Predicting the impact of climatic change on Arctic-breeding waders

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The Arctic is expected to warm more than the global average, by 2–7°C in mean summer temperature between 1961–1990 and 2071–2100. Such major climate change is likely to affect the waders that breed in the circumpolar tundra, especially the many species concentrated in the high Arctic. Their breeding habitat may be compressed towards the poles and might conceivably disappear altogether. We assess how the possible future direct and indirect effects of climate change could affect Arctic-breeding waders. We then review the evidence for existing effects of climate change on Northern Hemisphere waders, in particular changes in phenology and distribution. We conclude by identifying priority research areas.

INTRODUCTION

Wallace (1878) first noted the trend for decreasing species richness from the tropics to the poles, but waders are an exception to the general pattern as they breed more commonly in boreal and arctic areas (Kouki 1999). Some 50 wader species breed in the circumpolar tundra (Piersma & Wiersma 1996, Piersma et al. 1996) where they sometimes constitute as much as 40% of the bird species and 55% of all birds (Lindström & Agrell 1999), with the greatest proportions in the high Arctic. As the earth warms with climate change, biogeographic zones are expected to move pole-wards (Hughes 2000, IPCC 2001). Thus, whereas habitat types that are presently found near the equator may be expected to move simply northwards or southwards, boreal and arctic areas may be compressed towards the poles before possibly disappearing altogether. As yet, there have been no known extinctions of Arctic-breeding waders (Boyd & Madsen 1997). However, unless they prove to be particularly adaptable to changing environments, they may be among the species most at risk from a warming earth as their present breeding habitat is likely to change considerably. Waders also make some of the longest yearly migrations of any fauna, migrations that include flights of several thousand kilometres and that may include only a few stopover sites. The energy demands of waders are high during the breeding (Piersma & Morrison 1994), migration and wintering seasons (Piersma 1994). These factors also contribute towards making waders particularly vulnerable to global change. However, lengthened and/ or warmer breeding seasons may be beneficial for some waders. They may provide increased abundance of invertebrate food supplies, as well as possibly more time to moult and put on fat reserves before migration and more time to fit in replacement breeding attempts if unsuccessful initially.

If correct, the predicted change in climate over the next few decades is beyond anything witnessed in historical times. Thus, Danell *et al.* (1999) and Lawton (1996) consider that it is impossible to predict accurately future responses of biota to climatic change, but that it is more acceptable to suggest a range of scenarios of possible change. In a review of the biological consequences of climate change, Hughes (2000) suggested that the challenge for ecologists, physiologists and land managers is to predict the effects of human-induced climate and atmospheric change on species and on communities. He surmised that these predictions would have to include effects on physiology, distributions, phenology and individual adaptation. However, there will always be uncertainty with respect to the potential impacts on the relationships between species, as processes such as predation, parasitism and competition are likely to be unpredictable (e.g. Davis 1998a,b).

We broadly follow Lindström and Agrell (1999) in dividing the possible impact of global change on waders into direct (predominantly physiological) and indirect effects (habitat change, food availability, predators), though clearly both categories affect the distribution, phenology and need for individual adaptation of waders (Fig. 1). After listing some of the possible direct and indirect effects of climatic change on waders, we assess the evidence for existing effects of climatic change on waders. We then conclude by suggesting some priority research areas. This paper has been written because we believe that climatic change is probably the single greatest threat faced by waders at present. It is a threat to waterbirds and wetlands that is being increasingly recognised (e.g. Ramsar 2002). It is vital to identify the proximal biotic and abiotic pressures on these birds that may arise from climatic change. This should encourage the further exploration, compilation and interpretation of existing knowledge as well as the development of integrated multidisciplinary long-term monitoring programmes and largescale experimental manipulations that will be needed to enable us to predict with confidence the likely impacts of climatic change on waders.

GLOBAL CHANGE SCENARIO

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Fig. 1. Simplified pathways for change in wader distributions and abundance resulting from climate change. The diagram has been kept simple to avoid a complex web of possible interactions; for example, even though increasing atmospheric carbon dioxide will increase the productivity of plants (Myneni *et al.* 1997) that are an important constituent of wader habitat and diet, this pathway is not marked.

2001). The 1990s was the warmest decade since 1861 ($P \ge 90\%$) and the increase in global temperature in the 20th century was the largest in any century during the past 1,000 years (P = 66 - 90%). On average, between 1950 and 1993, night-time daily minimum and daily maximum air temperatures over land increased by about 0.2°C and 0.1°C per decade, respectively, and this has lengthened the freeze-free season in mid- and high-latitude regions. The increase in global sea surface temperature over this period was about 0.05°C per decade.

Since 1966, the extent of spring snow cover in the Northern Hemisphere has decreased by about 10%. Over the 20th century, there has been a reduction of about two weeks in the annual duration of lake and river ice-cover in the mid- and high latitudes of the Northern Hemisphere (P=90–99%). There has also been a widespread retreat of mountain glaciers and Northern Hemisphere spring and summer sea-ice extent has decreased by about 10–15% since the 1950s. Moreover there has been a 40% decline in Arctic sea-ice thickness during late summer and early autumn (P=66–90%).

Global average sea level rose by 0.1-0.2 m during the 20th century. Global ocean heat content has also risen. In addition, there is microseismological evidence for increased wave heights over the last half of the 20th century, which may provide an extra threat to coastal areas through increased erosive power (Grevemeyer *et al.* 2000).

Precipitation increased by 0.5-1% per decade in the 20th century over most mid- and high latitudes of the Northern Hemisphere (P=90-99%) and heavy precipitation events increased by 2-4% (P=66-90%). Since 1950, there has been a reduction in the frequency of extreme low temperatures (P=90-99%). In some regions, such as parts of Asia and Africa, the frequency and intensity of droughts have increased in recent decades.

Human influences are expected to continue to change atmospheric composition throughout the 21st century. The IPCC Special Report on Emission Scenarios (SRES) projects globally averaged surface temperature to increase by 1.4-5.8°C between 1990 and 2100. The projected rate of warming is much larger than the observed changes during the 20th century and is without precedence during at least the last 10,000 years (P=90-99%). Nearly all land areas will warm more rapidly than the global average, particularly those at northern high latitudes in the cold season (P=90-99%). The warming in the northern regions of North America, and northern and central Asia, for example, is expected to exceed global mean warming by more than 40%. Global average water vapour concentration and precipitation are projected to increase during the 21st century. By 2050, it is likely that precipitation will have increased over northern mid- to high latitudes and Antarctica in winter (P=66–90%), and larger year-to-year variations in precipitation will occur (P=90-

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99%). It is also likely that there will be an increase in extreme events such as more hot days, more intense precipitation, more drought and increased cyclone peaks, but fewer cold and frost days. Northern Hemisphere snow cover and ice extent are projected to decrease further. Glaciers and ice caps are projected to continue their widespread retreat during the 21st century. The Greenland ice sheet will lose mass (P=66– 90%). Global mean sea level is projected to rise by 0.09 to 0.88 m between 1990 and 2100.

In the important Arctic, Subarctic and Boreal breeding grounds of waders in Greenland, Alaska and Northern Asia, there is expected to be warming in excess of 40% above the global average from December to February 2071-2100. Some climate change models also predict such an increase in Northern Europe (for details of models used and geographic extent definitions see IPCC 2001: 595-596). Similarly, from June to August 2071–2100, the warming is predicted to be much greater than average in Greenland, and greater than average in Alaska and Northern Asia. These changes are expected to equate to increases of some 5-11°C and 2-7°C in mean winter and summer temperatures, respectively, from 1961-1990 to 2071-2100. Importantly, it is expected that between 1975-1995 and 2080-2100 there will respectively be 12-20°C and 4-8°C increases in daily minimum and maximum surface air temperatures in the most northerly latitudes.

FACTORS RELATED TO CLIMATE CHANGE THAT COULD AFFECT WADER POPULATIONS

Direct effects of global climate change

Climatic factors such as temperature, precipitation, wind conditions and solar radiation affect the physiological requirements of birds (Piersma 1994, Piersma & Morrison 1994, Wiersma & Piersma 1994). Low temperature, rain and strong wind lead to waders increasing their energy expenditure and may restrict the waders from depositing fat for migration or reproduction. Waders on their breeding and wintering grounds can regularly encounter relatively cold, wet and windy conditions. For a discussion of the possible effects on waders of increasing levels of UVB since the 1970s, especially at high latitudes, see Lindström & Agrell (1999). Lengthened or warmer breeding seasons may be in some ways beneficial for waders, allowing them more time to moult and for putting on fat reserves before migration, and perhaps more time to fit in replacement breeding attempts if unsuccessful initially.

Indirect effects of global climate change

Habitat change

Habitat change will occur as a result of climate change. Sea levels will rise predominantly as a result of ocean expansion with warming. Rising sea-levels will result in a shift in coastal geomorphology, manifest through the redistribution of coastal landforms including intertidal flats, saltmarsh and sand dunes (Pethick & Crooks 2000). Coastal tundra habitats will be lost. Tidal prisms and salinity regimes may be much altered, which could significantly alter the composition of estuarine communities (Kennish 2002). Furthermore, rising sea levels are expected to affect the shape of estuaries resulting in a change in their sediment composition (Austin



& Rehfisch 2003), that in turn would change invertebrate densities and community composition, thus affecting the composition and densities of wader communities (Yates et al. 1993). Austin & Rehfisch (2003) predict the likely effect of rising sea level on the numbers of wader that can be supported during the winter on two contrasting UK estuaries. Assuming that no sea defences are built and that existing ones are allowed to breach, the overwintering densities of waders such as Redshank Tringa totanus and Dunlin Calidris alpina that prefer muddy estuaries are predicted to decline with rising sea level and increasing intertidal sediment particle size, but the total numbers of waders that could be supported on the estuaries might potentially increase as a result of an increase in the area available for foraging. With rising sea level, higher densities and numbers of overwintering Eurasian Oystercatchers Haematopus ostralegus, a species found at high density on sandy substrates, are expected on increasingly sandy estuaries. If, as is very likely, management plans for the defence of estuaries against rising sea level are implemented, existing coastal squeeze of intertidal habitat (Carpenter & Pye 1996) may get worse with potentially serious implications for the numbers of wader that can be sustained during winter and passage periods in the estuaries of the UK and elsewhere. It is likely that this will be exacerbated by the erosion of sandy shores by rising sea levels (Brown & McLachlan 2002). Global sea level rise is also a factor in estuarine shoreline retreat along the northern coast of the Gulf of Mexico; the net effect of which has been the submergence of extensive wetland areas and the conversion of marsh habitat to an open water system (Kennish 2002). Nearly 60% of the wetland loss in the northern Gulf of Mexico is attributed to this process, and the relative sea level rise along the Louisiana coast alone has increased from a net $1-2 \text{ mm yr}^{-1}$ to 1 cm yr $^{-1}$ or more during the 20th century accounting for an annual loss of up to 73 km² of wetland area (White & Tremblay 1995 and Eisma 1998 in Kennish 2002). Even the lowest estimate of sea level rise accompanied by a period of greater storminess is likely to result in substantial loss of saltmarsh, especially if accompanied by a decline in sediment inputs as a result of increased water abstraction (Adam 2002).

Large-scale breeding, passage and wintering habitat changes are also likely as a result of vegetation responses to increased atmospheric carbon dioxide (Myneni *et al.* 1997) and climatic change (Hughes 2000, Huntley *et al.* 1995). Lindström and Agrell (1999) report that Cramer (1997) predicted a 65% decrease in tundra over a large area of the arctic and that it would become rare in Europe. This suggests that what is presently suitable breeding habitat for the many arcticbreeding waders may become much less common.

Prey distribution and abundance

At all stages of their lives, waders feed predominantly on invertebrates, especially molluscs, annelids, crustaceans and insects (Cramp & Simmons 1983). Insect distributions have already started to alter with climate change (Parmesan 1996, Parmesan *et al.* 1999). As insects have short generation times and the capacity for rapid dispersal, they should be able to follow changing bioclimatic zones. However, there is a danger that there will be a progressive decoupling of species interactions (e.g. between the insects and their plant or animal hosts) especially if one partner is cued by an unchanging daylength and the other by temperature (Harrington *et al.*

1999, Hughes 2000, Visser et al. 1998). The marine molluscs, annelids and crustaceans with pelagic free-swimming larvae such as some Littorina spp. should also be able to follow changing bioclimatic zones, perhaps unlike those of Arenicola marina, Nereis diversicolor, and the Gastropoda Pulmonata that are not active swimmers (Barnes 1980). Changes in sea temperatures can have major effects on marine populations, as witnessed during severe events such as El Niño, and give an indication of what might be expected from substantial global warming (Brown & McLachlan 2002). On South American beaches the abundance of many invertebrate species plummeted. However, this was followed by a rapid recovery when conditions returned to normal. Subtidal areas that were normally anoxic saw an increase in species abundance and diversity, and there was an extension in the vertical distribution of many species during El Niño events. These effects are related largely to changes in productivity, indicating that the consequences of elevated temperature may be indirect (Brown & McLachlan 2002). Brown & McLachlan (2002) suggest that the overall effects of global warming over the next 25 years may be more subtle than dramatic, with some redistribution of species. Animals from the tropics and subtropics may invade higher latitudes whereas towards the poles, there may be some distributional contraction. Changes in temperature regimes may affect the growth rates and breeding seasons of some invertebrates. Much increased winter temperatures should enable colonising species of invertebrate to invade new areas and species already present may show increased overwinter survival and growth rates and in some instances a greater number of generations per year. Even though some or perhaps many invertebrate species may go extinct, at least locally (Parmesan 1996), Lindström & Agrell (1999) suggest that, generally, higher temperatures will lead to an increase in the abundance and diversity of the insect prey that are particularly important to breeding waders (Holmes 1966, Holmes & Pitelka 1968). This may be true, but invertebrates are already super-abundant during the summer chick-rearing season. The critical period is during pre-breeding and egg-laying in early June, when more extensive snow cover in the high Arctic may delay invertebrate emergence and thus hamper waders, as opposed to the low Arctic populations that may benefit (Hans Meltofte pers. comm.).

Predators, disease, humans and other forms of disturbance

The warming in excess of 40% above the global average from December to February 2071-2100 expected in the Arctic, Subarctic and Boreal breeding grounds of waders is very likely to lead to their colonisation by a variety of species, including humans, that find present conditions unfavourable. Already there is evidence that, while the abundance of polar species is either stable or declining, that of more temperate species is increasing or else their distributions are expanding (Parmesan & Yohe 2003). Already, the range of the Arctic Fox Alopex lagopus in Canada may have contracted to the benefit of the Red Fox Vulpes vulpes (Hersteinsson & McDonald 1992). Moreover it is possible that other wader predators, such as Hedgehog Erinaceus europaeus, Badger Meles meles, Weasel Mustela nivalis, Polecat Putorius putorius, Wild Cat Felis catus and Lynx Lynx lynx, may also start colonising more northerly wader breeding habitats. Already waterbirds have to cope with increasing raptor numbers (Butler & Vennesland 2000) and further colonisation of the far north by Sparrowhawk *Accipter nisus*, a major predator of waders (Cresswell 1994), could significantly increase predation pressure on waders. As conditions get milder in the far north, the present relationship between high lemming abundance and low depredation of wader nests (Underhill *et al.* 1993) may become less clear and waders may be faced by regular predation pressure from a wider variety of predators.

Based largely on Piersma (1997), Lindström & Agrell (1999) suggested that the appearance of parasites in the northerly breeding habitats of waders expected with warming conditions could pose a serious threat to the survival of waders, largely as a result of the low immunological investment made by waders.

Since 1995, the global human population has increased by about 80 million people every year, a rate of 1.3% per annum (United Nations 1998). If this rate carries on and continues to coincide with deteriorating conditions in the tropics resulting from climate change, it is likely to lead to even greater numbers of human economic migrants attempting to reach wealthy northern hemisphere countries. This may lead to an increased tendency for humans to move into the sparsely populated Arctic, Subarctic and Boreal wader breeding grounds that will become increasingly attractive with warmer weather. Ongoing disputes between conservation and petroleum interests in Alaska highlight the pressures to which the largely pristine Arctic and Subarctic habitat may become subject. Humans are likely to bring increased pollution, including water eutrophication, and disturbance, arising from such activities as mining, drilling and recreation. As the weather gets warmer arctic tourism is likely to increase in what are now rarely visited areas. Disturbance may be especially concentrated along the coast where, in the UK, it has been shown to lead to a decline in Ringed Plover Charadrius hiaticula breeding success (Liley 2000). Also on the coast, increased human presence is likely to lead to the desire for more landclaim per se, for defences against rising sea levels, the development of aquaculture and shellfisheries, increased levels of bait-digging (the latter two providing competition for food with waders, for example, Atkinson et al. in press), saltpans, tidal power schemes and tidal barriers (Adam 2002, Kennish 2002). It is also likely to lead to the increased dissemination of introduced species, both plant and animal, some of which may have a deleterious effect on waders. The extensive spread of Spartina anglica and S. alterniflora, for example, has resulted in the loss of intertidal wader habitat (Goss-Custard & Moser 1988, Buchanan, this volume). Humans are also likely to wish to control the insects (Adam 2002) that are a very important constituent of the diet of breeding waders and their young (Holmes 1966, Holmes & Pitelka 1968).

EVIDENCE FOR EXISTING EFFECTS OF CLIMATE CHANGE

Birds have shown relatively great advances in spring phenology (Crick & Sparks 1999, Root *et al.* 2003) and the shifts in phenology expressed by species have been greater in the more northerly latitudes (50° to 72°N) than further south (Root *et al.* 2003). The timing of arrival and breeding of migrant waders is often responsive to ambient temperatures and, any long-term trends can often be explained by trends in climate, but in other cases there are no trends. For exam-

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ple, records of the first arrival of Common Sandpipers Actitis hypoleucos at four bird observatories around the British Isles show no trend over time or relationship with spring temperatures (Loxton & Sparks 1999). Similar results were found by Jenkins & Watson (2000) in Deeside (NE Scotland) for Common Sandpiper, Eurasian Oystercatcher, Northern Lapwing Vanellus vanellus and Redshank, although Eurasian Curlew Numenius arquata had shown a significant advance in arrival date of 25 days over the period 1974-1999. Sparks & Mason (2001) found major changes in phenology in a study based on first arrival dates recorded in bird reports for the county of Essex in SE England from 1950 to 1998. They found that arrival of Little Ringed Plovers Charadrius dubius and Whimbrels Numerius phaeopus have advanced by 6 and 22 days per decade, and 3 and 6 days per °C in relation to mean January to March temperatures, respectively. Analysis of long-term trends in average breeding date for waders in the UK (Crick & Sparks 1999) showed that although Ringed Plover Charadrius hiaticula exhibited no overall trend in laying date between 1944 and 1995, its laying date did become earlier in relation to mean monthly temperatures at a rate of 1.1 days per °C, temperatures in the relevant months having shown little trend over time. Although Eurasian Oystercatcher demonstrated a curvilinear trend in average laying date between 1962 and 1995 (peaking in the mid 1970s), this was not related to temperature but partially to May precipitation: becoming earlier at the rate of 0.06 day per mm. The laying dates of Lapwing showed no trend between 1962 and 1995 and were not related to temperature or precipitation.

There are two other studies of migrant wader arrival dates at higher latitudes in Europe. Barrett (2002) investigated trends of arrival near Tromsø, in Norway (at 69° N) between 1978 and 2000 to find that although Eurasian Oystercatcher arrival was advanced by 1.7 days per °C (in March), Northern Lapwing arrival by 2.8 days per °C (in March) and Redshank arrival by 1.8 days per °C (in April), none of these species showed any trends towards earlier arrival. The reason appears to be that temperatures have not shown any trend in his study area over the period. In contrast, Eurasian Golden Plover Pluvialis apricaria has shown a trend towards earlier arrival (at 0.35 day per year) but arrival was not related to temperature. This emphasises the need to interpret such trends carefully and to always consider alternative hypotheses. Further east, on the Kola Peninsula in Russia, at about 68° N, wader arrivals were also earlier in relation to warmer May spring temperatures: Greenshank Tringa nebularia, Common Snipe Gallinago gallinago and Common Sandpiper (Gilyazov & Sparks 2002). Between 1931 and 1999, there were significant advances for Common Snipe (7 days) and Common Sandpiper (6 days) but no trend for Greenshank. The only other information on a wader that we know of comes from the time series gathered in Wisconsin between 1936-47 and 1976-98 (Bradley et al. 1999): records of the "first peet" of American Woodcock Scolopax minor have advanced at the rate of 0.16 day per year.

The implications of earlier arrival and breeding of northern waders are currently unexplored. Earlier phenology may be beneficial if it provides waders with greater opportunities for multi-brooding or clutch replacement after failure. Furthermore, earlier breeding may provide juveniles and postbreeding adults with a longer period to improve their condition before migrating south at the end of the summer. However, there is the possibility that warmer temperatures may lead to increases in high latitude precipitation, such that snow



cover is retained for longer. Thus waders that attempt to arrive earlier on their breeding grounds may be faced by prolonged snow cover that could affect their survival. Furthermore, increased snow cover and delayed melt could delay their breeding, which may be detrimental given the short "window of opportunity" that they have for breeding at high latitudes before temperatures start to fall again. The mistiming of arrival in relation to delayed snow melt is analogous to observations made at high altitudes in Colorado, where American Robins Turdus migratorius arrived 14 days earlier in 1999 compared with 1981 due to warmer temperatures at lower altitudes. However, the interval between their arrival and the date that bare ground was first exposed had actually grown by 18 days. Warmer temperatures have led to greater snowfall and later snowmelt (Inouye et al. 2000). In addition, if the climate becomes more variable (Hulme & Jenkins 1998), then periods of extreme (and detrimental) weather may increase early in the season, causing greater stress on new arrivals and causing increased nest losses.

British Trust for Ornithology data show that breeding distributions of many birds in Britain have extended northwards with climatic change (Thomas & Lennon 1999). Arctic species of several taxa have tended to show range-size contraction (Parmesan & Yohe 2003). Johansen (1956) noted that arctic birds had spread further into the polar region and that even boreal species were penetrating into the Arctic and Boyd and Madsen (1997) suggested that this early distributional shift made it difficult to separate changes due to climate change from those due to earlier events such as human persecution. This may be an unnecessarily pessimistic view as these northerly movements could have been due to climate change as the arctic has been warming at least since the 1950s, with increased minimum daily temperatures, lengthened freeze-free seasons, increased sea surface temperature, reduced annual duration of lake and river ice cover and the widespread retreat of mountain glaciers and Northern Hemisphere spring and summer sea-ice extent (IPCC 2001). The extent of snow cover has also decreased since at least the 1960s.

Although systematic monitoring data for Ruff Philomachus pugnax are missing, Zockler (2002) suggested that its populations may be declining in all habitats across temperate Eurasia as a result of a northwards and eastwards shift in population towards the Arctic tundra perhaps linked to climatic change. A local study of Eurasian Golden Plovers and Common Sandpipers in the Pennine Mountains of England has shown that populations fluctuate in relation to changes in the North Atlantic Oscillation (NAO), which is a meteorological feature that determines the types of weather affecting NW Europe (Forchhammer et al. 1998). Eurasian Golden Plover numbers increase 2 years after warm and moist winters, presumably because juveniles survive better; but Common Sandpiper numbers increase after cool dry winters. The latter result is likely to be mediated through their food supplies or habitat, because the species migrates to Africa in winter.

In Britain, wintering wader distributions have changed since the 1970s (Austin *et al.* 2000). Since the mid-1980s, with an increase of 1.5°C in mean winter temperature in the UK, the estuarine distributions of seven out of nine common wader species have moved in an eastwards direction across the winter isotherms, with the smaller species showing the greatest shifts (Fig. 2, Rehfisch & Austin 1999, Austin & Rehfisch in prep.). The relationship could not be explained



Fig. 2. (a) Relationship between median longitude of population distribution and average number of days with ground frost recorded across 39 British weather stations. Comparison between the distributions of Ringed Plovers (b) at the median easting of 331 during the particularly cold 1979/80 winter and (c) at the median easting of 395 during the particularly warm 1989/90 winter.



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by the buffer effect (Gill et al. 2001) although the buffer effect could have been noted as a consequence of Blacktailed Godwits Limosa limosa moving eastwards with warmer winters. Between two winter surveys of Britain's non-estuarine coasts in 1984-85 and 1997-98 the distributions of eight wader species moved in an eastwards and/or northwards direction with increasingly mild winter temperatures and changes in mean rainfall, wind speed and wind-chill (Fig. 3, Rehfisch et al. in press). In both cases the authors suggest that the waders appear to be wintering closer to their breeding grounds that are predominantly to the north and east of Britain as the risk of cold-induced mortality has diminished in the east with milder winter weather. If the waders were starting to winter even further north and east, outside of Britain (Rehfisch et al. 2003a,b), this could help explain the recent decline in eight of the 14 common coastal waders. Tentative predictions made for some wader species suggest that their numbers on the UK's non-estuarine coasts might show considerable declines if the observed relationship between weather and distribution continues (Fig. 3, Rehfisch et al. in press). It is possible that, if the observed trend towards easterly and northerly wintering were to continue in Britain, the carrying capacity of easterly wintering grounds could be exceeded (e.g. Gill et al. 2002) encouraging waders to winter on the Continent of Europe.

PREDICTIONS AND CONCLUSIONS

There is an urgent need to explore the intrinsic and extrinsic factors that could potentially inhibit the adaptation of waders to climatic change. Birds are likely to be good indicators of the impact of climate change as they show the greatest known advance in spring phenology (Fig. 2 in Root et al. 2003). Waders are likely to be particularly useful indicators as the phenological shifts expressed by species in northerly latitudes are greater than those further south (Root et al. 2003) and Arctic species tend to show range-size contraction (Parmesan & Yohe 2003). Waders are thus likely to reward study as they will have to show relatively rapid changes in behaviour and life history traits if their populations are not to decline rapidly as a result of climatic change. They also occupy or visit those parts of the world where climate changes are greatest and are likely to continue to be greatest. Furthermore, their numbers, population trends and productivity (from age-ratios) can be monitored relatively easily on their wintering grounds. This, in conjunction with the present increase in data being gathered from their breeding grounds on their reproductive performance in relation to environmental variability by the "Arctic Breeding Conditions Survey" and "Pan-Arctic Shorebird Monitoring Program", may make the identification of causal relationships possible.

The future distribution and abundance of waders will be the result of a series of highly complex and interacting direct and indirect effects on the waders themselves, their habitat, prey, predators and other co-existing species, not least of which will be the potentially considerable impact of anthropogenic factors as man colonises the far north in increasing numbers as the weather becomes milder. Lindström and Piersma (in prep.) suggest that the sheer complexity of the information needed for each stage in the intricate web of interactions that will determine the future wader distribution and abundance makes it unreasonable even to attempt to generate realistic predictions of the impact of climate change



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on waders. Although they suggest that there are more urgent issues affecting waders, such as excessive shellfishery pressure, we feel that even relatively simplified population models will be useful for understanding some of the potential effects of future climate change. Following the approach of Rodenhouse (1992), a better understanding of these factors should make it easier to start developing the multi-parameter population models for individual species that will help increase our understanding of the complexities of the interactions between different components of a species' demography. Only once these parameters are understood should models that incorporate multi-trophic interactions be considered, for, as in all forms of modelling, errors at each stage of the procedure may be compounded in directions that could lead to results of uncertain value.

Having reviewed the impact of climate change on birds, Crick (in press) has detailed why the following factors should be prioritised in future studies (with our additional italicised notes): "(i) the lack of phenotypic/genotypic adaptability, (ii) dispersal ability (*if adequate staging posts exist along a migration route, this is unlikely to be a predominant factor for waders that migrate annually over long distances*), (iii) ecological specialisation, (iv) small population size, (v) increases in the frequency of extreme events, (vi) loss or decline in habitat quality, and (vii) changes in the range of other species including introduced non-native species." Clearly anthropogenic factors will be particularly important determinants of (vi) and (vii).

An alternative approach to understanding potential changes in the distribution of species is one based on empirical relationships between presence/absence or abundance of species with climate and habitat variables. The use of this climateenvelope or suitability-space approach allows ready assessment of the impact of climate change and habitat change based on future scenarios. Ideally, the dispersal capacity of species should be built into this bio-climatic modelling approach as the habitat-associated dispersal capabilities of some species of plants, prey and wader predators may not be great enough to keep up with a very rapidly changing climate. In combination with scenarios of changing land-use, this is broadly the approach being used in the UK to predict the possible change in the regional distributions of a wide range of selected species as part of the MONARCH project (Berry et al. 2001). Doubtless these and any other such predictions will be associated with a great margin for error but they should start providing opinion-makers with estimates of the scale of the likely changes.

Thus, assessment of the likely impact of climate change on wader populations and dealing with its impact is a multifaceted and long-term issue that requires the attention of researchers, government agencies and non-governmental organisations, preferably in conjunction with business and industry. These stakeholders should work collaboratively to ensure that the predictions of change are as sound as possible. Conservationists will then be in a position to use the models to develop the strategies that will help maximise the probability that the present populations (or at least viable populations) of waders are maintained, perhaps until greenhouse gas concentrations revert back to something approaching those of historical times. Such a reversion is not impossible. The glaciation of the Antarctic in Cenozoic times occurred relatively rapidly through a height/mass-balance feedback once atmospheric CO₂ had started declining from three times pre-industrial atmospheric level (DeConto &



Fig. 3. (a) Ringed Plover densities on the non-estuarine coast of each of Great Britain's counties during the winter of 1984–85 (height of bar proportional to density), and (maps b, c & d) predicted relative change in their numbers by 10-km square under various UKCIP climate change scenarios (Hulme & Jenkins 1998): (b) 2020 medium-low climate change vs 1961–1990 baseline; (c) 2080 medium-low climate change vs 1961–1990 baseline; (d) 2080 high climate change vs 1961–1990 baseline (Rehfisch *et al.* in press). All changes in (b) to (d) are <1, thus indicating declines.



Pollard 2003). In a rapidly changing world, conservationists applying the precautionary approach to the maintenance of viable populations of waders are likely to argue that large tracts of "protected" land will need to be set aside. These will have to cover the full range of habitats required during the migratory life-cycle of waders: extensive breeding areas, staging posts and suitable wintering grounds. Active management of the protected areas will be necessary to counteract conditions that are likely to be sub-optimal under changed climatic conditions.

Although the most urgent priority is to tackle the anthropogenic and other factors that are leading to direct pressure on wader populations, we feel that the potential impacts of a rate of climate change not previously witnessed in historical time is likely to be so overwhelming for waders and other fauna, including humans, that every effort must be made to evaluate and understand them. In our opinion, predictions of change that may point to the probable disappearance of many charismatic species, including waders, are potentially vitally important in highlighting the dangers of climate change to decision makers and the general public.

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