

Biodiversity Climate change impacts report card Technical paper

11. Impacts of Climate Change on Migration

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Summary:

- The UK hosts in the region of 250 migratory species; most of these are birds, but bats, butterflies, moths and dragonflies are also represented. Migratory behaviour is a flexible trait, with species varying greatly in their migratory tendencies and the distances covered, but, in broad terms, terrestrial migrants either migrate to the UK in the summer from further south, or in the winter from further north and east.
- Migratory species may be affected by factors operating on the breeding, non-breeding or stopover ranges and there are likely to be interactions between these. Migratory routes, use of stopover areas and resource availability in most non-breeding areas are poorly known, especially for bats, limiting our ability to quantify these effects. New tagging technologies will continue to improve our knowledge of migratory journeys and connectivity.
- Migratory birds rely disproportionately on coastal, wetland and tundra-type habitats, which show large seasonal peaks in prey resource, but are particularly likely to suffer from climate change.
- Some effects of climate on migratory behaviour have been well documented: most avian species are migrating less and summer migrants are arriving earlier (and some are departing later). The population impacts of these changes are likely to be species specific and depend upon the relative rate of change exhibited by other organisms, particularly their prey. Migratory insects, in contrast, are migrating with increasing frequency and this is leading to the colonisation of the UK by new species.
- All migratory species rely on wind currents to aid migration. There is evidence that these are changing, including an increased frequency of storms, but the population impacts of these are unknown.
- For birds and bats gathering fuel to complete the migratory journey may be a challenge, requiring good quality habitat. Many of the sites used by birds (and possibly other species) to do this (e.g. many estuaries, wetland areas, the Sahel) are among the areas most likely to be affected by climate change, through lowered water tables adversely affecting the ability of migrants to forage sufficiently. These habitats are often also under intense pressure from other anthropogenic threats, such as water abstraction or infrastructure development.
- In many cases, although documented population level impacts may be correlated with climate change, it has proven difficult to ascribe climate change as the sole cause, since there are often concurrent changes in land use and habitat quality that may have similar impacts. In general, impacts of changing land use may be greater than, or at least interact with, climate change. Successful adaptation to climate change will most likely depend on appropriate land management.
- Key knowledge gaps in our understanding of migration dynamics are: resource requirements and availability throughout the migratory cycle; whether individuals from different breeding locations also winter in geographically distinct areas; availability of models to accurately assess future impacts and the extent and importance of seasonal interactions and carry-over effects. Our knowledge in all these areas is much better for birds than for other taxa.

Migration is a flexible behavioural strategy evolved in response to ecological and biogeographical processes such as seasonality, spatio-temporal distributions of resources, habitats, predation and competition (Alerstam *et al.* 2003). Consequently, the annual movements of migratory species often span large distances, tracking the locations of suitable environmental conditions across the globe, leading to difficult challenges in their conservation (Runge *et al.* 2014). While this suggests that migrants may be able to easily track changes in their environment, their ability to do so is constrained not only by the timing of seasonal events, but also by the time-scale over which adaptation (evolutionary or otherwise) can occur (Sutherland 1998; Both & Visser 2001). As environmental changes (and responses to them) may occur at differing rates and extents in different parts of the migratory range, this can also result in conflicting drivers of change (e.g. Ahola *et al.* 2004; Zipkin *et al.* 2012). Understanding the impacts of climate change on patterns of migration, and ultimately migratory species, therefore requires knowledge of the relative effects of processes operating and interacting across locations separated by many hundreds, or even thousands, of kilometres (Robinson *et al.* 2009; Hostetler *et al.* 2014). Because migratory species integrate over multiple environments, they may be considered as 'sentinels' of climate change (Piersma & Lindström 2004). In this paper we aim to: (i) review the current migratory patterns of UK species (ii) explore the range and extent of climate induced changes to the migration patterns of UK species and the extent to which migratory species will be affected by other climate-induced changes, and (iii) highlight the priorities for research in this area.

1. Current migratory patterns of UK species

The current primary international legislation protecting migratory species, the Convention on the Conservation of Migratory Species of Wild Animals (CMS, www.cms.int), defines a migratory species as one in which '*a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries*'. Typically, migratory species cross such boundaries in order to travel between two distinct geographical locations in relation to reproduction cycle, changes in temperature and prey availability (Forcada 2002). Under this definition, migration is distinguished from other forms of movements, such as one-way dispersal movements (e.g. natal dispersal of young) and more unpredictable irruptive movements linked to annual or seasonal fluctuations in food supply, which may not always involve a return journey and can often lead to populations concentrating in different parts of their non-breeding range in different years (Newton 2008). Although migratory movements are usually assumed to occur over substantial distances (for instance, across range state boundaries), shorter distance migrations may also occur, for example along elevation gradients or between inland and coastal areas (Wernham *et al.* 2002), and among insects, migration is often considered to be movement between habitats (Chapman *et al.* 2010).

Not all individuals of the same species always exhibit the same migratory strategy. In populations of partial migrants, a subset of the population remain in the breeding area for winter (or move only short distances), whilst others leave for areas further away. Across their breeding ranges, partial migrants often exhibit a latitudinal cline in migratory tendency, with individuals from more northerly (in the Northern Hemisphere at least) populations more likely to migrate, or migrating further (so-called 'leap-frog' migration) than more southerly breeding individuals (e.g. Korner-Nievergelt *et al.* 2014). In birds, evidence suggests that at high latitudes it tends to be the more dominant individuals (typically older males) that tend to remain closer to their breeding territories throughout the year, while females and sub-adults make up the majority of the migratory population (Boyle 2008).

One consequence of migratory (and other) movements is that individuals may occur more, or even less, frequently in areas where they are not normally encountered, i.e. as vagrants or accidentals. This may be because of variability in the genes influencing migratory direction (e.g. Helbig 1996; Berthold & Helbig 2008), individuals forced off-course by

inclement environmental conditions (e.g. McLaren *et al.* 2006), or dispersive movements from nearby populations. Because of its geographical location, and a large enthusiastic nature-watching community, many species of vagrants are

Table 1: Summary of the number of terrestrial species with different migratory strategies occurring in Britain. Summer migrants are those that spend the summer here generally migrating from further south. Winter migrants come from the north and east to spend the winter. Marine migrants (seabirds) spend most of the non-breeding season offshore (these are covered by the MCCIP card). In partial migrants only a proportion of the population is migratory; passage migrants migrate to or through Britain in the spring-autumn, but do not usually breed, while vagrants occur only rarely. Resident species show no migratory tendency.

	Summe r	Winte r	Marin e	Partia l	Passag e	Vagrants	Resident s	Total
Birds								
Non-passerine	27	27	14	46	16	148	41	318
Passerine	23	8	-	25	14	171	31	273
Insects								
Butterflies	3	-	-	4	-	9	55	71
Moths	21	-	-	12	17	100+	c. 2,300	c. 2,500
Dragonflies	-	-	-	5	-	12	40	57
Mammals								
Bats	-	1	-	-	-	6	17	24

Sources: Birds - Parkin & Knox (2010), Wernham *et al.* (2002); Butterflies – Asher *et al.* (2001); Moths – Waring & Townsend (2003), Sterling & Parsons (2012); Dragonflies – Cham *et al.* (2014); Bats – Dietz *et al.* (2009).

recorded in Britain (Table 1), particularly from Europe and Asia, but also Africa and North America. Although the identity and frequency of occurrence of these vagrants may be affected by climatic processes, in general, they will not be considered further. We do note, though, that in some cases such vagrants may be important in establishing new populations, for example, black redstart *Phoenicurus ochruros* (a short distance migrant) was only recorded as an occasional vagrant in Britain until the 1940s, but is now a regular breeder in south-east England.

1.1 Birds

Birds are by far the most migratory group within the UK, with most species exhibiting some degree of migratory tendency; relatively few species (c. 10%) can be considered entirely resident (Table 1). The UK is at the centre of the East Atlantic (Africa-Eurasia) flyway, linking Arctic breeding grounds stretching from Canada to central Siberia, with wintering grounds in western Europe and further south throughout much of Africa (Davidson & Stroud 2006). Due to this position, its relatively mild climate and extensive areas of mudflats for feeding, the UK is both the final winter destination for many Arctic & Scandinavian breeding migrants as well as an important passage site for species continuing further south. The majority of species overwintering in the UK are waders and waterbirds; however, there are also a small number of passerine species, particularly thrushes, for which Britain and Ireland hold a substantial, but unquantified, proportion of the Eurasian population (Wernham *et al.* 2002); a recent BTO survey aimed to address this (<http://www.bto.org/volunteer-surveys/winter-thrushes>). In recent years, the number of over wintering waders in the UK has declined while the numbers of ducks, geese and swans have increased (Figure 1a).

During the summer months the UK's temperate climate provides breeding grounds for many species travelling north from Southern Europe and Africa (Wernham *et al.* 2002; Sanderson *et al.* 2006). Within the UK, and indeed across Europe, many of these migratory species are currently declining at a faster rate than resident populations, especially those wintering in more humid habitats (Figure 1b; Thaxter *et al.* 2010); these declines appear to be greatest in the south and east of Britain (Morrison *et al.* 2013). For example, of the ten bird species which suffered population declines of greater than 50% since 1994, seven are migrants (Risely *et al.* 2012). While the drivers of such declines are currently largely unknown, changes in the climatic conditions on breeding grounds, during migration

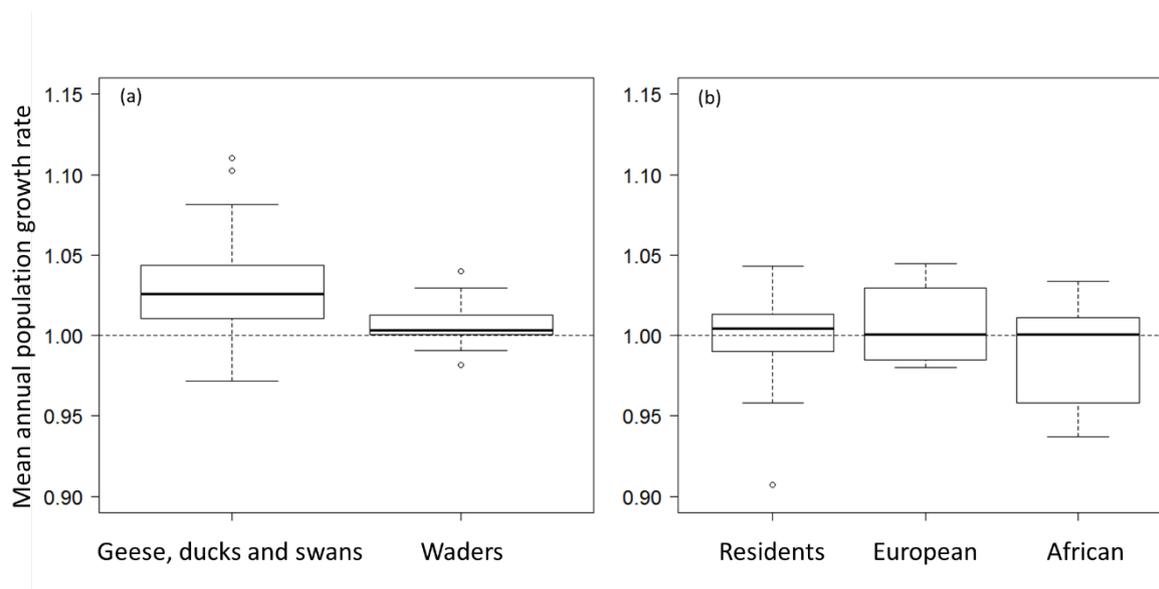


Figure 1: Changes in the population size of, (a) non-passerine winter migratory species of geese, ducks and swans ($n = 24$) and waders ($n = 18$) recorded under the Wetland Bird Survey (WeBS) between 1974 and 2010 and (b) passerine species of residents ($n = 22$), short-distance ($n = 8$) and long-distance ($n=18$) birds recorded by the Breeding Bird Survey (BBS) between 1995 and 2010. Populations with a growth rate of 1 (indicated by the dotted line) are stable.

and during breeding grounds, during migration and during the non-breeding season are all likely to be playing a role. The UK also hosts internationally important colonies of breeding seabirds (Mitchell *et al.* 2004), the migratory routes of which vary from localised movements within the North Sea (e.g. guillemot *Uria aalge*), to global journeys as far as Antarctica (arctic tern *Sterna paradisaea*). Climate impacts on these species are considered under the Marine Climate Change Impacts Partnership (MCCIP) reporting process (MCCIP 2010).

While we have detailed knowledge of the distribution and abundance of many migratory terrestrial birds within the UK, information on their non-breeding season movements is more limited. In general, the ranges of UK migratory species have been identified from recoveries of ringed birds and a small number of observations (Thorup *et al.* 2014). However, recovery rates for most species are extremely low and subject to severe sampling biases (Korner-Nievergelt *et al.* 2010). Presently much of our understanding of migratory routes, stop-over sites and connectivity comes from a limited number of site and species specific studies (e.g. Gunnarsson *et al.* 2005). However, recent developments in technologies such as geolocators and satellite tags have the potential to provide detailed records of movements of individuals throughout migratory ranges (Egevang *et al.* 2010; Bridge *et al.* 2011; Vardanis *et al.* 2011; Tøttrup *et al.* 2012) and greatly improve our understanding of these processes, for example in determining where on the migratory journey mortality occurs (Strandberg *et al.* 2010).

1.2 Insects

In the UK, there are a small number of species of Lepidoptera (butterflies and moths) which are classified as regular migrants (Table 1); in addition there are an increasing number of species (particularly in the Crambidae and Pyralidae moth families) that occasionally occur as irruptive immigrants, some of which are considered pest species (Sterling & Parsons 2012). As the lifespan of the adult (or imago) is relatively short, the migratory journeys of butterflies and moths may be carried out over a number of different generations and most individuals that reach Britain do not survive over-winter, although the frequency of those that do so is increasing as temperatures increase (Skelton 1999; Asher *et al.* 2001). During the spring, moths and butterflies travel from North Africa and the southern Europe with a variable number reaching UK to breed; the offspring of this generation then undertaking the southward migration during the autumn (Chapman *et al.* 2012; Stefanescu *et al.* 2012). The number of species of migratory Lepidoptera reported each year in the south of the UK has been rising steadily since the 1980s (Sparks *et al.* 2007) and populations of some species in Britain, e.g. painted lady *Cynthia cardui*, are largely reliant on continental immigrants. In Europe, distributions of migratory butterflies are generally not well explained by climate, in contrast to more sedentary species, and only two (false comma *Nymphalis l-album* and clouded yellow *Crocias croceus*) are considered at (moderate) risk because of changes in climate space (Settele *et al.* 2008).

There are five species of dragonflies in the UK with migratory individuals in their populations (Table 1). In recent decades the abundance of migratory dragonflies within the UK has been increasing, with species such as the migrant hawkler *Aeshna mixta* (which was rare in the UK until the 1940s), Red-veined Darter *Sympetrum fonscolombii* and Willow Emerald Damselfly *Chalcolestes viridis* migrating from mainland Europe in large numbers and recently establishing resident populations (Ott 2010; Cham *et al.* 2014). The migratory movements of British dragonflies are currently poorly understood, although some North American species (recorded as vagrants in Britain) are better studied (May 2012). However, since the mid-1990s, monitoring has been carried out by volunteers submitting records to the British Dragonfly Society's Migrant Dragonfly Project (<http://british-dragonflies.org.uk/content/migrant-dragonfly-project>). Such work aims to provide a better understanding of movements and range changes of species in relation to environmental change.

1.3 Mammals

Most migratory mammals are cetaceans (Learmonth *et al.* 2006), which are considered as part of the MCCIP process. However, the UK also hosts a number of species of bats that are migratory within Europe. Our knowledge of bat movements, though, is poor and a key area for future work (Sherwin *et al.* 2013). Nathusius' pipistrelle *Pipistrellus nathusii* is the only species that is known to make long-range movements to and from Britain, with British populations of other species largely appearing to be sedentary (Dietz *et al.* 2009). In continental Europe, Nathusius' pipistrelles migrate south-west in late autumn and winter before returning to eastern Europe in the spring. In the UK, the small summer breeding population is supplemented by migratory individuals in the winter, probably migrating from Scandinavia (Russ *et al.* 2001). Across Europe this species have been intensively studied for decades, with the longest movement recorded at 1,905 km (Dietz *et al.* 2009). However, within the UK, it has historically been under recorded and increasing records in recent years may reflect sampling effort as much as range expansion.

2. Ecological and population impacts of climate change

2.1 Length of journey and frequency of migration

Climate warming has been associated both with northerly areas becoming more suitable for colonization and increases in the number of migratory moths and butterflies reported each year in the south of the UK (Sparks *et al.* 2007). For example, two migrant butterflies, the clouded yellow and the red admiral *Vanessa atlanta*, have recently started to overwinter in England in increasing numbers (e.g. Skelton *et al.* 1999) and moths such as the cypress carpet *Thera cypressata* have recently colonized (Waring & Townsend 2003). Similarly, dragonflies appear to be undertaking longer, and more frequent, migratory journeys in Europe (Ott 2010). This has resulted in the colonization of Britain by at least two new species in recent decades with more sporadic breeding by several other species suggesting the potential for them to establish (Cham *et al.* 2014). It is **Very Likely** that these shifts reflect a northward movement of isotherms in Britain, though concurrent improvements in water quality may also have played a role (Hickling *et al.* 2005). The range of the one bat species known to migrate to Britain, Nathusius' pipistrelle, also appears related to climate, and is predicted to increase as climates warm and, indeed, may already have done so (Lundy *et al.* 2010).

For many migratory birds, it is **Very Likely**, that journeys are becoming shorter, at least for shorter-distance migrants (Figure 1). Wernham *et al.* (2002), estimated that 14 (of 41) migrant species had shortened their migration distance, based on an analysis of recoveries of ringed birds across a range of taxa. Similarly, Visser *et al.* (2009) suggested that migration distances have become significantly shorter for 12 of 24 migrant species breeding in the Netherlands, and Paprocki *et al.* (2014) document reduced migration in North American raptors. It is often unclear from these analyses, though, whether this represents a shift in wintering area, or individuals spending less time (arriving later and/or returning sooner) there, or both. Amongst species wintering here, Maclean *et al.* (2008) showed that the centroid of the wintering range of several migratory waders has shifted north-eastwards (i.e. closer to the breeding grounds) by an average of 115 km, and similar patterns are evident among migratory waterfowl (Pavón-Jordán *et al.* 2015). This has resulted in a decline in the number of waders wintering in Britain, with declines most notable in west coast estuaries (there have been corresponding increases on east coast estuaries for some species). Waders generally exhibit a high degree of philopatry, so such changes are likely to have come about through changes in juvenile settlement (Gill *et al.* 2013).

Shorter journeys will not only reduce the costs of migration, but may also allow individuals to better assess conditions on their breeding grounds (because they are closer) and so better time their return (Kullberg *et al.* 2015; Tellería *et al.* 2015). They may not, however, always be entirely beneficial. Ambrosini *et al.* (2011) documented a northward shift in wintering swallow populations of 3 - 9 km.yr⁻¹, which implied an increasing proportion were wintering in warmer, drier areas which may be more, and increasingly, unfavourable. Amongst trans-Saharan migrants however, there is **Limited Evidence** to suggest that that journeys may lengthen. Doswald *et al.* (2009) used climate envelope modelling to predict shifts in the breeding and wintering ranges of *Sylvia* warblers. For several species, these shifts resulted in a doubling of migration distances.

Finally, migratory tendency in some species is also decreasing (e.g. Lesser Black-backed Gull, Ross-Smith *et al.* 2014), although this can be difficult to demonstrate as it requires a population of marked individuals. Pulido & Berthold (2010) show that in German blackcaps *Sylvia atricapilla* this probably as a result of genetic selection. Climate change has the potential to select for alternative migratory strategies (Berthold *et al.* 1992), including populations becoming entirely sedentary.

2.2 Fuelling the journey

Migrants lay down large fat stores before beginning their journeys and particularly before crossing an ecological barrier, such as a large expanse of desert or water (Newton 2008; Schaub *et al.* 2008). For example, before crossing the Sahara Desert, garden warblers *Sylvia borin* more than double their body weights from 16-18g to 37g (Bairlein 1991). As carrying large amounts of fat reserves can carry large costs and make individuals more vulnerable to predation (McNamara & Houston, 1990), appropriate timing of fuel loading is important. The time taken to obtain the necessary pre-migratory body condition (i.e. fuel stores) will depend on the food availability in the surrounding environment and the effects of lower food availability before and during migration may not be equal across the population. For example, during migration juvenile swallows load less fuel than adults and consequently might suffer greater delays or mortality in years of poor resources (Coiffait *et al.* 2011). Such effects are **Likely** to be greatest prior to crossing an ecological barrier, thus, in the Afro-Palaearctic migration system, changes in the Sahel region and the Mediterranean basin may be particularly important (see 3.1).

2.3 Shifts in migratory schedule

Migratory species exist within tight annual cycles, with shifts in the time taken to complete one stage potentially impacting the time available for subsequent stages. One of the most widespread changes in the schedules of many migrants has been in the timing of spring arrival and it is **Virtually Certain** that birds are arriving earlier on their breeding grounds (Sparks 1999; Root *et al.* 2003; Lehikoinen *et al.* 2004; Rubolini *et al.* 2007; Sparks 2013). This is a consequence of earlier departure from the non-breeding areas (e.g. Altwegg *et al.* 2012; Fox *et al.* 2014), and a shortening of migratory distances, though the balance of these in particular species is unknown. In general, the (northwards) spring migration towards the breeding grounds is more constrained and hence likely to be impacted (see below), with birds flying at higher average speeds (Nilsson *et al.* 2013), although there appear to be some exceptions (Nuijten *et al.* 2014). Because of this, at least some suffer greater mortality at this time, particularly when barriers, such as the Sahara desert, have to be navigated (Lok *et al.* 2015), meaning that it is **Likely** that changes in spring migration conditions will have greater population impacts.

The mechanism whereby these shifts in migratory timing have occurred is a subject of some debate, variously being proposed to be due to individuals changing their behaviour (plasticity) or populations adapting to new conditions (evolution). Despite an abundant literature, no study so far has provided direct evidence for an evolutionary response of bird phenology to current climate change, and a lack of individual-based studies hampers our ability to distinguish between these (Charmantier & Gienapp 2014). Among shorebirds, however, the arrival dates of individuals tend to be highly consistent and advancement in migration date appears to be due to earlier arrival of new recruits (Gill *et al.* 2013); the same may be true of at least some passerines (e.g. Tøttrup *et al.* 2012). Advances in nest-laying dates may explain these changes, if benefits of early hatching facilitate early subsequent spring migration, rather than individual plasticity or rapid evolution of migration timings (Gill *et al.* 2013).

In the UK, migratory birds are arriving on their breeding grounds around two weeks earlier than thirty years ago (Sparks *et al.* 2007), a trend that is most notable in the earlier arriving migrants (Eddowes 2012). Advances (or delays) in arrival dates on breeding grounds could arise through both direct and indirect climatic processes. Direct processes include the impact of weather on departure decisions, progression speed or stopover duration (Ahola *et al.* 2004; Both 2010; Studds & Marra 2011), while indirect effects describe the cascade of effects due to changes in environmental conditions driven by climatic fluctuations (Gordo 2007). For example, droughts on non-breeding grounds could lead to a scarcity of food and later departure from wintering areas and/or stopover sites. The impact of these changes will depend on the relative degree of advancement in arrival times and breeding phenology (also

linked to climate, see 3.1), if arrival times are advancing at a slower rate, then breeding success may be reduced (Visser & Both 2005).

The quality and availability of foraging areas varies through space and time making synchronisation between the migration routes and food peaks a critical component of migratory journeys. The spring migration of many geese and other herbivorous waterfowl to their northern breeding sites follows a 'green-wave' as individuals track a climatic gradient and take advantage of the spring growth of plants at each stopover site (van der Graff *et al.* 2006; Kölzsch *et al.* 2014). If changes in spring phenology occur at different rates along this wave, then the synchronisation of migration with food availability *en route* could be greatly impacted (van der Jeugd *et al.* 2009). Currently, little is known about the population level impacts of such mismatches, although changes in plant phenology are known to have affected the breeding of at least some migratory populations of Arctic mammalian herbivores (Post & Forchhammer 2008).

Other species may rely on conditions at only a handful of locations *en route*. Recent tracking studies of swifts *Apus apus* have revealed their dependence on a restricted stopover area in western Africa, where foraging conditions are thought to be particularly profitable, on their northwards journeys (Åkesson *et al.* 2012; Appleton 2012). Synchronisation of timing of arrival at this area and peak prey emergence may therefore be a crucial component of the migratory journeys of many British and European breeding swifts. Shifts in the synchronisation of conditions along migratory routes and on breeding have also been observed. Late migrating northerly populations of European pied flycatchers *Ficedula hypoleuca* have not advanced their breeding date, but conditions during their migration have changed considerably during the last decades leading to earlier arrival in Fennoscandia (Hüppop & Hüppop 2003; Ahola *et al.* 2004; Jonzén *et al.* 2006). These populations now arrive under colder conditions than in the past, which may entail increased mortality costs, especially for early arrivals (Møller 1994; Brown & Brown 2000).

Thus, it is **Very Likely** that changes in the timing or cues used for migration have the potential to severely disrupt the migratory journey and reduce the number of individuals that are able to complete it successfully. Such cues are likely to be particularly important for the (spring) journey to the breeding grounds, for two reasons: (i) it is usually completed in a much shorter time interval, so the 'margin for error' is less and (ii) impacts on mortality have less scope to be compensated for by density-dependent processes, as probably happens on the wintering grounds following the southward autumn migration.

Evidence for changes in departure dates (implying a shift in the length of the breeding season) is more mixed (**About as Likely as Not**), with delays only occurring in some species, particularly the shorter-distance migrants (Bairlein & Winkel 2001; Jenni & Kéry 2003; Sparks & Mason 2004; Sparks *et al.* 2007; Lehikoinen & Jaatinen 2012). This may partly reflect the fact that the southward autumn migration is undertaken with much less time pressure so journey times tend to be longer and the higher level of variability between individuals in when they commence autumn migration (probably related to the timing of when they finish breeding or moulting e.g. juveniles and adults). Generally we might predict advances in timing of breeding would lead to earlier departure dates from breeding grounds, however flexibility and variation in the number of breeding and re-nesting attempts and the duration of post-breeding moult may mean this is not universally the case (Morrison *et al.* 2015).

2.5 Weather conditions en route

The speed, direction and altitude of migration can be influenced by the climatic conditions *en route* and there is increasing evidence that birds time their departure, from breeding and non-breeding sites to utilise favourable conditions (e.g. Shamoun-Baranes *et al.* 2006). During migration, tailwinds greatly reduce the cost of migratory flight and thus the rate at which body stores are metabolised (Newton 2008). Consequently, in the UK, peak southward migrations by birds tend to occur with cool northerly tailwinds, while peak

northwards migration tends to occur with light winds near the centre of a high (Richardson 1990). Similarly, migratory species of butterflies and moths exploit the prevailing winds, commonly travelling along 'wind highways' and taking advantage of favourable winds at high elevations (Chapman *et al.* 2008, 2010; Stefanescu *et al.* 2012). Winds greatly assist in the crossing of migratory barriers, such as seas or deserts, and migrants making long sea crossings tend to set off in more favourable conditions than those carrying out shorter journeys over land (Bairlein 2008). Migrants (both birds and insects) can adapt their behaviour to changes in wind speed and direction by departing at a time when, and flying at an altitude where, the winds are favourable and changing their flight headings to compensate for drift (Gill *et al.* 2014; Chapman *et al.* 2015). Birds therefore might be able to compensate for small changes in the strength, direction and timing of prevailing winds during migration (McLaren *et al.* 2012). While greater changes in wind-tracks are **Likely** to increase energy demand, or deliver individuals to the wrong locations or at the wrong time (Liechti 2006), we currently have **Limited Evidence** of population impacts, although Drake *et al.* (2014) demonstrate that wind conditions during spring migration are the best predictor of apparent annual adult survival, male arrival date, female clutch initiation date and, *via* these timing effects, annual productivity in North American yellow warblers *Setophaga petechia*. There is also **Some Evidence** that the frequency of storms in the Caribbean region is related to variation in population numbers of passerines breeding in eastern North America (Butler *et al.* 2000).

Over the past 40 years, the frequency and speed of tailwinds over central Europe has increased. A number of studies have highlighted correlations between timing of arrival on breeding grounds and the North Atlantic Oscillation (NAO) (Forchhammer *et al.* 2002). The NAO is a measure of atmospheric circulation across Europe (specifically, it is the difference in atmospheric pressure between the Icelandic Low and Azores High pressure systems). In years when the NAO is positive, westerlies tend to be more frequent leading to cool summers and mild and wet winters in Britain. In contrast, if the index is low, westerlies are suppressed and winters tend to be colder. Thus, a possible mechanism underlying correlations between arrival and the NAO are the favourable wind conditions associated with higher NAO years which allow species to carry out faster migratory journeys arriving at breeding grounds earlier (Gordo 2007). During positive NAO years, storms track further south toward the Mediterranean Sea, bringing increased storm activity and rainfall to southern Europe and North Africa. Many African migrants cross the Mediterranean region directly after crossing the Sahara, meaning their fuel reserves may already be depleted. Deterioration in conditions in the Mediterranean basin may therefore have a disproportional impact on migrants and increase the importance of the Mediterranean fringe of North Africa as a potential stopover area.

Changes in the frequency and strength of storms are may be of particularly relevance to migrating raptors, which are mainly restricted to soaring flight during migration. Many raptors migrate along geographical bottlenecks (e.g. Strait of Gibraltar) taking advantage of atmospheric updrafts (Newton 2008). Consequently, large numbers of individuals travel along similar routes, increasing the populations' vulnerability to changes in wind and dust storms in a few key areas, e.g. Saharan borders (Goudie & Middleton 2006; Strandberg *et al.* 2010). Migrating raptors are **Likely** to be most badly affected by wind farms (developed at least in part as climate change mitigation measures), especially where these are situated along key migration routes (e.g. de Lucas *et al.* 2012); migratory bats are also **Likely** to be at risk (Kunz *et al.* 2007; Sherwin *et al.* 2013).

2.6 Climatically induced habitat change

The distribution of biomes and habitats follow climate patterns closely (e.g. Huntley 1991). Consequently, species ranges also follow climatic patterns, and when these patterns alter, species distributions have been shown to alter too (e.g. Parmesan 1996; Root 1998; Huntley *et al.* 2007; Doswald *et al.* 2009; Pateman 2013; Gillings *et al.* 2015). It is **Virtually Certain** that shifts in climatic conditions have had an impact on both the availability and quality of

migrants' habitat across their breeding and non-breeding grounds (Figure 1). Of the bird species listed in the Appendices (I and II) of the CMS, 84% rely on habitats particularly vulnerable to climate change (coastal, wetland, montane or tundra) at some point in their life cycle and many species use more than one habitat (Robinson *et al.* 2009). The most common threat faced is changes in water regime, reflecting the importance of wetland sites to migratory birds, but climate-induced changes in prey resources are also likely to be a key threat. For many insects, including migratory ones, climate change will remove, or relocate barriers that limit current distributions, resulting in range shifts or spread (Robinet & Roques 2010).

Degradation of stopover sites may cause increased competition for resources, resulting in longer stopover periods or departure of individuals with lower fat reserves, reducing the distance they can safely travel before the next stop (Newton 2004; Wilson & Cresswell 2006). This may restrict the ability of long-distance migrants to advance arrival dates in order to respond to changes on the breeding grounds (Both *et al.* 2010). Impacts are likely to be greatest where stopover habitat is discrete and limited in extent. For example, estuarine habitats where threats due to climate change (sea-level rise) will exacerbate already intense pressure from land claims, resource management and infrastructure development (e.g. Kennish 2002; Barter 2003; Swart & van Andel 2008). Of course, climate change may also have positive effects, since warmer winters can lead to higher over-winter survival (Clark 2004), and it is **Likely** that this is affecting (probably positively) migration phenology, particularly of short-distance migrants where the greatest changes have been seen (Kullberg *et al.* 2015).

One projected consequence of climate change is increased desertification at mid to low latitudes adjacent to existing deserts (IPCC 2007). Such areas can be critically important for migratory birds, refuelling and resting both before and after the crossing. For many of the UK's Afro-Palaearctic migrants, the Sahel region of Africa provides vital resources before undertaking their journey across the Sahara Desert. In recent years, however, lower rainfall, coupled with over-grazing, has increased the rate of desertification in this region and breeding numbers of trans-Saharan migrants, such as whitethroats *Sylvia communis*, are significantly lower in drier years as a result of decreased survival (Winstanley *et al.* 1974; Zwarts *et al.* 2009). Furthermore, there is evidence to suggest that whitethroats are starting their spring migration across the Sahara from more southerly departure points than 30 years ago as a result of drought and habitat degradation, increasing the challenge posed by the desert crossing (Ottonson *et al.* 2002). As deserts already pose significant barriers to migrants, further increases in their extent are **Likely** to increase the costs of migration even more.

For migratory butterflies, stopover sites may be used by individuals making a single journey, or by populations where the migration is multi-generational. In the former case, use of stopover sites is related to individual condition (McCord & Davis 2012), but the population consequences of this (if any) are unknown. For the latter, deterioration of conditions on stopover sites could have population level impacts as a result of reduced productivity, but this does not seem to have been demonstrated yet. The available evidence suggests that bats do not undertake long continuous movements; rather that the journey is interrupted at frequent intervals at 'stopover' points (Fleming & Eby 2003). Thus the maintenance of suitable migration corridors, which include adequate stopover points, is **As Likely As Not** to be a more important conservation requirement for migrating bats than for birds.

2.7 Impacts on prey availability

As with resident species, migratory species are **Very Likely** to be affected by changes in prey availability. Because of their dependence on wetland habitats (which often yield a marked seasonal peak in resource abundance), migratory birds are **Very Likely** to be disproportionately affected by predicted trends for reduced precipitation and lowered water tables, both on the breeding grounds (Smart & Gill 2003; Pearce-Higgins *et al.* 2010;

Rhymer *et al.* 2010) and on the non-breeding grounds (Peach *et al.* 1991; Szep 1995; Robinson *et al.* 2008). For example, reduced rainfall is thought to have led to declines in the garden tiger moth *Arctia caja* (Conrad *et al.* 2002), which are a key prey resource for the migratory cuckoo *Cuculus canorus* and may have contributed to its decline. In peatlands, desiccation has been associated with lowered abundance of Diptera (Carroll *et al.* 2011), an important component of the diet of many migrants (Pearce-Higgins *et al.* 2010). While warmer temperatures will contribute to lowered water tables through greater evapotranspiration they may also increase prey abundance through higher overwinter survival and extended growing seasons (Bale *et al.* 2002).

A much stronger effect of temperature on prey resources used by birds (given that many species prey on ectothermic invertebrates) is on the phenology of prey abundance. In those species and habitats exhibiting a seasonal peak in prey abundance, there is a well-documented tendency for this peak to occur earlier, resulting in a need to breed earlier if the period of maximum prey availability is to be exploited (e.g. Crick & Sparks 1999; Thackeray *et al.* 2011), though this does not appear to apply in all habitats (Halupka *et al.* 2008; Both *et al.* 2010). Migrant species are particularly constrained in this regard because of their need to arrive on the breeding grounds before the breeding can commence, and there is some evidence that populations that have adjusted their migratory arrival time have more positive population trends than those that have not (Møller *et al.* 2008). Changing spring temperatures may also be causing mismatches in timing of arrival on breeding grounds of interrelated populations. In some populations the synchronisation between the timing of spring arrival of, the migratory brood parasite, the common cuckoo, and its hosts is changing (Saino *et al.* 2009). In particular short-distance, but not long-distance, migratory hosts have advanced their arrival more than the cuckoo. This mismatch may be contributing to the decline of cuckoo populations in some areas, but an analysis of nest record data suggests this is not the case in Britain (Douglas *et al.* 2010).

2.8 Importance of carry-over effects

Current evidence suggests that high levels of mortality occur during migratory journeys (Silllett & Holmes 2002; Lok *et al.* 2015). However, it is **Likely** that the conditions experienced before and during migration can also have strong but non-lethal effects on an individual's success in the following season (Harrison *et al.* 2010). For example, red knot *Calidris canutus* on the west Atlantic flyway arriving with lower reserves on their northern breeding grounds have lowered breeding success and survival in subsequent seasons (Baker *et al.* 2004). Individuals that winter in poor quality habitats have also been shown to be in poorer body condition during the subsequent breeding season, and may thus have lower breeding success than those that wintered in higher quality habitats (Marra *et al.* 1998; Gunnarson *et al.* 2005; Inger *et al.* 2010; Alves *et al.* 2013). Consequently, changes in the climatic conditions experienced during the non-breeding season can influence population demography not just through increased mortality but also, indirectly, via reduced productivity (Ockendon *et al.* 2013; Finch *et al.* 2014). To date most of the studies exploring carry-over effects have taken place in avian systems, with the role of carry-over effects in the population dynamics of other migratory taxa remaining largely unexplored.

3. Maintaining an ecological network

The *Making space for nature* report (Lawton 2010) highlights the importance of increasing the connectivity of England's ecological network (in addition to making sites larger and improving habitat quality therein) for the conservation of its biodiversity stating:

'To maximise the capacity of our wildlife to cope with climate change we need to establish an ecological network that is as robust and resilient as possible to current conditions.'

Adaptation to climate change is likely to be achieved through altered patterns of land-use, requiring management across the entire network of sites used, to increase the population

sizes of threatened species, reduce the risks of local extinction, and provide colonists for new sites (Lawton *et al.* 2010). The changing distributions of migratory species within and around the UK will require a flexible approach to habitat management and the continued protection of, and designation of new, protected areas for these species. In this regard, conservation of migratory species will be similar to sedentary species, though wetland habitats (both coastal and inland) are disproportionately important to them. Migratory species are further constrained as this network needs to contain sites of sufficient quality that the rapid fuel deposition required for migration is possible. Appropriate habitat management may enable adaptation to the impacts of climatic changes, for example, management of woodland structure to maintain suitable microclimates for invertebrate prey could potentially increase food availability during the breeding season.

In addition, the required ecological network for migratory species will extend beyond the shores of the UK. For many species this is **Likely** to mean that the appropriate conservation measures will need to occur in non-breeding areas, where social development pressures can be intense (e.g. western Africa, Norris *et al.* 2010). Thus, international measures, for example the Afro-Eurasian Waterbird Agreement (AEWA) and the recently concluded African-Eurasian Migratory Landbirds Action Plan (AEMLAP, both daughter agreements of the CMS) will be required; fully implementing these existing measures is a key challenge (Davidson & Stroud 2006). In addition to suitable habitat at either end of their journey, migratory species require an ecologically coherent habitat network that they can use *en route*, the expanse and location of which may change for individual species between spring and autumn migration. The required degree of connectivity between areas will vary

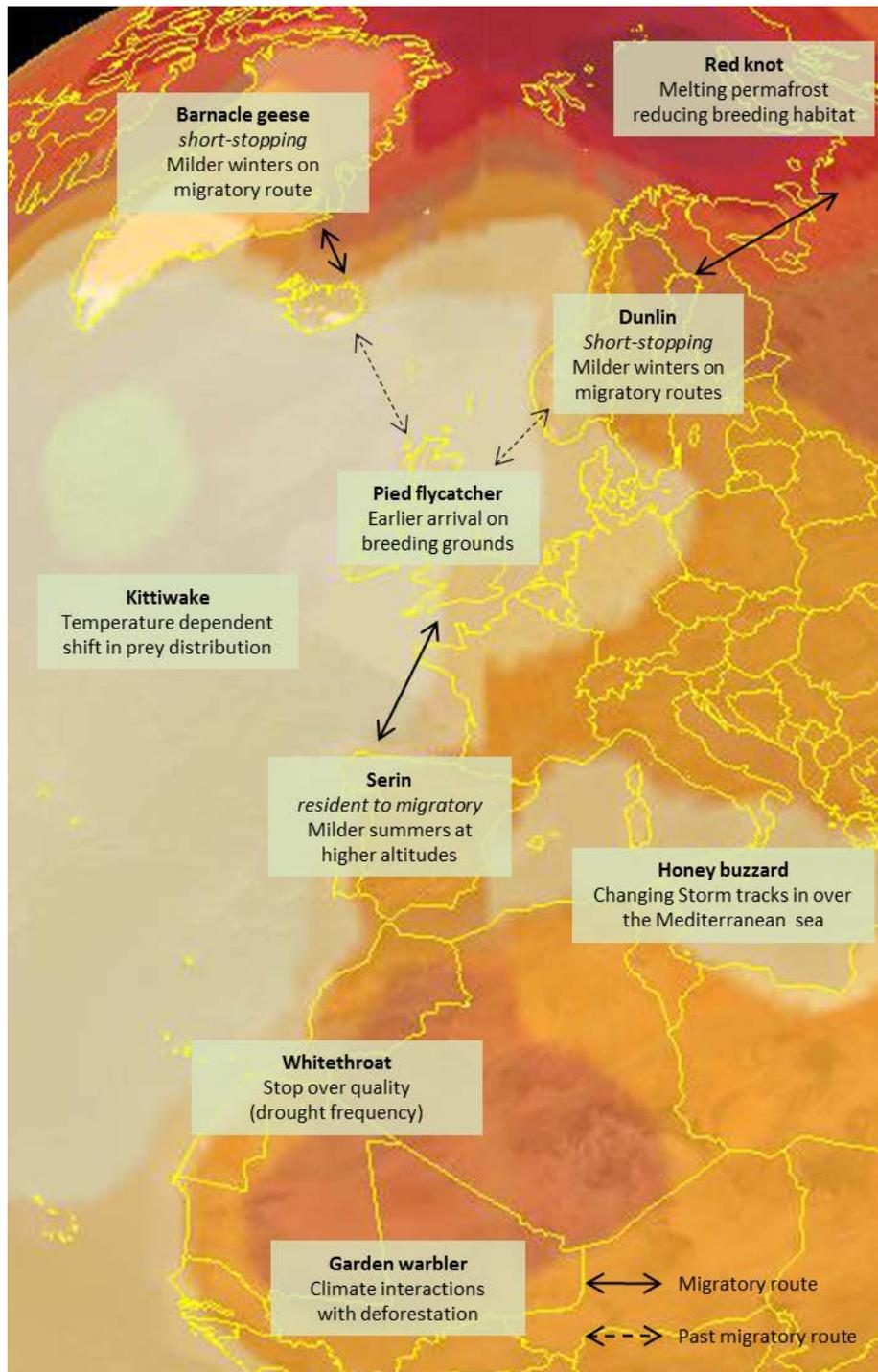


Figure 1: Examples of key impacts of climatic changes on migration patterns of British migratory birds (although serin is not currently a British breeding bird it is predicted that it could become so). The base map is IPCC temperature projections under a high emissions (A2) scenario for 2090 (Source: www.ipcc-data.org).

between species and will have important implications for the potential of populations to adapt to change conditions (Webster *et al.* 2002). The quality of these habitats is particularly important for

migrants that use a limited number of widely separated, and often highly productive stopover sites, such as migratory shorebirds (e.g. Baker *et al.* 2004). It may be, though, that conservation of migratory species does not require permanent land protection, but more dynamic strategies, such as seasonally targeted management measures may suffice (Bull *et al.* 2013).

4. How strong is the climate change signal for observed changes in migration patterns?

Disentangling the importance of changing climatic conditions from processes such as habitat destruction and management intensification on migratory species is a critical step in forming appropriate conservation strategies and requires a mechanistic understanding of population change (Travis 2003; Kleijn *et al.* 2010; Evans & Pearce-Higgins 2013). Many of the mechanisms underpinning the relationships between changes in the behaviour of migratory species and climatic conditions, however, remain unclear. Robinson *et al.* (2009) identified that 73% of all bird species highlighted as being affected by climate change are also under threat from other anthropogenic factors. Climate change impacts may thus be most evident in species which are already constrained by human patterns of land-use, for example, climate induced lowering of water tables in lowland wet grassland is a greater conservation threat because in England and Wales semi-natural grassland is estimated to have declined by 97% from 1934 – 1984 (UK BAP 2010).

4.1 Differentiating effects and impacts

Much of the literature on migration focuses on quantifying the *effects* of climate change on the behaviour or life-history of individuals. By contrast, few studies have quantified the *impacts* of climate change on population, *i.e.* the degree to which population status has changed as a result of climate-related effects. There are many well documented effects of climate change, including on migratory species (indeed these were some of the first to be observed), but the presence of individual-level effects does not necessarily mean climate change will have impacts at the population level (Reed *et al.* 2013). Quantifying population level impacts is difficult; the best evidence comes from long-term demographic studies (Both *et al.* 2006; Nevoux *et al.* 2008; Pearce-Higgins *et al.* 2009). Demographic data will be required from a broader range of species if the relative impact of climate, habitat and other changes are to be disentangled (Baillie 2001; Mustin *et al.* 2007). Indeed, in most cases, changes may not be attributable to a single cause. For example, in Northern lapwings *Vanellus vanellus*, although the proximate driver of a 50% decline in population in Britain was a series of cold winters reducing juvenile survival, a long-term decline in nesting success on the breeding grounds meant the population was unable to recover and the reduced population size persisted (Robinson *et al.* 2014). It is also possible that the observed changes in migratory patterns are driven by non-climatic factors. For example, the increasing frequency of over-wintering blackcaps in the UK could be driven by milder winter climates in the late 90's and early 2000's increasing survival and/or higher provisioning through increases in garden bird feeders (Cannon *et al.* 2005), augmented by assortative mating (Bearhop *et al.* 2005).

4.2 How confident are we of climate change impacts on migration

Effects of climate change on migration have been widely documented, thus there is **Robust Evidence**, with **High Agreement**, to support the broad statement that climate change is having an effect on migration and migratory species. Most of these effects (and the best documented ones) relate to the timing and extent of migration, though see Knudsen *et al.* (2011) for a critical review. These effects differ between insects and birds: the frequency and degree of movement in insects is increasing, while for birds it is tending to decrease. It is **Likely**, with **Moderate Agreement**, that these effects (on their own) are generally positive in the UK, though this has been more clearly demonstrated for insects. Amongst birds, it is **Likely** that an ability to adjust the migratory schedule is related to population status; those

showing the greatest adjustment might be least likely to be declining. As a consequence, long-term monitoring of such patterns may provide a useful indicator of climate change effects (Newson *et al.* 2009).

Effects on the abundance and timing of prey availability have also been demonstrated (Both *et al.* 2006; Visser *et al.* 2006) for some species. In general, increasing temperatures have mostly influenced timing of peak prey abundance, while less precipitation and lowered water tables have reduced availability of prey (especially of soil-dwelling invertebrates). It is **Very Likely** that timing mismatches will affect some populations reliant on highly seasonal prey resources, but there is **Limited Evidence** concerning how widespread these effects will be; more knowledge is required on seasonal resource use and availability throughout the migratory cycle for most species. It is **Very Likely** that impacts of reduced water availability will be widespread, particularly in the seasonally productive wetland habitats preferentially exploited by migrants, but probably also elsewhere. Temperature mediated habitat changes are **Likely** to be having an impact on the breeding ranges of Arctic breeding migrants, some populations of which pass through or winter in the UK, (Lindström & Agrell 1999). It is unknown to what extent birds will adapt to these changes, or whether long-distance and short-distance migrants will differ in this regard.

Effects on the migratory journey itself are less well-documented, perhaps because they are harder to study. Migration is greatly facilitated by wind patterns. These are **Likely** to change, but there is **Limited Evidence** that this will have an impact on the probability of successful migration. Extremes of weather are predicted to occur more frequently, and while more storms (at least during the migratory period) may have an effect on migratory numbers it is **Unlikely** that this will have a major population impact.

Whilst it is **Virtually Certain** that climate changes are having some impact on some populations it is unclear whether more of these will be positive or negative in terms of population status. Climate change is only one factor impacting on populations, and although climate effects have been related to changes (both positive and negative) in population status in some species, it is often hard to exclude the effects of other concurrent changes in land-use, habitat management and water quality, for example. There is **Limited Evidence** on whether climate change is having greater impacts on the breeding or non-breeding grounds; it is **Very Likely** that effects in these areas will interact (so called 'carry-over' effects), but it is currently unclear to what extent these will have a population-level impact. Throughout, we have drawn largely on avian examples; this is partly because birds represent a greater portion of our migratory fauna (in terms of number of species), but also because the current state of knowledge is greater. Climate change impacts on insects and, especially, bats are poorly studied.

4.3 Are the changes likely to be led by UK or global climate changes?

In general, the climatic processes driving changes in migratory patterns are **Likely** to be operating over regional and global scales e.g. impacts of NAO on arrival date. However, interactions with local-scale processes such as habitat change will also be important in determining the impact of climate change on migratory species. For migrants, the interactions between local and regional processes can occur at multiple locations during their annual cycle. Recent analyses indicate that it is **As Likely as Not** that changes in breeding season habitat are at least partly responsible for declines seen among Afro-Palaearctic migrants (Morrison *et al.* 2013). It is **Unlikely** that these habitat changes are driven primarily by climate change, but it **Likely** that they will interact with changes in phenology by reducing network resilience.

5. Priorities for future research

Knowledge of the likely impacts of climate change varies greatly between taxonomic groups: there is much knowledge, and some degree of confidence about the effects and impacts on bird populations, less so for other groups (Robinson *et al.* 2009; Knudsen *et al.* 2011;

Sherwin *et al.* 2013; Chapman *et al.* 2015). Many of the impacts of a changing climate will apply to species irrespective of their migratory status, thus consideration of migratory species cannot be done in isolation from non-migratory taxa, however, migratory species face additional constraints relating to the length of the migratory journey and conditions *en route*, particularly the location and quality of stopover areas, where sufficient food must be available for the next leg of the journey. We identify below some key areas for future research, these focus largely on migratory birds and bats, where the greatest conservation issues are perceived. In contrast, migratory insects, tend to be generalist (or even pest) species with increasing ranges; research priorities on the impact of climate change in these taxa are more focussed on sedentary habitat specialists (Warren & Bourn 2011; Wilson & Maclean 2011).

1 - Quantifying resource requirements throughout the migratory cycle

There is a pressing need to understand the resource requirements of many migratory species throughout their life-cycle, and especially on stop-over/fuelling sites and whether these are vulnerable to climate change, which may be most likely for species migrating here from Africa. Among bats even qualitative knowledge about the resources, let alone quantitative information, may be lacking (Krüger *et al.* 2014). It is presumed that most mortality for migrant species occurs during migration, however, quantifying the extent and exact timing of mortality has not been demonstrated for most migratory species and so the drivers remain unclear. For example, do conditions operating *en route* lead directly to mortality, or do lowered resource levels on the wintering grounds or stopover sites lead to birds departing in poor condition (or failing to depart at all) indirectly driving mortality?

2 - Understanding migratory connectivity

Although the broad pattern of migratory routes is reasonably well established for most species (at least among birds), the areas used in the non-breeding seasons by specific breeding populations is often poorly defined. Are individuals and populations faithful to particular areas or routes, or is there a large degree of mixing and movement? Such knowledge is necessary if conservation action in the non-breeding season is to be targeted effectively and also to help determine where ecological drivers of change are operating.

3 - Improving our knowledge of bat migration

Although only one species of bat is known to have a migratory population involving Britain, many others are (sometimes long-distance) migrants in continental Europe; our knowledge of bat movements is poor, so other species may also migrate to (or from) Britain. Work is currently being undertaken on Serotine *Eptesicus serotinus*, which is the main reservoir host for the viral bat rabies pathogen EBLV1, to better understand its ecology and movements in this regard, but there remains a pressing need to better understand movements of British bats and whether the distance or frequency of these movements is changing. This will require a stronger level of information exchange on species movement across Europe.

4 - Improving the predictive power of climate impact models

Models of the impact of climate change have largely focussed on the observed pattern of increasing temperatures and the resultant bioclimatic shifts in distribution and although some have incorporated relevant life-history traits, very few have considered the underlying demographic drivers (Eglington *et al.* 2015). Accurately predicting the precise impacts of climate change on any given species is likely to be unfeasible, except in general terms. Rather, such models should be used to help plan effective conservation strategies in the light of expected changes, considering both direct climate change effects and indirect effects via climatically driven land use change. Doing this successfully for migrants will be particularly challenging.

5 - Understanding carry-over effects

The degree to which effects carry over between seasons is currently poorly understood. For birds, changes in the timing of breeding can have consequences for the timing of moult, and hence migration and individuals that experience poor conditions in winter may start the breeding period at a disadvantage, and have lowered reproductive potential. These effects are beginning to be shown to be important and are likely to provide some of the mechanisms by which changing climatic conditions will impact on population size. Understanding the role of density dependence will be necessary to fully predict the impact of changing climates, particularly where individuals from different breeding populations mix and consume shared resources (Sutherland & Dolman 1994).

6 – Understanding the role of migrants in disease transmission

Numerous pathogens of migratory birds and bats exist, and are expected to increase their geographic range as a result of climate change (Fuller *et al.* 2012; Wood *et al.* 2012). For example, within Europe there is preliminary evidence that the movements of migratory ducks are reduced in harsher winters increasing the probability of transmission of H5N1 (Keller *et al.* 2009; Reperant *et al.* 2010); widespread evidence of such processes is, however, currently relatively weak. The increase in prevalence of diseases which can cross over into humans, such as West Nile Virus may be of particular concern, and outbreaks in areas that act as key stopover areas for species migrating to or through the UK could increase the likelihood of their transmission (Bessell *et al.* 2014). Ultimately however, the influence of climate change on the role of birds in spreading such diseases will depend on changes in the distribution of the disease prevalence relative to migratory routes and the suitability of conditions within the UK (e.g. vector activity) (Bessell *et al.* 2014). More studies are needed to understand how climate change will influence such ecological processes and their interaction with pathogen dynamics in migratory species (Altizer *et al.* 2011).

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