may function, we considered the case of possible climate change impacts on migratory shorebirds. We reviewed the literature for evidence of the mechanisms of climate change impacts and considered the feasibility of incorporating such detail into predictive models.

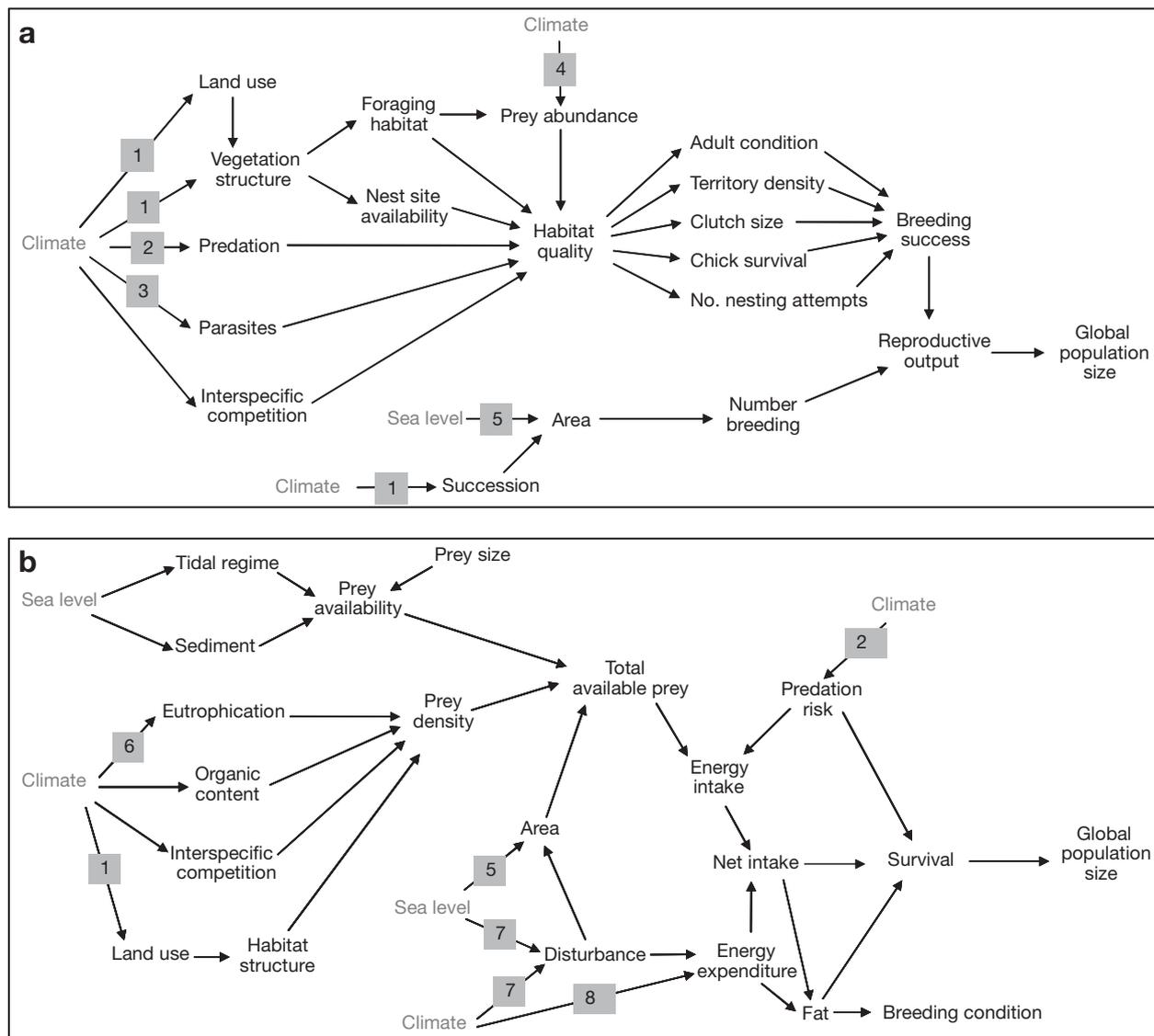


Fig. 1. Mechanisms of climate change effects on wader population size during the (a) breeding and (b) non-breeding seasons. Numbers 1 to 8 refer to possible specific climate change effects and are reviewed in Sections 2.1 to 2.8. Arrows without numbers represent likely effects for which there is insufficient evidence in the literature to make meaningful statements regarding future climate change

2. REVIEW OF CURRENT LITERATURE

2.1. Land use, vegetation structure and succession

2.1.1. Tundra and montane

Approximately one-quarter of the world's shorebirds breed in tundra and boreal habitats of the arctic and sub-arctic (Hayman et al. 1986). The open nature of these habitats, with complex, mosaic-like vegetation structures, provides well-camouflaged nesting sites for these ground-nesting species, and the short pulse of invertebrate abundance following snow-melt provides the conditions for rapid chick growth during a very short season (Schekkerman et al. 2003).

Climate warming in the arctic is likely to occur at rates that are 1.5 to 2 times faster than the global mean, and, in montane environments, is likely to parallel that in the surrounding regions, such that high-latitude mountains will experience greater warming than more tropical mountains (IPCC 2001, Kaplan & New 2006). The high level of endemism and species adaptation to the arctic and alpine environments, the degree of temperature dependence in their distribution, and the geographical impossibility of many species moving polewards means that global climate change will have highly significant implications for these ecosystems (IPCC 2001, Callaghan et al. 2004a, Kaplan & New 2006). Where possible, the dominant response is likely to be one of relocation rather than adaptation, driven by the local expansion of intrazonal outlier populations and the northward or upward movement of entire vegetation zones (Callaghan et al. 2004a,b,c). Organisms that are 'arctic specialists' generally show poor competitive ability and so are very vulnerable to invasions from the south, their ranges will most probably narrow and they may face local, or even complete, extinction (Callaghan et al. 2004a,d).

The International Tundra Experiment is a collaborative multi-site experiment designed to examine experimentally the variability in the response of tundra ecosystems to climate change across geographic and climatic gradients (Arft et al. 1999). Meta-analyses of these experiments have shown consistently that plants in the arctic and alpine tundra are sensitive to warmer summer temperatures and that even moderate temperature increases lead to rapid and sustained responses by vegetation in the form of short-term increases in vegetative growth, accompanied by more gradual increases in sexual reproduction (Arft et al. 1999, Walker et al. 2006). These responses vary along the climatic gradient: plants in warmer low arctic sites, where competition for resources is high, show the strongest vegetative response, while plants in cooler high arctic sites with more bare ground to colonise invest more in

reproduction (Arft et al. 1999). Furthermore, in the short term, the strongest vegetative response is from herbaceous forms, while over longer time periods the greatest response is from woody plants. Over time this can change the height and structure of the canopy, with negative implications for lower plant species, especially lichens and bryophytes, which may be lost entirely as the vegetation shifts to shrub dominance (Arft et al. 1999, Callaghan et al. 2004c,e, Walker et al. 2006). The response to elevated temperature of an increase in woody plant dominance is also consistent with the paleoecological record and natural temperature gradients. In areas of tundra already experiencing climate change, evidence from satellite measurements, aerial photos and indigenous knowledge all indicate that arctic vegetation is already becoming shrubbier and more productive (Callaghan et al. 2004c,e, Walker et al. 2006). Species diversity, evenness and richness declined in response to experimental warming, which is inconsistent with natural temperature gradients (Walker et al. 2006). However, species diversity in the arctic is generally low, and the gradient from boreal forest to polar deserts is associated with an increase in the abundance of 'super dominant' species (Callaghan et al. 2004a,c). Such species occur in a wide range of habitats and are likely to respond to climate change with increased productivity and abundance, thus strongly affecting ecosystem processes and leading to new communities with different structures to those currently existing (Callaghan et al. 2004a,c).

Treelines are a bioclimatic boundary against which other thermal life zones can be defined, irrespective of latitude, and past periods of climate change were associated with a very rapid advance of the treeline (Callaghan et al. 2004b,d, Körner & Paulsen 2004). Treeline expansion is partly related to an increased frequency of warmer summers, leading to reduced summer snow retention and earlier snow melt and, thus, enhanced seed viability and juvenile growth. Winter temperatures must also be considered, as there is evidence that treelines previously limited by winter desiccation have advanced as a result of increased winter temperatures, leading to enhanced survivorship and growth (Kullman 2001, 2002, 2007). This, combined with sea level rise, has led to a significant reduction in the area of tundra (Callaghan et al. 2004b,d). Model predictions suggest that even using conservative estimates of the rate and extent of future climate warming, the arctic forested area will expand, largely at the expense of tundra, while tundra will be limited to mountainous and coastal areas where treelines are largely limited by factors other than climate (Holtmeier & Broll 2005, Lloyd 2005, Kaplan & New 2006). There may be time lags exceeding 150 yr between the onset of warming and the development of vegetation that

can be functionally classified as forest. This time lag varies due to regional variation in the response rates of vegetation to the warmer climate through environmental, reproductive, or physiological factors (Lloyd 2005). The treeline advance in the Scandes mountain chain in Sweden, however, has been closely associated with 20th century warming, with no appreciable time lag (Kullman 2001, Holtmeier & Broll 2005, Lloyd 2005). Evidence from recent advances of the tree lines in Alaska and Canada has shown significant regional and local variation in the timing and rate of advance, most likely caused by local topography, with additional effects of shelter and snow richness in the case of high-altitude treelines (Kullman 2001, Gamache & Payette 2005, Lloyd 2005). Since the great majority of high-latitude breeding shorebirds are dependent upon open habitat, the expansion of woodland habitats is likely to severely reduce the extent of suitable habitat (Gunnarsson et al. 2006). While, in the long term, global warming will facilitate treeline advance to greater latitudes and altitudes, this response will vary regionally and according to topography. At the landscape and local level, the effects of topography may override global warming, particularly due to harsh wind exposure conditions and geographical barriers, and regionally short-term cold extremes may slow down or even reverse the trend (Kullman 2002, Callaghan et al. 2004b,d, Gamache & Payette 2005, Holtmeier & Broll 2005, Lloyd 2005).

2.1.2. Coast and wetlands

Global climate change will have an impact on the community composition of the vegetation of saltmarshes, as a result of changes in the distribution and abundance of species, as well as the influence of climatic changes on interspecific interactions (Adam 2002, Bertness & Ewanchuck 2002). These effects will be highly species specific, however, and so it will be difficult to predict entire community responses (Bertness & Ewanchuck 2002). Some possible general trends include the expansion of thermophilic species to higher altitudes and latitudes and range contraction of species currently restricted to higher latitudes (Adam 2002).

The structure of saltmarsh communities is a key aspect of their suitability for nesting shorebirds. For example, in the UK, 45% of the redshank *Tringa totanus* population breeds in saltmarshes (Brindley et al. 1998), largely in the mid- and upper-saltmarsh zones, where the vegetation is complex enough to allow nest concealment (Smart 2005). Changes in temperature and rainfall may also alter the distribution of salt-pans (Adam 2002), which can be key habitats for foraging shorebirds (Masero et al. 2000).

2.1.3. Agriculture

Scenario modelling has not been able to identify common, convergent futures for European agriculture, but it does indicate that there may be radical changes in agriculture and rural land use in the coming decades that result more from socio-economic than climatic factors (Sutherland 2004, Holman et al. 2005, Audsley et al. 2006, Busch 2006). It seems likely that the main effects of both climate and socio-economics will be in the agriculturally marginal areas of Europe, though the precise nature of changes will be heavily dependent on policy decisions, global trade, agricultural productivity and potential shifts to biofuel production (Rounsevell et al. 2005, Audsley et al. 2006, Busch 2006).

Climate change will increase the vulnerability of both wildlife and farmers, and as such it is highly likely that future policies will be required to resolve conflicts between conservation and agriculture (Berry et al. 2006, Rounsevell et al. 2006). Agricultural management in Europe looks set to diversify with potential changes from food to energy production, extensification, land abandonment and habitat recreation, all of which benefit some species, while agricultural intensification in some areas could reduce habitat quality and increase fragmentation, with potentially detrimental effects to others (Rounsevell et al. 2005, Berry et al. 2006). The major climate trend does, however, suggest a likely northward expansion of arable farming despite increasing viability of grassland farming, which reflects changes in agricultural management (Audsley et al. 2006, Busch 2006). In alpine environments, the long-term trend for landscape homogenisation through the loss of open areas to woodland looks set to continue unless the abandonment of grasslands is prevented by the presence of cattle farming (Giupponi et al. 2006).

The arable and pastoral landscapes of Europe are home to large populations of breeding shorebirds, such as lapwing *Vanellus vanellus*, black-tailed godwit *Limosa limosa*, snipe *Gallinago gallinago*, redshank *Tringa totanus* and ruff *Philomachus pugnax*. Virtually all of these species are currently declining in population size, frequently as a consequence of the drainage and intensive management associated with modern agricultural methods (Thorup 2005). Future developments, such as increased land abandonment and habitat recreation, may therefore provide an opportunity to improve breeding habitats for these species (e.g. Smart et al. 2006), although current efforts to halt the declines of these species through improved agricultural land management have had mixed success (Kleijn & Sutherland 2003). For shorebirds, the widespread requirement of wet foraging habitats within breeding areas will mean that attempts to improve habitats must

also take changing precipitation frequency and the consequent availability of water into account (Smart et al. 2006, Eglington et al. 2007).

All the conclusions drawn from scenario modelling of the future of agricultural land use in Europe are hampered by model-based uncertainties resulting from insufficiencies in the data sets, and variability in predictions from different climate models (Audsley et al. 2006, Rounsevell et al. 2006), making the potential impacts on biodiversity even harder to predict.

2.2. Predation

According to the Roselaar-Summers bird–lemming hypothesis, breeding success of arctic ground-nesting birds will fluctuate in response to cycles in lemming *Dicrostonyx* spp. and *Lemmus* spp. abundance (Roselaar 1979, Summers 1986). Populations of predators, especially arctic foxes *Alopex lagopus*, increase dramatically after years of high lemming abundance. The bird–lemming hypothesis states that, in lemming-poor years, predators will switch to eggs and chicks, such that breeding success will be highest when lemming numbers are increasing or remaining high, but will be poorest in years immediately following a lemming peak, when predators are still abundant but there is little alternative prey to sustain them (Blomqvist et al. 2002, Ims & Fuglei 2005). A number of studies of arctic-breeding waders have subsequently provided evidence to support this hypothesis (Underhill 1993, Blomqvist et al. 2002).

Small mammals in the arctic tundra are dependent upon deep snow cover as a means of protection from both low ambient temperatures and predators (Ims & Fuglei 2005). While there are no long-term data on arctic lemming populations, it has been shown that the cyclic population dynamics of voles in Scandinavia have been decreasing in amplitude since the early 1970s, and that this is associated with increasingly mild and wet winters and the associated shortening of the period of snow cover (Hörnfeldt et al. 2005). As these cyclic population dynamics are so heavily dependent upon long, cold winters, it is possible that a small change in climate may have a large disruptive effect, especially as climate change will also facilitate the invasion of more generalist predators, such as the red fox *Vulpes vulpes* (Callaghan et al. 2004a, Ims & Fuglei 2005).

Niehaus & Ydenberg (2006) used long-term data to examine the importance of changes in the timing of snowmelt for the interactions between western sandpipers *Calidris mauri* and their predator, the peregrine falcon *Falco peregrinus*, during migration. They found that peregrines respond more strongly to changes in

snowmelt, such that earlier snowmelt years are more dangerous for the sandpiper as they are more likely to encounter peregrines. This may be another important climatic consideration in the success of migratory shorebirds that breed at high latitudes.

2.3. Parasites

As climates change there is potential for distributional changes in the local abundance of parasites, vectors and hosts, and this may lead to changing areas of coexistence, which may ultimately affect infection rates (Poulin & Mouritsen 2006).

Mendes et al. (2005) found that in shorebirds, avian malaria is most prevalent in freshwater inland habitats, which are used by overwintering birds from more southerly breeding latitudes, with arctic breeding species restricted to more coastal, marine and saline habitats. As parasites and pathogens are relatively scarce in arctic and marine environments, these birds can invest more in thermoregulation and growth, but, as a result, may be more susceptible to infections if the prevalence of malaria, or other parasites and diseases, changes as a result of climate change (Piersma 1997, Callaghan et al. 2004a).

Evidence from biological transmission models developed to understand the risk of spread of human malarial infections in the future suggests that both seasonal transmission and geographical distribution of malaria will change, particularly due to changes in temperature and precipitation (Martens et al. 1995, 1999, Rogers & Randolph 2000). Increases in the length of the transmission season may be particularly important at current border areas, and the greatest proportional changes are forecast to occur in temperate zones, where vectors currently exist but temperatures are not sufficiently high to allow transmission (Martens et al. 1999). Rogers & Randolph (2000) have suggested that, given the current effects of climate on malarial distribution, there will be remarkably few changes to the prevalence of malaria, even when considering the most extreme climate change scenarios. It is important to note, however, that these predictions relate to human malaria, and, while some of the vectors may be the same, the disease is caused by different parasites in birds.

2.4. Prey abundance

2.4.1. Uplands

Breeding success in golden plover *Pluvialis apricaria* has been shown to be linked with the flush of tipulid (Tipulidae) hatching, as weight gain and survival of

golden plover chicks is shown to be positively correlated with the abundance of tipulid adults (Pearce-Higgins & Yalden 2004). Modelling of climatic influences on golden plover and tipulid phenology suggests that by the end of this century there is the potential for a mismatch between the timing of first laying and tipulid emergence, which, without an adaptive response, may reduce the success of early breeding attempts (Pearce-Higgins et al. 2005). Given the key importance of tipulids for a wide range of upland-breeding birds (Buchanan et al. 2006), changes in the timing of emergence of these species could have far-reaching implications for avian productivity in the uplands.

2.4.2. Coastal, intertidal and rocky shore

Changes in climate and weather may cause distributional changes to common intertidal species in the UK, particularly where species are living close to the limit of their geographical extent and may expand when climatic constraints are relaxed (Kendall et al. 2004). Analysis of long-term data from the western English channel at Plymouth has shown that periods of relatively short-term warming (such as those from the 1920s to the 1950s, and from the 1980s onwards) can be associated with increased abundances of fish, plankton and intertidal organisms more typical of warmer waters, and that conversely during cooling periods (e.g. 1962 to the 1980s) northern cold-water species become more abundant (Hawkins et al. 2003). Overall food abundance is unlikely to decline as similar species replace each other in parts of their distribution, and so, in most cases, the impacts on wading bird distribution may be small (Kendall et al. 2004). However, it is possible that small-scale variability in thermal stress as a result of regional variation in the timing of low tide may overwhelm large-scale climatic gradients and lead to complex patterns of species distributions, as opposed to simple range shifts (Helmuth et al. 2006).

Alterations of the phase relationship between temperature and photoperiod are likely to occur as a result of global warming, and will have significant effects on spawning of estuarine invertebrates at temperate northern latitudes (Philippart et al. 2003, Lawrence & Soame 2004). This also has the potential to lead to miscuing with other important events such as phytoplankton blooms (Philippart et al. 2003). The most likely effects will be changes in fecundity, spawning success and recruitment, and these may lead to a reformulation of estuarine food webs and possibly a reduction of the resilience of the system to additional disturbances, having serious implications for overwintering birds (Philippart et al. 2003, Lawrence & Soame 2004). Cli-

mate warming and increased storminess may also lead to a decline in abundance and productivity of brown algae, affecting some waders directly through a loss of feeding grounds for small and easily desiccated invertebrates, and also indirectly as a consequence of the reduction in dead algae acting to boost bacterial production in sediments (Kendall et al. 2004).

Sea level rise may lead to reduced prey availability only where shore topography prevents the upward migration of the biota (Kendall et al. 2004); however, modelling has shown that reduced feeding opportunities, spatially and temporally, may differentially affect overwintering survival of wading bird species, depending on available prey biomass (Durell et al. 2006).

2.5. Area

Galbraith et al. (2002) provide evidence that future sea level rise may reduce the area of intertidal habitat and thus adversely affect the ability of many coastal sites to continue to support large numbers of migrating and wintering shorebirds. Even assuming a conservative 2°C rise in temperature in the next century, their model projects 20 to 70% losses of current intertidal shorebird habitat in the United States. They predict that the most severe losses will occur where steep topography and sea walls prevent inland migration of the coastline, and that anthropogenic effects will also be important. It may prove difficult to predict the impacts on particular shorebird populations, as, while some staging sites will lose habitat, others may gain it, and the overall effect on the flyway will thus be complex (Galbraith et al. 2002).

Saltmarshes are also likely to be severely impacted by sea level rise. Their long-term stability is determined by relative sea level, which is the relationship between mean sea level and the sediment surface (Adam 2002, Morris et al. 2002). The ability of such habitat to persist with sea level rise depends upon dominant macrophytes accreting sediment to regulate elevation, though other factors, such as tidal range, will also be important (Adam 2002, Morris et al. 2002). Altered tidal inundation patterns will influence the structure of the vegetation and may lead to complete loss of saltmarshes in some areas (Smart & Gill 2003). Morris et al. (2002) describe a theoretical model that predicts a saltmarsh at maximum productivity will be less stable than a less productive marsh that is situated above its optimum sediment level. Saltmarshes in SE England have been eroding at about 40 ha yr⁻¹ for the last 50 yr. The direct effects of sea level rise and the indirect effects of climatic change are both likely to reduce the availability of suitably complex saltmarsh structures for nesting shorebirds (Smart & Gill 2003).

Modelling has suggested that under a variety of future climate scenarios, coastal wetlands will experience losses, but that losses due to sea level rise alone are likely to be relatively small compared to potential losses due to human activities (Nicholls et al. 1999, Adam 2002, Nicholls 2004). While there is considerable uncertainty, both model- and data-based, socioeconomic and policy factors are highlighted as important in determining the magnitudes and impacts of sea level rise (Adam 2002, Nicholls 2004).

A critical issue is whether the current coastal defences are retained, resulting in coastal squeeze, or whether new areas of coastal habitat can be formed inland of the current habitats, in which case, in theory, the area of coastal habitat could stay similar overall. With housing, industry and infrastructure concentrated along the coast, it seems inevitable that overall there will be considerable reductions in coastal habitat for feeding birds. Loss of coastal habitats will have an impact on migratory shorebirds in a number of ways: the reduction in habitat is likely to result in increased depletion and interference and, thus, increasing mortality (Sutherland 1996). A range of species breed within saltmarshes and any habitat loss is likely to impact them. The great majority of shorebirds feed on intertidal habitats, particularly mudflats, beaches and rocky shores, during migration and in winter, and these habitats are already under pressure from industrial and recreational development.

2.6. Eutrophication

The interaction between climate and eutrophication is complex and will vary greatly between estuaries, with the vulnerability of individual sites likely to be affected by changes in temperature, sea level, ocean exchange, freshwater runoff, nutrient loading and physical circulation (Howarth et al. 2000, Scavia et al. 2002). Evidence from the Hudson estuary in the north-eastern United States suggests that climate change will lower summer freshwater discharge and, thus, increase the likelihood of eutrophication (Howarth et al. 2000). In Chesapeake Bay, Miller & Harding (2007) showed that years with more frequent warm and wet weather have phytoplankton blooms that are greater in magnitude and cover a larger area than years that are colder and drier.

Eutrophication may affect the response of saltmarsh species to climate warming and may result in the loss of macrophyte beds to coarser sediments and unvegetated areas dominated by opportunistic invertebrates (Adam 2002, Dolbeth et al. 2003, Cardoso et al. 2004). An increase in dense and contiguous macroalgal mats may have direct or indirect effects on wading birds (Cabral et al. 1999).

2.7. Disturbance

Global warming is expected to result in changed patterns of human behaviour. If high temperatures and good weather conditions increase in frequency, there are likely to be greater numbers of tourists visiting temperate coasts more often (Coombes et al. 2004). Conversely, should precipitation levels and frequency increase, the number of visitors to coastal areas is likely to decline. Species breeding in temperate habitats favoured by tourists, such as beaches or upland areas popular with hill walkers, are likely to be particularly affected by such changes. For example, piping plovers *Charadrius melodus* in the United States declined dramatically, in part as a result of recreational development and disturbance on their beach nesting habitats (Haig et al. 2005), and extensive efforts are now underway to protect and expand the remaining populations. Liley & Sutherland (2007) developed a population model of ringed plovers *Charadrius hiaticula* breeding on beaches in eastern England, and showed that local population sizes were impacted by human presence, both as a result of avoidance of highly disturbed areas and trampling of nests. In upland habitats, Pearce-Higgins et al. (2007) showed that the breeding distributions of golden plover *Pluvialis apricaria* and dunlin *Calidris alpina* were influenced by visitor pressure in heavily visited areas, but also that these effects could be minimised by the provision of facilities such as well-surfaced paths.

Evidence for impacts of human disturbance in the non-breeding seasons is less clear, with responses varying between species. Gill et al. (2001a) showed that human presence had no impact on current patterns of resource use and distribution of wintering black-tailed godwits *Limosa limosa*, but Stillman et al. (2007) demonstrated how human disturbance could have population-level impacts on oystercatchers *Haematopus ostralegus*. A key issue in understanding how changing patterns of human distribution will impact biodiversity is the interaction between disturbance and density-dependent population dynamics (Mallord et al. 2007). The behaviour-based models used in these types of studies will, therefore, be of increasing importance in predicting the potential impacts of novel levels of human use of these habitats (Gill 2007).

2.8. Energy expenditure

The vast distances over which migratory shorebirds travel, and the wide range of habitats and conditions that they can experience on these journeys, makes managing energy budgets of critical importance

(Piersma & Lindström 2004). Maintaining the required energy levels to survive harsh conditions and fuel long journeys, often in tidally constrained systems, is a balancing act that can easily be altered by climate change. The energy requirements of maintaining body temperature and sufficient fuel reserves are strongly determined by air temperatures, solar radiation and wind speeds (Wiersma & Piersma 1994). Harsh weather conditions are a key driving force of energy budgets, both at arctic breeding grounds (Piersma & Morrison 1994) and winter sites (Wiersma & Piersma 1994, Kelly et al. 2002), and the mortality during severe weather can result from both direct impacts, for example, through sustained net energy losses (Camphuysen et al. 1996), and indirect impacts, such as individuals being forced to forage in areas with higher predation risks (Yasue et al. 2003).

In the UK, data on daily temperature extremes indicate that there has been a marked reduction in the frequency of cold days (mean temperature $<0^{\circ}\text{C}$), particularly between November and March (Watkinson et al. 2004). Continuation of this trend may, therefore, result in reduced incidence of high levels of shorebird mortality. However, the complex effects of weather conditions on prey abundance and activity (Beukema 1979, Beukema & Dekker 2005) and the physiological and ecological requirements of long-distance migration (Piersma & Lindström 2004) are likely to make energetic effects of climate change very difficult to predict.

3. DISCUSSION

Just as destroying ecological value is usually easier than restoring it, predicting that an area will no longer be suitable because a key resource will be missing is easier than predicting that an area will become suitable. As this review highlights, there are many complex interactions and multiple ways in which climate change can impact different aspects of species' ecology, behaviour and distribution. The approach presented here (see Fig. 1) is suggested as an important first step in quantifying and ranking the relative importance of ecological interactions in determining species' responses to climate change. In order to weight the different pathways for their relevance to demography, these diagrams would need to be species-specific rather than the more generic shorebird model we have shown here. The available literature on these topics provides some evidence for how parts of the pathways can be quantified for individual species, and for identifying the habitats and species of likely greatest concern. However, there are also many important gaps in current knowledge. Quantifying the details of these

pathways for individual species is clearly not going to be feasible given the need for rapid action to develop strategies for protecting biodiversity in the face of climate change; however, these details have significant potential to alter the outcome of simple climate envelope approaches. We would therefore suggest that methods such as using expert opinion, for example, the Delphi technique and nominal group technique (Sutherland 2006), to assign probabilities to key interactions are likely to be necessary in the short term along with setting priorities for the important research gaps.

A key aspect involving ecological details that will improve predictions of distribution changes is the spatial dynamics of range shifting. Using a spatial patch occupancy model, Travis (2003) demonstrated the potentially catastrophic synergistic effects of climate change and habitat loss. On a fragmented landscape, the threshold rate of climate change that a species can survive is substantially reduced. Recent work has extended this approach; for example, McNerny et al. (2007) explored how species might move across landscapes characterised by different patterns of habitat loss. K. Mustin et al. (unpubl. data) simulated the range shifting of a metapopulation structured on an environmental gradient (see Holt & Keitt 2000) and showed that species with ranges structured in this way may show accelerating rates of range expansions. Clearly, incorporating within-patch dynamics will be crucial for many species, but, as yet, there is remarkably little work relating this to range shifting dynamics. In one recent exception, Best et al. (2007) considered how the form of within-patch density dependence determines a population's range shifting behaviour. The first few attempts to incorporate additional ecological realism into what are still relatively simple models already demonstrated that the predictions we make on a species' ability to track changing climate are sensitive to the precise manner in which the processes involved are modelled, and also to our ability to properly parameterise the models. There is undoubtedly a need for a greater level of detail to be built into future modelling approaches, but, in terms of making predictions for specific species (as opposed to much more strategic predictions made by those models described above), data availability is likely to be a constraint.

This review has highlighted the major role of socio-economic factors and policy responses in determining many climate-mediated changes in species distribution (Adam 2002, Nicholls 2004, Sutherland 2004, Holman et al. 2005, Rounsevell et al. 2005, Audsley et al. 2006, Busch 2006). These types of factors will be particularly difficult to include in predictive models of species distribution under climate change, and represent one of the major challenges associated with making

meaningful predictions. For migratory shorebirds, these issues may be particularly difficult to resolve because of the complex interactions between breeding and non-breeding sites (e.g. Gill et al. 2001b, Gunnarsson et al. 2005). However, it is apparent that the high level of dependence of shorebirds on arctic tundra and wetlands as breeding habitats may well make them particularly vulnerable in the face of changing vegetation structures and reduced water availability.

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