Commentary

Unravelling the mechanisms linking climate change, agriculture and avian population declines

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During the last decade or more, much research has attempted to predict the likely consequences of climate change for biodiversity. Many studies have focused on modelling species distributions as a function of climate (climate envelope modelling), and then used future climate projections to model the potential change in the distribution of that species were it closely to track the change in climate. This approach has usefully highlighted the potential magnitude of the conservation problem that may result from climate change (Erasmus et al. 2002, Thomas et al. 2004, Harrison et al. 2006) and identified species traits associated with projected vulnerability to change based on the relative size and overlap of current and projected future ranges (Huntley et al. 2007, 2008, Jetz et al. 2007, La Sorte & Jetz 2010). However, it provides little information about the likely mechanisms by which such changes will occur, and yet this mechanistic information is required to develop appropriate management actions. Identifying and quantifying the mechanisms through which climate change will influence population change is therefore one of the major challenges we currently face.

For most species, the main impacts of climate change are likely to operate indirectly, through alterations in key factors such as prey availability (e.g. Frederiksen *et al.* 2006, Pearce-Higggins *et al.* 2010), predation risk (e.g. Martin 2001) and disease (e.g. Cattadori *et al.* 2005). Human land-use is also heavily influenced by climatic conditions, and many indirect effects of climate change are therefore likely to operate through enforced and adaptive changes in agriculture, forestry and other sectors. The potential power of such land-use change to drive population changes is clearly illustrated by consequences of agricultural intensification for European open-country birds (Donald *et al.* 2001). Changing climatic conditions are very likely to influence agricultural management and drive land-use change, which may increase the pressure on vulnerable bird populations, but these mechanistic links have rarely been examined.

In this issue of Ibis, Kleijn et al. (2010) describe how the Black-tailed Godwit Limosa limosa, a rapidly declining bird of intensively managed farmland in the Netherlands, was first affected by agricultural intensification and, more recently, by interactions between climate change and agriculture. This case study neatly demonstrates that climate change does not act in isolation, but interacts with a range of other processes to produce potentially complex consequences for species (e.g. Mustin et al. 2007). This has two important consequences for ecologists. First, whilst broad patterns from climate envelope models indicate the potential direction and magnitude of shifts in species distributions (Green et al. 2008, Gregory et al. 2009), projections for individual species may have a high degree of uncertainty associated with them, particularly if they are based upon generic bioclimatic variables (Heikkinen et al. 2006) or exclude other potential drivers of change (Anderson et al. 2009). This means that, secondly, species-specific studies of the likely mechanisms by which climate change will impact upon populations can provide more detailed information about how individual species are likely to respond to climate change (e.g. Pearce-Higggins et al. 2010), and thus inform adaptive management. Ornithologists have been at the forefront of developing mechanistic models of population-level responses to environmental change (Sutherland 1996, Norris 2004). Identifying the routes through which climate change is likely to influence these processes, as in the Kleijn et al. study, provides a basis both for incorporation of climate change impacts into these models and for the development of potential management solutions to adapt to the effects of climate change.

We have long known the problems that Black-tailed Godwits in the Netherlands face as a result of agricultural intensification. This species breeds primarily on lowland grasslands that receive a high amount of fertilization, and are subject to frequent mowing or grazing (Kleijn et al. 2001). Mowing results in the loss of nests and young chicks (Kruk et al. 1997), whilst chicks that avoid direct mortality may also suffer reduced survival as a result of increased predation and reduced food availability (Schekkerman & Beintema 2007, Schekkerman et al. 2009). The severe impact of changes in mowing dates on productivity of Black-tailed Godwits and other meadow birds in Western Europe led to the development of agri-environment initiatives ranging from postponement of farming operations to direct protection of nests. However, these measures have not been sufficient

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to halt the population declines (Kleijn *et al.* 2001, Verhulst *et al.* 2007).

Kleijn et al. (2010) describe the changes that have taken place within the Godwit population since the 1940s, and explore the influence of agricultural intensification and recent warming trends. Between the 1940s and 1970s, a period of relatively stable climatic conditions, Godwit breeding phenology advanced by around 2 weeks, probably as a result of agricultural intensification (particularly the high degree of fertilization) improving adult resources for breeding or providing earlier cover for nesting (Beintema et al. 1985, Kleijn et al. 2010). However, in contrast to changes observed in Northern Lapwing Vanellus vanellus breeding in the same areas (Both et al. 2005), and other waders such as European Golden Plover Pluvialis apricaria (Pearce-Higgins et al. 2005), recent increases in spring temperatures have not resulted in any further advance in Godwit laying dates since the 1980s. The Black-tailed Godwits breeding in the Netherlands winter in West Africa and Iberia, and have also experienced severe environmental changes in their passage and wintering sites (Zwarts et al. 2009). Throughout this non-breeding range, extensive drainage of freshwater wetlands has resulted in a reduction in natural prey availability, with Godwits now almost entirely dependent upon rice as the main food source (Lourenco & Piersma 2008). Given the strong links that can exist between breeding and non-breeding season processes in migratory birds (Gunnarsson et al. 2005, 2006), the timing of arrival and nesting in Dutch Godwits may well be constrained by the conditions they are now experiencing in the non-breeding season, as Kleiin et al. discuss.

In the Netherlands, recent warming has continued to improve agricultural conditions and extend the growing season earlier into the spring. This means that median mowing dates advanced by about 15 days between 1982 and 2005 as a result of more rapid grass growth, and now occurs at about the same time as median Godwit hatch dates. This has several detrimental consequences for the Godwits. First, an increasing proportion of nests and young chicks suffer mortality as a result of mowing, resulting in an almost seven-fold increase in the loss of clutches attributed to farming from the late 1980s to late 1990s (Teunissen et al. 2005). Secondly, more chicks have to survive in an unsuitable landscape of mown or heavily grazed grasslands, resulting in increased predation risk and reduced food availability. Thirdly, the uncut vegetation, which was the favoured foraging habitat, is now denser and therefore less accessible to chicks, as a result of more rapid spring growth. As a result of this reduction in foraging quality, chick condition and survival has also declined since the late 1980s.

This mechanistic study provides an opportunity to identify how management to adapt to climate change

might be implemented. Such an approach builds on the models applied to declining farmland birds, where the identification of the demographic mechanisms underpinning population declines (e.g. Siriwardena et al. 1998, Peach et al. 2003, Potts & Aebischer 1995) and their links to agricultural management (e.g. Green 1996, Wilson et al. 1997) informed the development of potential management solutions (e.g. Green et al. 1997, Morris et al. 2004). The most powerful of these involved the development of population models to explore the potential consequences of different management options (e.g. Green et al. 1997), used to predict the consequences of variation in grassland management upon Corncrake Crex crex productivity, a system not too dissimilar to that of Dutch Godwits. Widespread implementation of appropriate agri-environment schemes based upon that model has led to successful Corncrake population recovery in Scotland (O'Brien et al. 2006), and this same modelling approach can be applied to inform climate change adaptation. Kleijn et al. discuss the potential options for management to improve conditions for Godwits but suggest that introducing delays in mowing or grazing to return to the phenology of the 1980s would be insufficient because the current higher temperatures increase grass growth rates, and increased sward density reduces food accessibility and chick survival rates. Creating the mosaics of tall and open swards that Godwits need is likely to require raising groundwater levels to retard plant growth (Jackson 1985, Schekkerman et al. 2008). The information presented in the Kleijn et al. study is key to the development of appropriate adaptation strategies, perhaps informed by a population model to assess the relative costs of different management options (e.g. Ratcliffe et al. 2005). More studies like this are therefore urgently needed to allow robust predictions of population responses to climate-induced environmental changes, for it is through such studies that science can best inform policy.

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