Understanding declines in the population size of migratory birds

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Declaration

I declare that the work in this thesis is my own and has not been submitted elsewhere for the award of any other degree.

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Abstract

The common sandpiper is an Afro-Palearctic migrant that is declining across Europe. Studies have suggested that environmental conditions during winter are likely to be important determinants of their population trends, but these trends differ between breeding regions suggesting that wintering conditions are not the only important factor. We investigated the factors affecting common sandpipers during each of their lifecycle stages to obtain a complete overview of the factors affecting their status. During the breeding season, we found that disturbance appears to have an important effect on the probability of a nest hatching successfully. Further, we found that heavy rainfall in the week after hatching reduced the probability of chicks fledging, presumably through the influence of poor weather on thermoregulation and foraging. Common sandpipers are known to be associated with areas of high water quality. In winter, common sandpipers were more likely to be found in areas of low salinity and high pH, and had higher foraging success in these areas, suggesting that water chemistry might be an important influence on their habitat selection. Further, we showed that common sandpipers are territorial in winter, which has previously only been suggested based on anecdotal evidence. Studies of many other species have shown that the conditions during migration are likely to be a key driver of population trends. We investigated the migration of individuals across multiple populations using geolocators, tagging common sandpipers in England and Senegal, and combining these data with published data from individuals tagged in Scotland. We revealed that there is a large amount of overlap in the non-breeding distributions of individuals from these populations. Also, we showed that birds appear to use wind to facilitate their migration in autumn, but actively fly against prevailing conditions in spring. Finally, we investigated changes in the timing of wading bird migration at a flyway scale using the eBird citizen science dataset. We showed that, contrary to the findings of many studies, the timing of migration seems to be becoming later at a flyway scale and suggest range shifts as the primary driver. Understanding the influence of conditions at each lifecycle stage is paramount for determining the drivers of declining migratory bird populations. Further, investigating the mechanisms driving population trends in individual species will help us to understand the patterns we see at larger spatial scales.

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Chapter 1 Introduction

Migratory bird species are good indicators of environmental health and provide valuable ecosystem services, but many have suffered significant population declines in recent decades (Wilcove & Wikelski 2008, Vickery *et al.* 2014, Kleyheeg *et al.* 2019, Rosenberg *et al.* 2019). These declines are often linked to climate change and various forms of habitat loss, but there is a lot of recent research trying to understand these complex relationships more clearly (Wilcove & Wikelski 2008, Vickery *et al.* 2014). Migratory birds are particularly susceptible to the effects of climate change as they rely on multiple distinct sites throughout their lifecycle. Changes in the conditions at one lifecycle stage might not be mirrored across all stages, either because of differing rates of temperature change or because of varying levels of anthropogenic disturbance (Wilcove & Wikelski 2008, Vickery *et al.* 2014, Van Gils *et al.* 2016, Patchett *et al.* 2018). Therefore, understanding the reasons for their declines is extremely difficult because they are likely to be dependent on factors operating across large spatial and temporal scales (Norris *et al.* 2004). Indeed, the influence of conditions at one stage is likely to depend on the conditions experienced at other lifecycle stages (Piersma 2002, Newton 2006, Senner *et al.* 2015). More work is urgently needed to understand these processes if future conservation measures are to be successful (Vickery *et al.* 2014).

Reasons for declines in migratory birds

Climate change and phenology

One of the biggest threats to migratory bird populations is human-induced climate change. Evidence suggests that wildlife populations have already undergone important changes because of warming climates, and these are likely to continue as greenhouse gas emissions increase (Parmesan & Yohe 2003). For example, temperature changes might cause significant range contractions for some species and has already changed the timing of migration in many (Parmesan & Yohe 2003, Huntley *et al.* 2008, Vickery *et al.* 2014, Mayor *et al.* 2017). Warming global temperatures have advanced the start of spring across the globe, as measured by bud burst, greening and insect emergence, and many bird species have advanced the onset of migration and breeding as a result (Both *et al.* 2004, Gordo 2007). For many migratory species, advances have not occurred at the same rate as those seen in plant or insect phenology, creating mismatches between the chick-rearing period and the time of maximum food availability (Parmesan & Yohe 2003, Root *et al.* 2003, Saino *et al.* 2011, Mayor *et al.* 2017). Migrant species may also be constrained because arrival dates sometimes depend on endogenous rhythms rather than temperature cues. This means that in some cases, egg-laying advances due to temperature have not been matched by arrival date, preventing further advances (Gwinner 1996, Both & Visser 2001). In areas where food peaks have advanced most rapidly, constraints have caused significant population declines (Both *et al.* 2006); this is especially true in highly seasonal habitats (Both *et al.* 2009).

While there have been long-term changes in the arrival dates of many migratory species, some also show phenotypic plasticity. This is important considering that climate change is likely to make weather less predictable, and arrival at the wrong time can prove extremely costly (Møller 1994, Cohen *et al.* 2014). Early arrival when conditions are favourable can advance the onset of breeding and provide more time for its completion, increase the likelihood of second broods for multi-brooded species, provide access to better quality mates and increase recruitment into the population (Cowley 2001, Parmesan & Yohe 2003, Balbontín *et al.* 2007, Morrison *et al.* 2019). However, early arrival to the breeding grounds can also mean encountering adverse weather conditions, which can kill large numbers of individuals (Møller 1994, Newton 2006). Correlations between weather conditions on the wintering grounds and breeding grounds could provide cues for migrating birds (Saino & Ambrosini 2008), and the conditions experienced during migration are likely to mediate migration speed by increasing or reducing foraging efficiency (Rubolini *et al.* 2007, Balbontín *et al.* 2009). Understanding the relationship between arrival dates, survival and reproductive success of migratory species, and how this relationship is affected by changes in the predictability of weather, will be important for determining the true impacts of climate change.

Pressures during breeding

Vickery *et al.* (2014) suggested that the degradation of breeding habitats was one of the most important factors affecting migratory birds. This degradation is likely to be primarily due to agricultural intensification, which includes the homogenisation of habitats, increasing fertiliser and pesticide use, and changing grazing and cutting schedules (Wilson *et al.* 2005, Vickery *et al.* 2014). Habitat mosaics, a combination of agricultural land and other habitat types, can be beneficial or negatively affect individuals depending on the species. For some species, these mosaics are important as individuals require distinct areas for nesting and foraging; maintaining a patchwork of different habitat types in the right configuration is therefore likely to be important for conservation. This means that even the abandonment of agricultural regions in favour of more ‘natural’ habitats could result in declines in the population size of certain species (Vickery *et al.* 2014). However, birds nesting in habitat mosaics can also suffer from higher predation rates because of the greater predator densities associated with anthropogenic landscapes (Angelstam 1986, Paton 1994, Saracco & Collazo 1999; but see Fahrig 2017). Furthermore, agricultural intensification results in increased pesticide use and decreased marginal habitat that is key for many invertebrate species; if managed effectively, habitat margins have the potential to ensure year-round food availability for birds (Wilson *et al.* 1999, Wilson *et al.* 2005, Vickery *et al.* 2009).

Despite the breeding season being the most well-studied lifecycle stage for most, if not all, avian migrants (Vickery *et al.* 2014), there is still a lot more to understand regarding intra-specific variation in the factors affecting reproductive success. For example, for many species there is likely to be significant mortality in the post-fledging stage, but the causes of this are currently under-studied (Cox *et al.* 2014). It is increasingly apparent that there is substantial variation in life-history traits between species, populations of the same species and individuals within the same population (Chevallier *et al.* 2011, Morrison *et al.* 2013, Hewson *et al.* 2016, Morrison *et al.* 2016). Conservation measures are likely to be most easily implemented on European breeding grounds. Therefore, it is vital to understand the relative importance of breeding ground conditions on the population trends of migratory species compared to conditions in the non-breeding season. For example, a study on Willow Warblers (*Phylloscopus trochilus*) found that improving breeding productivity rather than overwinter survival was most important for reversing population declines and is where conservation schemes should be focussed (Morrison *et al.* 2016).

Pressures during migration

Relatively little is known about the factors that affect birds during migration, despite the fact that migration is the stage during which most mortality is likely to occur (Sillett & Holmes 2002, Klaassen *et al.* 2014, Lok *et al.* 2015, Loonstra *et al.* 2019). The miniaturisation of GPS trackers and geolocators has meant behavioural studies are becoming more feasible, even for the smallest passerines (see below; DeLuca *et al.* 2015). This is necessary considering the growing evidence that there is considerable intra-specific and interspecific variation in migratory strategies and that these can impact population trends (Balbontín *et al.* 2009, Mckinnon *et al.* 2013, Hewson *et al.* 2016, Hou & Welch 2016).

The large number of developing countries crossed during migration is likely to pose particular problems for migrating birds. These countries may not have the same protected area coverage as in more developed countries (Runge *et al.* 2014) and, therefore, birds may be more at risk from agricultural intensification, hunting and land reclamation through the draining of important wetlands (Zwarts & Van Horssen 2009). For example, declines in some migratory waders have been linked to degradation of important stopover areas due to agricultural intensification, urbanisation and land reclamation (Murray *et al.* 2014). Of particular relevance to Afro-Palearctic migrants is the fact that northern Africa is an important stopover site for many species but has exceptionally low protected area coverage (Runge *et al.* 2015). This is also problematic because of the large potential hunting pressure in the region (Mcculloch *et al.* 1992). However, even in developed countries, species of conservation concern suffer from hunting, indicating that a species receiving protected status is not always enough to completely eliminate its impact (Mcculloch *et al.* 1992, Barbosa 2001, Hirschfeld *et al.* 2019, Jiguet *et al.* 2019). Overall, we know relatively little about the non-breeding ecology of many species, meaning that we are unlikely to understand the true effects of the overexploitation of resources or land use change without further research (Baker *et al.* 2004, Burton *et al.* 2006).

Migratory timing and moult schedules are probably governed by seasonal peaks in food availability (Baker *et al.* 2004, Barta *et al.* 2008, Bairlein 2016, Thorup *et al.* 2017, Pageau *et al.* 2020) and are likely to differ between spring and autumn migration (Conklin *et al.* 2013, Hewson *et al.* 2016, Prochazka *et al.* 2017). Individuals will shift their migratory timing in order to track temporal and geographic changes in their food supply and, as such, effective protected areas would need to be flexible between years to accommodate between-year variation (Karpanty *et al.* 2006). To do this, an in-depth understanding of species-specific migratory behaviours is necessary.

Pressures on the wintering grounds

Many of the recent declines experienced by Afro-Palearctic migrant populations have been linked to changes or environmental factors on the wintering grounds (Zwarts & Van Horssen 2009, Thaxter *et al.* 2010, Morrison *et al.* 2013), which is sub-Saharan Africa for most British and European species (Jones 1995, Wernham *et al.* 2002). Declines in British migrants have been linked to their bioclimatic wintering zone in Africa, with those in arid regions declining more than those in humid areas (Ockendon *et al.* 2012). Significant population crashes of many species in recent decades have been linked to droughts in the arid region of the Sahel, because they are dependent on the rains to flood waterways and increase insect abundance; droughts reduce overwinter survival rates and correlate with smaller breeding population sizes (Zwarts & Van Horssen 2009). Recently, however, average rainfall has increased but has not been mirrored by population trends, suggesting that other factors on the wintering grounds or elsewhere may be important (Giannini *et al.* 2008, Patchett *et al.* 2018). It is likely that a combination of landscape and climatic changes have been important (Thaxter *et al.* 2010, Ockendon *et al.* 2012, Vickery *et al.* 2014), but identifying the mechanisms causing population declines is difficult because of the lack of long-term studies investigating bird distributions relative to habitat changes in Africa.

Landscape changes due to damming, land reclamation, and deforestation for agriculture, wood fuel and livestock have been widespread and are likely to have had an impact on wintering migrant birds through habitat fragmentation and degradation (Burton *et al.* 2006, Murray *et al.* 2014, Vickery *et al.* 2014). The link between habitat degradation and population declines is likely to be complex (Wilson & Cresswell 2010), with at least some species being robust to change (Wilson & Cresswell 2006). Farmland birds like whinchats (*Saxicola rubetra*), for example, may benefit from anthropogenic agricultural change on the wintering grounds as it increases the amount of suitable habitat (Hulme & Cresswell 2012). The degree to which a species is affected by conditions in a given location is likely to depend on the way in which it uses that site (Vickery *et al.* 2014). Additionally, populations affected by habitat loss may incur significant and direct impacts on their survival even though other nearby sites appear initially suitable (Burton *et al.* 2006), as is likely with the reclamation of wetlands for rice farming, for example (Tourenq *et al.* 2001).

Migration theory

Winter

There are relatively few studies investigating the wintering ecology of migratory birds, but understanding these could provide valuable insights for conservation (Sorensen 2014, Vickery *et al.* 2014, Willemoes *et al.* 2018). Overwinter survival is thought to be the primary cause of decline for many species (Zwarts & Van Horssen 2009). However, it is sometimes difficult to evaluate the relative contributions of within-winter mortality and mortality during migration. In whinchats, one of the few species for which survival during migration has been estimated, return rates to the breeding grounds are lower than within-winter survival, at 52% and 98-99%, respectively, suggesting high importance of mortality during migration (Blackburn & Cresswell 2016c); similarly high within-winter survival rates have been found in Neotropical migrants (Holmes *et al.* 1989, Sillett & Holmes 2002). Indeed, recent studies have suggested that most mortality is likely to occur during migration, as expected considering the large associated energetic costs (Newton 2006, Lok *et al.* 2015, Xenophontos & Cresswell 2016, Loonstra *et al.* 2019, Robinson *et al.* 2020).

Although there are relatively few species-specific studies investigating fine-scale wintering settlement decisions, wintering site fidelity is thought to be common (Cramp *et al.* 1983, Cresswell 2014). Ringing studies in Africa during the European non-breeding season have reported high recurrence of individuals of some species in multiple years (Sauvage *et al.* 1998). Site fidelity during the non-breeding season is likely to improve survival due to familiarity with the environment (Robertson & Cooke 1999). Recent studies have shown that certain species are site faithful on a very fine scale (e.g. Blackburn & Cresswell 2016a) but others may return to wider regions or even not at all (Berthold *et al.* 2002). High fidelity does not necessarily mean individuals will return to only a single site during the entire non-breeding season, but might use different sites as the season progresses (Cresswell 2014). Furthermore, even if wintering ranges are large, there may be core sites that are consistently visited each year (Cresswell 2014, Meyburg *et al.* 2015). However, some studies suggest that individuals might return to the same site across years even if there are more suitable sites nearby, perhaps due to constraints imposed during their first migration (Lok *et al.* 2011). Understanding settlement decisions after a juvenile's first migration might therefore be crucial for understanding larger-scale demographic and phenological patterns (Thorup & Rabøl 2007, Lok *et al.* 2011, Cresswell 2014, Gill *et al.* 2019).

Site fidelity could be governed by food supply (Newton 2010); individuals returning to a wintering site know that it is likely to have sufficient food resources for survival. However, species dependent on highly seasonal habitats are unlikely to be site faithful as the location of their food source may vary between years (Berthold *et al.* 2002). Prior knowledge of a wintering site may also improve survival through predator avoidance. A study comparing migratory and resident Eurasian siskins (*Carduelis spinus*) in winter, showed that the former had a higher predation risk through reduced vigilance and less efficient foraging behaviour (Pascual *et al.* 2014). Although this compares resident and migratory populations, it is not impossible that an individual with multiple years' experience of a wintering site could have more efficient predator avoidance behaviours due to familiarity with the area.

Winter territoriality

Avian territoriality is a well-studied phenomenon on the breeding grounds, where territory quality is an important determinant of reproductive success (Van De Pol *et al.* 2006, Sergio *et al.* 2009). Territoriality in wintering birds is far less well studied. Whinchats for example, defend territories during the winter and will consistently return to the same or neighbouring territories in consecutive years (Blackburn & Cresswell 2016b). It has been hypothesised that territory quality in whinchats is dependent on the number of perches available to them, which are important for foraging and used in territory defence as song posts (Blackburn & Cresswell 2016c). However, wintering territory quality is not a limiting factor for whinchats (Blackburn & Cresswell 2016c), but may be for other species (Sherry & Holmes 1996). For most migrants, maintaining territories during winter is unlikely to be as important as during summer. This is because on the wintering grounds the energetic constraints on birds are likely to be lower than during summer as individuals are not reproducing and may have lower overall energy requirements (Piersma 2002, Wikelski *et al.* 2003). Indeed, it seems that there is intra-specific variation in the degree of territoriality for many species (Colwell 2000, Willemoes *et al.* 2018).

Migration routes and connectivity

Migration routes can have important implications for migratory species, especially as for some species there is intra-specific variation in the route chosen (Finch *et al.* 2014, Hewson *et al.* 2016, Van Bemmelen *et al.* 2019). For example, differences in survival between migration routes can lead to population-specific declines (Hewson *et al.* 2016). Furthermore, low diversity in migration routes at the population level, i.e. the majority of the population using similar stopover sites at the same time, can increase susceptibility to declines because a greater proportion of individuals are likely to be affected by any degraded habitat that they encounter (Runge *et al.* 2014). Migration bottlenecks can cause flyways to be abandoned due to climate change affecting habitat suitability, with numbers diverted towards other routes (Verkuil *et al.* 2012), and can result in significant population declines (Baker *et al.* 2004, Murray *et al.* 2014). This migratory connectivity also operates between breeding and wintering locations (Webster *et al.* 2002, Gilroy *et al.* 2016). This can be separated into ‘strong’ or ‘weak (diffuse)’ connectivity which is when a high or low proportion of a breeding population winter together (or vice versa), respectively (Webster *et al.* 2002, Finch *et al.* 2017). Weak migratory connectivity for a breeding population is likely to create a buffer from habitat degradation in any single wintering location (Finch *et al.* 2017, Patchett *et al.* 2018). Density-dependent population dynamics may operate across lifecycle stages and therefore it is important to quantify the amount of migratory connectivity to understand population trends (Taylor & Norris 2010).

Colour ringing, ring recoveries, stable isotope analyses and tracking devices show that, in general, migratory connectivity is low for breeding populations (Gunnarsson *et al.* 2004, Finch *et al.* 2017), but is species dependent (Johnson *et al.* 2016, Kolecek *et al.* 2016, Prochazka *et al.* 2017). However, in some species, it appears that individuals might migrate using the same routes and stopover sites, but disperse once on the wintering grounds (Van Bemmelen *et al.* 2015), in which case migratory connectivity between breeding and wintering could appear low but the species still be dependent on very specific regions. There is likely to be considerable intra-specific variation in migration routes and wintering destinations, and more tracking studies of individuals from different parts of a species' range are therefore needed (Hewson *et al.* 2016, Finch *et al.* 2017, Van Bemmelen *et al.* 2019).

Staging and stopover sites

Stopover sites are important determinants of population change, because of direct mortality due to poor conditions or a lack of suitable habitat, and because they can exacerbate or buffer conditions experienced at subsequent lifecycle stages through carry-over effects (Norris *et al.* 2004, Tøttrup *et al.* 2012, Morrison *et al.* 2013, Finch *et al.* 2014). In some species, conditions experienced at stopover sites appear to be more important than conditions on the wintering grounds (Robinson *et al.* 2003, Schaub *et al.* 2005, Finch *et al.* 2014) and can influence subsequent reproductive success (Newton 2006).

The way in which stopover sites are used is likely to differ between spring and autumn migration because of differing selection pressures (Mcnamara *et al.* 1998, Conklin *et al.* 2013, Nilsson *et al.* 2013). During spring migration there is high selection for early arrival at the breeding grounds, whereas in autumn, they are likely to select migration routes that minimise energetic costs (Mcnamara *et al.* 1998). Indeed, spring migration is generally shorter than in autumn, primarily driven by decreased stopover duration, rather than increased flight speed (Nilsson *et al.* 2013). This could be achieved in a number of ways including better stopover site foraging conditions, increased feeding intensity or a greater energy deposition before the start of migration (Nilsson *et al.* 2013). In some species, however, fuel deposition rate does not differ between autumn and spring migration, suggesting that something other than food intake at stopover sites causes faster spring migration (Eikenaar *et al.* 2015). Faster spring than autumn migration could be because individuals have more time to deposit sufficient energy stores during winter, unrestricted by the energy requirements of breeding, or that they are simply under more significant time constraints.

Carry-over effects

Carry-over effects, when factors at one migratory stage influence the same individual at later stages, can operate over different timescales. For example, it might be that early-life conditions create behaviours that persist throughout the rest of an individual's life (Harrison *et al.* 2011). As discussed above, for example, the settlement decisions of juveniles in winter after their first migration could determine their future wintering sites (Cresswell 2014, Gill *et al.* 2019). However, carry-over effects can also have shorter-term effects, such as through particularly bad weather conditions at one stage affecting an individual's ability to survive at a subsequent stage. Indeed, in this case the effects of the first stage might not persist if conditions at subsequent stages are favourable, these are also referred to as reversible-state effects (Senner *et al.* 2015). The effects of the interactions between conditions at different lifecycle stages have been found to impact both resident and migratory species, although they are probably more prominent in the latter considering the high energy expenditure required for migration (Newton 2006). Given that in many migratory species the majority of their lifecycle is spent outside the breeding grounds, it is highly likely that the conditions experienced there have a major influence on life-history traits (Alves *et al.* 2013a).

Carry-over effects have been widely documented for a range of species but their impacts show large amounts of variation (Harrison *et al.* 2011, Senner *et al.* 2014). Conditions at the wintering grounds can both advance and delay arrival to the breeding grounds for example, the exact effects varying between species and even between individuals within the same population (Marra *et al.* 1998, Balbontín *et al.* 2009, Norman & Peach 2013). Energetics models have found that individuals wintering in poor quality habitats are more susceptible to migratory costs, suffering delayed arrival to breeding grounds and reduced survival (Alves *et al.* 2013a). Declines in reproductive success as a result of poor wintering conditions could result from declines in body condition or through the knock-on effects of delayed arrival on the timing of breeding (Ebbinge & Spaans 1995, Cowley 2001, Townsend *et al.* 2013, Swift *et al.* 2020). Carry-over effects have also been shown to operate between breeding seasons, with individuals in favourable conditions in one year benefitting the next (Latta *et al.* 2016), or suffering because of increased reproductive outputs (Inger *et al.* 2010, Catry *et al.* 2013). However, for some species there are few permanent effects on individuals (Senner *et al.* 2014, Senner *et al.* 2015). For example, delayed autumn departure in the Hudsonian godwit (*Limosa haemastica*) was not correlated with arrival back to the breeding grounds the following year, meaning that individuals are able to 'recover' lost time, perhaps through favourable conditions during winter (Senner *et al.* 2014). Further work monitoring individuals year-round could reveal how weather conditions experienced during migration affects migration schedules.

Macroecological patterns

In order to understand the changes that are occurring to populations, we need to investigate the patterns occurring at larger spatial scales (Kelly & Horton 2016). While following individuals year-round is paramount for understanding the mechanisms driving change in migratory populations, it might fail to reveal macroecological patterns (Kelly & Horton 2016, Bauer *et al.* 2019). This is because no study will be able to follow every individual in a population or deal with the biases that come with using many of the available tracking technologies (Bridge *et al.* 2011). Therefore, recently there has been increased focus on the potential of citizen science and weather surveillance radar data to understand larger patterns (Sullivan *et al.* 2014, Bauer *et al.* 2019). The analysis of citizen science datasets has become increasingly useful in recent years, with studies revealing large-scale patterns in migratory behaviours in relation to geographic barriers, climate change and fine-scale weather patterns (La Sorte *et al.* 2014, La Sorte *et al.* 2015, Horton *et al.* 2019b, La Sorte *et al.* 2019). Furthermore, these data have been used to map large-scale species distributions and to understand changes in the total numbers of individuals migrating (Sullivan *et al.* 2014, Horton *et al.* 2019b). This macroecological view of migration is focussed on understanding changes occurring to all migratory individuals, which is likely to be important considering the ecosystem services that migratory species provide (Wilcove & Wikelski 2008, Bauer *et al.* 2019). Indeed, migratory species transfer nutrients across vast, geographically and ecologically distinct sites, and it is in their numbers that these benefits are provided (Wilcove & Wikelski 2008, Viana *et al.* 2016a).

Large-scale datasets from citizen science schemes and weather surveillance radar also have their biases (Johnston *et al.* 2019). While these biases can be partially addressed (Johnston *et al.* 2019, Johnston *et al.* 2020), they cannot reveal the same amount of detail as individual-based studies. Understanding the mechanistic drivers of patterns using these unstructured data is therefore difficult and means that future work needs to combine information from both large-scale datasets and those obtained from individuals. These new, large-scale datasets could be used in tandem with more traditional methods so that we can get an overarching view of the changes in migratory species.

Tracking individuals using light-level geolocators

Geolocators and GPS devices have revolutionised the way in which we are able to monitor the behaviour of migratory species throughout their lifecycles (Bridge *et al.* 2011). Some such devices now weigh less than a gram, which means that all but the very lightest birds can be tracked safely. Tracking studies have provided us with a wealth of knowledge regarding differences in migratory behaviour between species, populations and even individuals within the same population (Hewson *et al.* 2016). Further species-specific tracking studies are now necessary if we are to understand this diversity of migratory traits.

Light-level geolocator devices record light levels against an internal clock which are then used to determine geographic locations. From these light levels, day length and solar noon can be calculated, which provide daily estimates of latitude and longitude, respectively (Hill 1994, Lisovski *et al.* 2019). The battery for many models can last for most, if not all, of an individual's non-breeding season allowing year-round tracks and the timing of migratory behaviours. These can provide greater temporal resolution than other methods, such as GPS or satellite tags which can only give relatively few positions over the same length of total tracking time (Bridge *et al.* 2011).

There are several issues with geolocator data, however. Firstly, geolocators are archival and data are stored internally, meaning they must be retrieved for the data to be downloaded. The successful study of any animal is therefore highly dependent on site fidelity and the ability to recapture them (Bridge *et al.* 2011). This issue severely limits the potential applications of such devices, especially for studying species of conservation concern for which there may be high mortality during the non-breeding season. Geolocators are also relatively inaccurate (+/- 150km), especially during the spring and autumn equinoxes when night and day length are the same globally, and are therefore not suitable for studies intending to reveal fine-scale information about stopover and wintering locations (Rakhimberdiev *et al.* 2016). Accuracy is also dependent on the behaviour of the individual carrying the device, because of the analysis' reliance on determining sunrise and sunset times. For example, the legs of forest-dwelling species are likely to be shaded at dawn and dusk, thereby affecting the accuracy of location estimates (Bridge *et al.* 2011, Lisovski *et al.* 2012b). Further, the behaviours and habitat choice of individuals may change throughout the year, meaning that the associated biases are also likely to change (Bridge *et al.* 2011).

Negative effects of geolocator attachment

Recently, there have been an increasing number of studies investigating the consequences of geolocator attachment (Weiser *et al.* 2016, Brlik *et al.* 2019, Geen *et al.* 2019). In species where the geolocator is a high proportion of the carrier's body weight, survival and return rates are reduced (Costantini & Møller 2013, Weiser *et al.* 2016). For Arctic-breeding waders, return rates were more likely to be affected when the geolocator weighed 2.5-5.8% of their body mass than if they were 0.3-2.3% (Weiser *et al.* 2016). Certain groups may be more susceptible to the negative consequences of geolocator attachment; for example, it appears that aerial foraging species such as barn swallows (*Hirundo rustica*) and swifts (*Apus apus*) are more affected by geolocators than terrestrial feeders (Costantini & Møller 2013), likely because of the manoeuvrability required to catch insects mid-flight.

The preferred method of mounting geolocators varies between groups of species and each may have different consequences for individual survival and reproductive success. Studies in wind tunnels have found that back-mounted geolocators, such as those used on aerial feeders, significantly increase drag (Bowlin *et al.* 2010). The authors suggest that the effects of drag may be the primary reason for reduced return rates in certain species, rather than weight. Some back-mounted geolocator models have small stalks on which the light sensors are mounted, ensuring the sensor protrudes above the bird's feathers. Long-stalked geolocators further increase drag and cause reduced survival in some species (Scandolara *et al.* 2014).

For wading birds, leg mounted geolocators appear to have greater negative effects than back-mounted geolocators but are still commonly used (Clark *et al.* 2010, Costantini & Møller 2013). Leg-mounted geolocators can either be mounted on a ring or leg flag, perpendicular or parallel to the leg. In a review of the effects of carrying geolocators on wading bird species, perpendicularly mounted geolocators on flags had greater negative effects on nesting success than if mounted parallel, appearing to be caused by egg damage (Weiser *et al.* 2016). However, parallel mounted devices reduced return rates and were more likely to cause leg injuries. Importantly, these negative effects were only present for the very smallest wader species, but when present, were substantial (Weiser *et al.* 2016). Costs to nest success could potentially be mitigated by adding ring spacers to the leg in order to reduce rubbing against the eggs, and rounding the edges of leg flags and filing the contact points of the geolocators in order to prevent piercing egg shells (Clark *et al.* 2010, Niles *et al.* 2010). Negative effects on birds could also be reduced by only attaching geolocators to the heaviest individuals or by delaying attachment until after the adults finish incubation (Pakanen *et al.* 2015), but doing this could also create biases (Bridge *et al.* 2011).

Geolocators may also have non-lethal effects on reproductive success, as the added weight of geolocators can place extra physiological constraints on individuals during migration. For example, geolocator-tagged northern wheatears (*Oenanthe oenanthe*) have been shown to arrive from migration and start egg laying significantly later than control birds (Arlt *et al.* 2013). Geolocator attachment can also increase stress and reduce overall body condition as suggested by higher corticosterone levels and lower body weight for geolocator-tagged thick-billed murres (*Uria aalge*; Elliott *et al.* 2012). Similarly, some waders carrying tibia-mounted geolocators developed calluses on their tarsus, although had no reduction in overwinter survival (Weiser *et al.* 2016). In tree swallows (*Tachycineta bicolor*), however, there were apparently no short-term effects of geolocators on individuals, with feeding visits, nestling growth and nestling size the same between experimental and control birds, yet return rates of geolocator birds were significantly lower than untagged birds (Gómez *et al.* 2014). The potential effects of carrying a tracking device is therefore incredibly complex and highlights the need for the continuous monitoring of individuals when undertaking tracking studies.

Study species: the common sandpiper

The common sandpiper (*Actitis hypoleucos*) is an Afro-Palearctic migrant wader which is identified by brown upperparts, plain white underparts, its constant ‘bobbing’ up and down and distinctive flight with stiff, bowed wings and shallow flaps (Cramp *et al.* 1983, Holland 2018). It is considered sexually monomorphic although a recent study has found that females are larger than males (Meissner & Krupa 2016); wing lengths above 117mm indicate a female and wings of less than 111mm indicate males. However, there is a substantial amount of overlap and, even with the addition of other biometrics, using discriminant functions to sex common sandpipers will only correctly sex 77% of birds (Meissner & Krupa 2016).

Common sandpipers breed from Ireland to Siberia and from 40°N to 70°N, with individuals found at sea level to over 4000m (Cramp *et al.* 1983). All populations are thought to migrate, with western populations wintering in Africa and eastern populations in Southeast Asia, Australia and India (Holland 2018). There even appears to be longitudinal segregation between birds in continental Europe, with Russian birds wintering in east Africa and western European birds in West Africa (Wernham *et al.* 2002). During the breeding season, common sandpipers are found on rivers and upland reservoirs, whereas in winter they can be found on any water body, from puddles to rivers and the coast, although they are predominantly associated with freshwater habitats (Cramp *et al.* 1983, Wernham *et al.* 2002, Holland 2018). The European population consists of approximately 882000 pairs and the British population of 13000 pairs (Wernham *et al.* 2002, Hayhow *et al.* 2015, Harris *et al.* 2020b). In Britain they become more common in the spring and autumn as migrants from more northerly breeding grounds pass through (Wernham *et al.* 2002, Holland 2018).

Common sandpipers are in decline despite being listed as Least Concern on the IUCN Red List, but the causes are unclear (International 2008). In the UK, their population size has declined by 50% since the mid-1980s which has resulted in them being amber listed here (Harris *et al.* 2020b). This decline is greater in the English population, with the Scottish population declining more slowly (Baillie *et al.* 2010, Harris *et al.* 2020b), a similar pattern to that seen in a number of other Afro-Palearctic migrants (Morrison *et al.* 2013). For many of these species, population size and overwinter survival has been strongly linked to Sahelian rainfall (Zwarts & Van Horssen 2009, Ockendon *et al.* 2014); this is likely to be the case for common sandpipers considering their reliance on aquatic invertebrates (Yalden 1986, Holland 2018), but it has not yet been investigated. The North Atlantic Oscillation (NAO) has been suggested as an important correlate of their breeding numbers, with a high NAO corresponding to a smaller breeding population and lower overwinter survival (Forchhammer *et al.* 1998, Pearce-Higgins *et al.* 2009). Pearce-Higgins *et al.* (2009) suggested this was likely to be caused by the effects of the NAO on African wintering grounds, with high NAO corresponding to colder and drier conditions. This means that population size would likely be affected by Sahelian rainfall as suggested above, but the true relationship cannot be understood until more work on the wintering grounds is carried out.

In a long-term study of common sandpipers in the Peak District, UK, annual adult survival was approximately 75%. However, populations seemed extremely susceptible to snow in spring which caused survival to drop to 50%, from which the population took a long time to recover (Holland & Yalden 1994, Holland & Yalden 2002). Population trends differ within the UK, making them more important to understand (Harris *et al.* 2020b). In a study of two breeding populations, one in the centre of the common sandpiper's British range and another on the edge, the former had higher recruitment despite survival and reproductive rates not being significantly different between the two (Dougall *et al.* 2005). The population size in the central region was more variable than the edge population but recovered better from population crashes, indicating it might be more buffered to population declines. Additionally, in the more recent study by Pearce-Higgins *et al.* (2009), adult overwinter survival rates were negatively correlated with the NAO, but not at all study sites, indicating that climate change alone was unlikely to be the primary cause of decline. Indeed, the impacts of wintering conditions may vary across breeding populations because of interactions between weather conditions experienced at different lifecycle stages (Dougall *et al.* 2005, Pearce-Higgins *et al.* 2009, Morrison *et al.* 2013, Finch *et al.* 2014, Morrison *et al.* 2016).

Breeding ecology

In the UK, male common sandpipers arrive at the breeding grounds a few days before females, from the beginning of April through to May, and settle on territories quickly (Mee 2001, Holland 2018). Unlike many other species, arrival dates to Europe are not correlated with the NAO (Vähätalo *et al.* 2004). Males and females with prior experience of a breeding site generally arrive at the breeding grounds before inexperienced individuals, suggesting either that prior experience of a breeding site allows earlier arrival or that inexperienced individuals are first year birds (Dougall *et al.* 2010). Return rates also differed between adults and juveniles in the Peak District population. Adult return rates were very high in the 1990s, with male rates greater than female (72% and 62%, respectively), but juvenile returns were much less common, although varied between breeding sites (Holland & Yalden 2002, Dougall *et al.* 2005).

Early in the season birds are often seen displaying, with their ‘wing-salute’ display appearing to be used for both courtship and territory defence (Mee 2001, Wernham *et al.* 2002, Holland 2018). Chases are also likely to reflect courtship or aggression, with individuals attempting to establish territories and attract partners. Competition for the best territories is likely to be high and one of the main factors driving early arrival, with females partnering with males occupying bigger territories (Mee 2001, Holland 2018). Common sandpipers are largely monogamous, with only infrequent instances of polyandry and extra-pair paternity (Mee *et al.* 2004). Birds usually re-mate in subsequent years if both mates return from the wintering grounds, but there is no evidence of assortative mating (Mee 2001). Although most individuals arrive unpaired, there is evidence to suggest that some may form pairs prior to arrival on the breeding grounds (Mee 2001). Furthermore, there is a high level of synchrony between individuals which bred together in previous years (Mee 2001).

Synchrony in pair arrival appears important; when one member of a pair that has previously bred together arrives a few days late, the earlier bird pairs with another individual. When both members of a pair arrive within a few days of one another they pair together again (Mee 2001).

Territories are linear along upland rivers, about 200-500m in length and are generally associated with shingle beaches and shallow water, which are important for feeding (Cramp *et al.* 1983, Yalden 1986, Mee 2001, Wernham *et al.* 2002, Holland 2018). Adult territory fidelity is very high, with many adults returning to the exact same territory or the adjacent territory in subsequent years in the Peak District study (males: 84% and females: 74%; Holland & Yalden 2002). Males will do this regardless of their breeding outcome the previous year; females tend to change if their previous breeding attempt was unsuccessful or their mate does not return (Mee 2001, Holland 2018). Juveniles are less site faithful with most dispersing approximately 3km and some as far as 200km, but the degree of fidelity may differ between breeding regions (Holland & Yalden 1994, Holland & Yalden 2002, Dougall *et al.* 2005). Once established, territories are stable throughout the season and there is some evidence to suggest that the number of fledglings per territory is positively correlated with the number of territories in the population (Holland & Yalden 2002). Agonistic behaviour between individuals occupying neighbouring territories occurs almost exclusively at territory boundaries, with rare intrusions into the centre (Mee 2001). Territory defence involves singing and displaying by both sexes, sometimes even resulting in prolonged ‘fights’ (Cramp *et al.* 1983, Holland 2018). Interestingly, neighbouring pairs forage next to one another in nearby fields, but agonistic behaviour resumes when in their territories along the river’s edge, suggesting that river banks are the commodity being defended (Dougall *et al.* 2010). Territorial behaviour continues right through until chicks fledge, meaning they have an important role to play in chick rearing and protection, probably because good territories will have a mix of shingle for foraging and vegetation to provide cover for young chicks (Dougall *et al.* 2010, Holland 2018).

After pairing, members of both sexes will start prospecting for nests, usually within 30m of the riverbank, but sometimes as far as 100m away. They will normally build their nests in early May under some form of vegetation, and these are shallow cups with a diameter of 10-12cm and depth of 3-4cm, lined with vegetation and other debris (Holland 2018). Females lay, on average, 4 pyriform eggs in approximately 6 days, with both sexes contributing to incubation starting from the penultimate egg. Incubation bouts are relatively long, with males tending to incubate overnight and females during the day; there are ‘changeovers’ in incubation bouts between partners that consistently happen within a short timeframe (Mee 2001). Incubation normally lasts between 21-22 days (Cramp *et al.* 1983), with males contributing more time than females; in some cases females may even desert the nest during incubation or shortly after hatching (Holland 2018).

Eggs usually hatch within 24 hours of each other, from mid-May to the beginning of June (Mee 2001, Dougall *et al.* 2010). If the first breeding attempt fails early in the season, pairs will produce a replacement clutch and these normally hatch by the beginning of July (Dougall *et al.* 2010). The ability to re-nest after clutch failure could be one of the main factors selecting for early arrival in females (Mee 2001, Morrison *et al.* 2019). Chicks usually stay in their nest for the first day after hatching but then spend the next few days in wet, insect-rich areas like streams and need regular brooding (Dougall *et al.* 2010). Mortality during this time is high despite both parents guarding them, and decreases as the chicks age (Yalden & Dougall 2004). Once chicks are older, they may only be guarded by a single parent with the other foraging nearby, although the more distant parent is still likely to play a role in predator detection (Dougall *et al.* 2010). Chicks can normally fly after 19 days, by which time usually only the male is present, remaining until the chicks fledge after 26-28 days (Cramp *et al.* 1983, Dougall *et al.* 2010). Surprisingly, lifetime reproductive success in this species is low, estimated at only 3.46 fledglings per female in the long-term study in the Peak District, just enough to maintain the population (Holland & Yalden 1994).

Adults and juveniles leave the UK relatively quickly, with breeding sites largely empty by the end of July (Dougall *et al.* 2010). It is likely that failed breeders leave far earlier than those that are successful, as suggested by the sighting of a colour-ringed bird from the Peak District population in Morocco on the 15th June 1979 (Dougall *et al.* 2010). There are also an increasing number of sightings in the UK in winter and, although their origin is currently not known, it has been suggested that these are UK breeders (Dougall *et al.* 2010).

Migration routes, phenology and stopover sites

Common sandpipers are normally solitary or found in very small flocks throughout their migration from Europe to West Africa (Cramp *et al.* 1983, Wernham *et al.* 2002). Autumn migration to the wintering grounds starts in July, with the first to depart being failed breeders, and recoveries in Morocco in September indicate that it is spread over a relatively long period (Wernham *et al.* 2002). Spring migration to the breeding grounds starts in March with birds arriving at the breeding grounds in Western Europe in April and May (Wernham *et* *al.* 2002). There are currently ten geolocator tracks from individuals tagged in Scotland, with most of them wintering along the West African coast (Summers *et al.* 2019). During autumn migration they used stopover sites in England, Ireland and the Iberian Peninsula, spending on average more time in the last than the first two. The median date they left Scotland was the 9th July and all arrived in West Africa by the 13th August, which is broadly consistent with passage dates from the Gulf of Gdańsk, Poland, and Ottenby, southern Sweden (Meissner 1996, Wernham *et al.* 2002, Iwajomo & Hedenström 2011). The median migration duration in spring was 17.5 days, with later leaving birds staging for less time on their way south. The tracked birds spent most of the wintering period on the coast of Guinea-Bissau and were therefore probably using the extensive mudflats of the Bijagós Archipelago (Summers *et al.* 2019). Previous expeditions to this area have found it to be extremely important for wintering waders, including common sandpipers (Zwarts 1988).

In spring, the tracked common sandpipers used similar stopover sites to those used in autumn, stopping over primarily on the Iberian Peninsula, but also using Morocco, France and England (Summers *et al.* 2019). The median duration of spring migration, 16 days, was slightly shorter than in autumn. This is consistent with studies suggesting that birds could be under higher selective pressures during spring, although there could be greater differences if, for example, fuelling time is taken into account (Wernham *et al.* 2002, Conklin *et al.* 2013, Nilsson *et al.* 2013, Lindström 2020). The median date of arrival to Scotland was the 2nd May. Interestingly, Summers *et al.* (2019) found that the spring migration of several individuals was hindered by adverse wind conditions and suggested that this could impose limitations on their population size, as also found for other species (Lok *et al.* 2015, Loonstra *et al.* 2019).

The findings from these tracked birds provide new insight into the migration schedule of common sandpipers in Britain (Bates *et al.* 2012) and suggest they employ a ‘hopping’ migration strategy with multiple short stopovers rather than one long staging site (Warnock 2010, Ortiz De Elgea & Arizaga 2016). However, these tracks are unlikely to be representative of the entire British population as migratory strategies differ between populations in many species (Balbontín *et al.* 2009, Hewson *et al.* 2016, Van Bemmelen *et al.* 2019). Furthermore, there are reports suggesting common sandpipers employ a more ‘jumping’ migration strategy – long flights with few, long stopovers (Moreau 1967, Warnock 2010) – and at least one bird from the Scottish population flew non-stop between Scotland and West Africa (Summers *et al.* 2019). Identifying the exact migration strategy used by common sandpipers from sightings on migration is difficult because most are of birds of unknown origin and the strategies employed could be population specific (Wernham *et al.* 2002).

Stopover sites used by common sandpipers appear similar to the regions used by other Afro-Palearctic species, such as southern Europe and northern Morocco (Wernham *et al.* 2002, Summers *et al.* 2019). Individuals may be faithful to passage sites between years (Van Steenwegen 1978, Catry *et al.* 2004) and they are likely to be used for both spring and autumn migration (Wernham *et al.* 2002, Bates *et al.* 2012, Summers *et al.* 2019). Like other species on migration, individuals increase their fat stores very rapidly during stopovers in order to continue their onward journey, with rates of 1.7g per day for Scottish birds (Bates *et al.* 2012). Such rapid fat accumulations (up to 60% of their body mass) have been reported for common sandpipers originating from different breeding populations at stopover sites across Europe, with a maximum of 1.93g per day in Valladolid, Spain, and a minimum of 0.7g per day at the Bay of Txingudi, Spain (Meissner 1996, Balmori 2005, Iwajomo & Hedenström 2011, Ortiz De Elgea & Arizaga 2016). The maximum and minimum rates reported by Balmori (2005) and Ortiz de Elgea and Arziga (2016) were very different considering both sites are located in northern Iberia and suggests that the birds stopping at each employ different migration strategies or originate from different breeding regions, and therefore arrive with different fuel loads. In the UK, common sandpipers attain a body weight of 80g before departing for migration, approximately 30g more than their mean weight (Holland 2009, Bates *et al.* 2012). A study of individuals at a passage site in Sweden caught birds with a maximum weight of 79.5g and found their flight range was over 6000km (Iwajomo & Hedenström 2011), easily allowing for non-stop flights to stopover sites further south.

Phenology and migration strategy differ between adult and juvenile common sandpipers. Adults depart from the breeding grounds and pass through stopover sites earlier than juveniles (Meissner 1996, Balmori 2005, Dougall *et al.* 2010, Iwajomo & Hedenström 2011, Bates *et al.* 2012). Iwajomo and Hedenström (2011) found that adult fuel loads at a stopover site were significantly greater than those of juveniles and that they showed a different trend in fuel load as the season progressed. They found an increase in fuel load throughout the season for juveniles but not for adults, which suggests that the two use different migration strategies (Iwajomo & Hedenström 2011). Furthermore, they found that juvenile head and bill length did not change throughout migration through a stopover site, but did change in adults (Iwajomo & Hedenström 2011). They suggested that this may be because there was a higher proportion of (larger) females early in the season, but more males late in the season (Iwajomo & Hedenström 2011). This is likely considering females depart from the breeding grounds before males (Dougall *et al.* 2010).

The timing of migration has changed in different ways for many migratory species (Lehikoinen *et al.* 2004) and there appears to be contrasting patterns in the migration schedules of common sandpipers, with several studies reporting advances in spring and autumn migration (Adamík & Pietruszková 2008, Iwajomo & Hedenström 2011) and another reporting no change (Sparks *et al.* 2007). Even at breeding sites where no changes have been seen, phenology is still likely to be changing as climate may only impact certain aspects of a species' lifecycle (Both & Visser 2001). For example, Bussiere *et al.* (2015) found that the duration of their stay in South African wintering quarters has shortened, which might not be reflected in the duration of the breeding season if more time is spent during migration. Conditions on the wintering grounds are known to affect the timing of arrival to breeding grounds in several species (Balbontín *et al.* 2009, Mondain-Monval *et al.* 2020) and it is therefore likely that there will be knock-on impacts on breeding ecology.

Wintering ecology

British common sandpipers are thought to winter primarily in southern Senegal or the Gambia, but there are increasing numbers of winter residents in Britain, probably because of milder winters (Bates *et al.* 2012, Balmer *et al.* 2013). Most observations of wintering common sandpipers claim them to be evenly distributed, about 200m apart, on any freshwater, saline or marine water body, with a preference for flowing water, from sea-level up to 2000m (Cramp *et al.* 1983). A study of wintering birds on the Miño estuary, Iberian Peninsula, Spain, suggested their diet consisted primarily of marine invertebrates, selected because of their energetic profitability (Arcas 2004).

The scattered distribution of common sandpipers during winter implies territoriality, which is supported by observations of individuals remaining at the same site for long periods and obvious aggression between neighbours (Cramp *et al.* 1983, Holland 2018). Tests with dummy birds placed close to solitary individuals strongly suggested territoriality by eliciting aggressive behaviour from the resident (Cramp *et al.* 1983). Both sexes appear territorial, with most observations suggesting territories are defended by solitary individuals. However, aggressive interactions appear to change as the breeding season approaches, with individuals starting to pairing up to defend territories against other birds (Cramp *et al.* 1983). This is corroborated by Mee (2001), who suggested that individuals may pair prior to arrival on the breeding grounds. Although territorial during the day, common sandpipers form communal roosts at night (Cramp *et al.* 1983, Holland 2018).

In a series of major ringing expeditions to the Parc National des Oiseaux du Djoudj, Senegal, (hereafter 'Djoudj'), Sauvage *et al.* (1998) found that common sandpipers were likely to be site faithful. They were the most recaptured wader of all the birds studied (9/65 or 14% after one year), with one bird caught in three subsequent winters. Furthermore, there is some evidence to suggest site fidelity in British wintering common sandpipers, with one bird ringed in Hampshire in 1974 found dead there in the following year (Wernham *et al.* 2002). Winter territoriality is likely to be common in many Afro-Palearctic migrants (Sauvage *et al.* 1998, Cresswell 2014, Blackburn & Cresswell 2016b), but there are very few species-specific studies confirming or refuting this hypothesis.

Aims

In this thesis we aim to understand the factors influencing the British common sandpiper population during breeding, winter and migration. In Chapter 2 we investigate the factors affecting breeding success, including the effects of anthropogenic disturbance and rainfall on nests and chicks. In Chapter 3 we study their wintering ecology, about which extremely little is known, in order to understand the factors influencing their presence and foraging success. To investigate the migration behaviour of common sandpipers we attached geolocators to individuals in England and Senegal. We investigate the influence of carrying these tags in Chapter 4, and report their migration routes and destinations in Chapter 5. In this chapter, we also compare the migrations of these birds to those of individuals tagged in Scotland, in order to investigate the amount of overlap between individuals from different populations and the influence of wind conditions during autumn and spring migration (Summers *et al.* 2019). We then investigate the influence of climate change and weather conditions on the timing of migration in wading bird species from across the Afro-Palearctic and Nearctic flyways using the eBird citizen science dataset (Chapter 6). Finally, in Chapter 7, we combine the information from Chapters 2 through 5 to discuss the potential influence of each lifecycle stage on the recent declines in the British population of common sandpipers. Here, we also investigate the possibility of bottlenecks during the non-breeding season and carry-over effects driving population declines, and discuss the importance of spatial scale for future studies of bird migration.

Chapter 2 Factors affecting breeding success in the common sandpiper and the potential impact of disturbance

Introduction

There has been considerable recent effort to understand the causes of decline in many migratory bird species (Vickery *et al.* 2014). Their population trends are particularly difficult to understand given their reliance on multiple, distinct geographic regions throughout their lifecycle (Wilcove & Wikelski 2008). Climate change is altering the conditions at each stage of the lifecycle, with its effects exacerbated by human modification of natural habitats through, for example, agricultural intensification, urbanisation and tourism (Vickery *et al.* 2014, Patchett *et al.* 2018). These factors have been shown to affect migratory species across all stages of their lifecycle and can have implications for survival and reproductive success (Inger *et al.* 2010, Catry *et al.* 2013, Vickery *et al.* 2014). However, studies have reported contrasting responses to these pressures across species (Ockendon *et al.* 2012, Morrison *et al.* 2013, Ockendon *et al.* 2014, Mayor *et al.* 2017), meaning that the effects of complex interactions between lifecycle stages are hard to understand. Therefore, to determine the reasons for global population declines in migratory birds, we need to understand the mechanisms driving changes at each lifecycle stage.

For many species, the energy required during the breeding season is higher than at other times of the year (Piersma 2002, Carey 2009, Pearce-Higgins *et al.* 2010), meaning that the effects of environmental change could be magnified in breeding regions (Carey 2009). For example, the reproductive phenology of most bird species has evolved to coincide with maximum food availability, to ensure a plentiful supply for their chicks (Carey 2009). However, climate change has advanced spring phenology, with many species unable to match these advances (Mayor *et al.* 2017). Generally, earlier arrival from migration increases reproductive success (Aebischer *et al.* 1996, Saino *et al.* 2004, McKellar *et al.* 2013, Velmala *et al.* 2015; although see Reneerkens *et al.* 2016), but given the recent effects of climate change it is paramount to understand the influence of the timing of reproduction across different species (Badeck *et al.* 2004, Both *et al.* 2004). Furthermore, the influence of reproductive timing might be affected by other factors, such as increased unpredictability of weather conditions across northern latitudes (Cohen *et al.* 2014). This is likely to impose significant costs, with heavy rainfall increasing the amount of food and energy chicks need to survive, especially for species using open nests (Schekkerman *et al.* 2001). After hatching, young are also susceptible to bad weather because they have not yet developed their full adult plumage and are thus unable to keep warm (Visser & Ricklefs 1993). Additionally, chicks need to be brooded by adults during large rainfall events, reducing food intake rates (Beintema & Visser 1989, Schekkerman & Boele 2009). Understanding how the timing of migration and weather conditions affect reproductive success is therefore crucial for predicting how environmental change might impact productivity.

Another major challenge faced by breeding populations is the influence of increasing human populations (Angelstam 1986, Boarman *et al.* 2006, Vickery *et al.* 2014). Ground nesting species are particularly vulnerable to a range of predators (Batáry & Báldi 2004), and often rely on camouflage to improve nest survival (Colwell *et al.* 2011, Troscianko *et al.* 2016). Some individuals will flee as predators approach the nest, relying on the eggs being camouflaged in their surroundings; in others, the incubating adult will not leave the nest readily and instead relies on plumage camouflage to hide from predators (Byrkjedal 1987, Larsen & Moldsvor 1992, Troscianko *et al.* 2016). The similarity in colour between the habitat surrounding the nest and the colour of the eggs or the adult's plumage has been shown to increase nest survival in a number of species (Troscianko *et al.* 2016). Other tactics involve incubating adults walking away from the nest before taking flight when approached by a predator or performing wing displays mimicking an injured bird; both are an attempt to divert the predator away from the actual nest site (Larsen & Moldsvor 1992, Frid & Dill 2002, Smith & Edwards 2018). Predation is therefore likely to play a key role in the population dynamics of ground nesting species.

In the northern hemisphere, the potential for anthropogenic disturbance is increasing as human population size is growing and the amount of unfragmented, natural habitat is in decline. Disturbance by humans on foot, as opposed to those using vehicles, appears to be the most problematic for birds, as it usually results in antipredator responses (Rodgers Jr & Smith 1995, Frid & Dill 2002, Beale & Monaghan 2004, Stankowich & Blumstein 2005). This disturbance can cause incubating adults to leave nests, reducing nest attentiveness which can increase vulnerability to predators (Langston *et al.* 2007, Price 2008). Furthermore, human disturbance can increase predation rates through other mechanisms, including by increasing the number of domestic predators such as cats and dogs, and others which are attracted to waste (Boarman *et al.* 2006, Langston *et al.* 2007, Borges & Marini 2010). High levels of human disturbance negatively affect population size and nesting success for some bird species (Beale & Monaghan 2004, Mallord *et al.* 2007, Whittingham *et al.* 2020), but there are no consistent trends across species and orders (Ibáñez-Álamo *et al.* 2012). Some studies report only short-term effects on adults, with no direct effect on nest survival (Smith-Castro & Rodewald 2010, Ledwoń *et al.* 2016); others report significant effects, particularly during egg laying and early incubation (Safina & Burger 1983, Carney & Sydeman 1999, Syrová *et al.* 2020). The effects of disturbance might also be mediated by the level of habituation, with its effects reduced in high-disturbance areas (Syrová *et al.* 2020). For some species, human disturbance may be beneficial by deterring predators and reducing predation rates (Sandvik & Barrett 2001, Richardson *et al.* 2009). However, this seems to occur only in specific cases, perhaps when the predator is more susceptible to disturbance than the focal species (Sandvik & Barrett 2001). Additionally, predators can become habituated to human presence so that predation rates might increase over time (Richardson *et al.* 2009). The effects of predation and disturbance are likely to operate in tandem and, therefore, understanding their relative influences is important for determining the drivers of population trends.

The common sandpiper (*Actitis hypoleucos*) is a ground nesting, wading bird species whose population is in significant decline (Vickery *et al.* 2014, Harris *et al.* 2020b). It breeds throughout Europe and much of temperate Asia, moving south to winter in Africa, southern Asia and Australasia. Common sandpipers have relatively high adult survival rates (Méndez *et al.* 2018), but these are negatively correlated with winter North Atlantic Oscillation (NAO), likely through its association with colder and drier conditions throughout Europe (Pearce-Higgins *et al.* 2009). However, the effect of the NAO is not consistent across different populations in the UK, indicating that wintering conditions are not the only cause of decline (Pearce-Higgins *et al.* 2009). This means that factors on the breeding grounds are likely to be at least partly responsible for ongoing declines. Previous studies of two separate breeding populations suggested that low recruitment was the main driver for the decline in one population but the population remaining stable in another (Dougall *et al.* 2005). Furthermore, common sandpiper populations may be susceptible to recreational disturbance, but it is unclear whether this can affect breeding success (Yalden 1992). Understanding more about the factors affecting reproductive success and population productivity can hopefully provide information regarding the steps necessary to conserve British and European populations.

Here, we investigate the factors affecting reproductive success in a population of common sandpipers in the Yorkshire Dales National Park, UK. This area is a tourist hotspot in the north of England with an extensive network of public footpaths, thereby providing the opportunity to study the effects of human-related disturbance. During the breeding season of common sandpipers, the area is visited by large numbers of hikers, dog walkers and anglers, each of which is likely to be considered a threat by incubating birds. Here, our aims were to investigate (1) the factors affecting hatching success, including the influence of human disturbance, (2) whether the response of incubating adults to disturbance events differed between successful and unsuccessful nests, and (3) the factors affecting fledging success and, primarily, the effect of rainfall.

Methods

Study population and nest monitoring

All fieldwork was carried out in the River Lune catchment within a 6.5km radius of Sedbergh, Cumbria, UK (54.3236˚N, 2.5282˚W), in the breeding seasons of 2017, 2018 and 2019 (Figure 2.1). This individually marked study population of approximately 20-25 pairs was monitored closely from April to July each year. At the start of the season, surveys of each river and tributaries were carried out 2-3 days per week in order to record the timing and identity of returning individuals. At least 80% of the nests in the population were found in each year (n = 24-27, including replacement nests i.e. second attempts following failure of the first) and monitored through to fledging or failure. The majority of nests were found by flushing incubating adults from areas where high activity had been noted, or by watching them return to the nest during focal observations. A small number were found prior to incubation, by flushing the female during egg laying; none of the nests found during laying were subsequently abandoned. Most of the nests that were missed had failed before we could find them, but the identity of the breeding pair could still be established from previous or subsequent attempts in the same territory in that year. Over 90% of unmarked adults were caught each year and fitted with a British Trust for Ornithology (BTO) metal ring on their right tarsus, a yellow colour ring engraved with two unique black characters on their left tarsus, and a plain red colour ring on their right tibia. We targeted individuals on their breeding territories by setting mist nets across rivers or by using wire mesh walk-in nest traps. Parents share incubation duties and, in most cases, one individual sits on the nest overnight and in the morning, before switching with its partner for the afternoon (Mee 2001). This meant that we could target specific individuals during different parts of the day.

We avoided nest trapping within the first week of incubation to limit the chances of desertion.

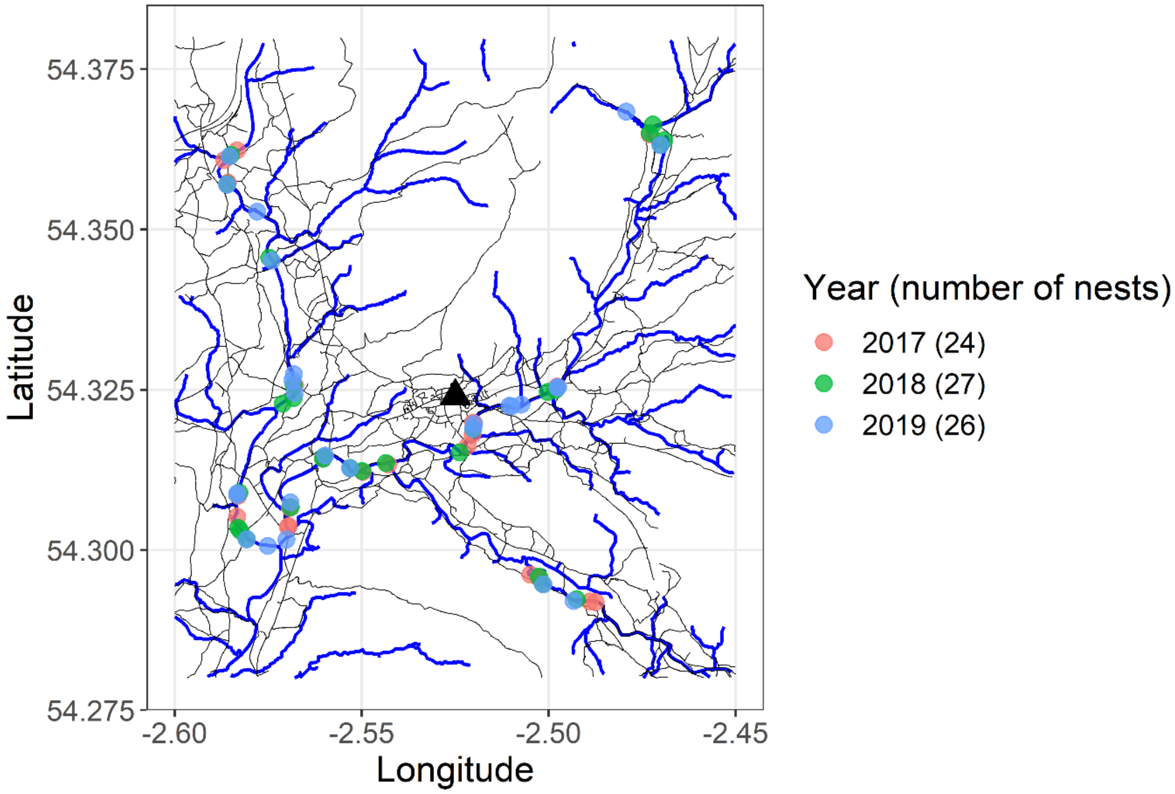


Figure 2.1 The study site around the town of Sedbergh (black triangle) and the locations and number of nests found in each year of the study period. Solid black lines are either public footpaths or roads; solid blue lines are the rivers and their tributaries.

Each nest was visited once every four to five days until the latter stages of incubation (see below); hatching success was then determined by visiting the nest every day. During the study period, we had only two known cases of a nest being abandoned, and one case of a nest being flooded. Therefore, our hatching success measure primarily reflects predation rates. Chicks usually remain in the nest for up to 24 hours after hatching, during which the nest was visited and the chicks caught, ringed and measured using the same methods as for the adults. Chicks were ringed with a BTO metal ring and the yellow engraved ring, placed on the same parts of the legs as adults, but were not fitted with the red colour ring in order to minimise visibility to predators. Territories that successfully hatched young were visited once every five days until the adults were no longer seen alarm calling or until the chicks were seen flying. The fledgling period reported in the literature is 19 days (Robinson 2005), but on several occasions we observed chicks flying when 17 days old ('day 17'); we therefore took this to be the minimum age of fledging. If no adults were seen alarm calling before day 17 on two consecutive visits to the territory, then we concluded that the chicks had been predated. When adults or chicks were seen during the last visit to the territory prior to day 17, but not after, we counted the chicks as having successfully fledged.

For each nest that we found, we measured the distance of the nest from the nearest river using a Hawke laser range finder LRF 400 (± 1m), hereafter 'distance from the river'. This was to determine whether there were any effects caused by proximity to the river, for example due to increased risk of predation by semi-aquatic mammals such as American mink (*Neovison vison*) and Eurasian otter (*Lutra lutra*) or by flooding. As distance from the river was affected by water levels, all measurements were taken on days when the river levels were typical. In order to determine the potential for vegetation cover to mediate the risk of nest predation, we placed a 6cm diameter white cardboard disc over the eggs and took a photo from waist height using a camera phone. These photos were then viewed on a computer and the amount of the disc that was covered by vegetation was estimated to the nearest 5%. This provided an estimate of the amount of vegetation covering the nest, hereafter referred to as 'nest cover'.

Estimating hatching date

Common sandpipers, like many other wading bird species, have inconspicuous nests which require very little construction, thereby making them difficult to find during egg laying. Furthermore, their young leave the nest within approximately 24 hours of hatching, which means that for ringing chicks, nests need to be visited as soon after hatching as possible (Dougall *et al.* 2010). For nests found during egg laying, we could estimate the day on which the first egg was laid ('first egg date', FED) and hatching date by allowing for a laying period of six days followed by 22 days of incubation (Cramp *et al.* 1983). However, many of the nests that we found had already started incubation. In order to organise nest visits and predict the timing of hatching for ringing chicks, we used an equation based on changes in egg mass relative to volume in the common snipe (*Gallinago gallinago*; Green 1984). To do this, on the first visit to a nest we measured the widest and longest point of each egg (the width and length, respectively) using Vernier callipers (± 0.1 mm), to determine their volume. We also weighed each egg using a set of scales (± 0.1 g) on the first, and at each subsequent, visit. Each time the eggs were weighed (median number of visits per nest = 4), we used the following equation to determine an index of egg mass relative to its volume on that day:

$$Egg\ mass\ volume\ index = \frac{mass}{(length * width)^2}.$$

This index could then be used to predict hatching date (see Green 1984 for the predictive equation).

Calculating first egg date for failed nests

For many species, the timing of migration is correlated with the timing of breeding, which in-turn affects reproductive success (Verhulst *et al.* 1995, Morrison *et al.* 2019). Therefore, the timing of reproduction is an important factor to consider when studying breeding ecology. While the equation based on common snipe (Green 1984) was useful for determining when to start daily nest visits and record hatching, the day of hatching was not always accurately predicted. For our models of reproductive success (see below), we wanted to determine the influence of FED. For nests that successfully hatched, we could back-calculate from the hatch date to obtain FED. However, for nests that failed prior to hatching, we created an equation to predict hatch date based on egg volume and mass measurements, similar to Green's (1984) equation for common snipe, and then back calculated from these predictions to obtain FED.

Creating and validating a predictive equation

To create the predictive equation, we used the measurements and weights of clutches that successfully hatched over the entire three-year study period (*n* = 37). For each successfully hatched clutch that we measured and weighed, we had the volumes of each egg and the changes in mass up until hatching. Occasionally, on the day of hatching, there were fewer chicks in the nest than the number of eggs and therefore, we were only able to determine hatching success at the nest level rather than for each egg separately. We used these egg measurement and mass data to produce an equation to predict hatching at the nest level. For this, the measures of each egg were averaged across all eggs in a clutch to give a mean egg mass volume index for each nest for each visit. We then regressed the actual number of days until hatching against the egg mass volume index. We used the slope and intercept from this model to create a predictive equation (i.e. $y = slope * x + intercept$), which was used to generate predicted hatching dates for each nest. We regressed the predictions from this model against the true number of days until hatching to assess its accuracy (Figure 2.2a, Table 2.1).

Table 2.1 General linear model regressing predicted against actual days until hatching. The mean and standard deviation of the differences between the predicted and actual number of days until hatching are presented (predicted – actual).

Intercept	Slope of days to hatching	Adjusted R^2	P-value	Mean difference	Standard deviation of difference
1.43	0.82	0.82	<0.001	4.29×10^{-3}	2.38

The model was highly significant, had a high R^2 value and a very small mean difference between the predicted and actual number of days until hatching (Table 2.1). The equation used to predict hatch date was:

$$Predicted\ days\ until\ hatching = 220436.00x - 94.45$$

where x is the egg mass volume index for the nest, as calculated using the method described above. To determine the potential biases associated with our equation, we plotted the difference between the predicted and actual days until hatching (predicted – actual) versus the actual number of days until hatching (Figure 2.2b). This shows that at the early stages of incubation, our equation slightly underestimates the number of days until hatching, whereas at late stages it overestimates the number of days until hatching (Figure 2.2b); but in either case it was only ever by a few days (Table 2.1).

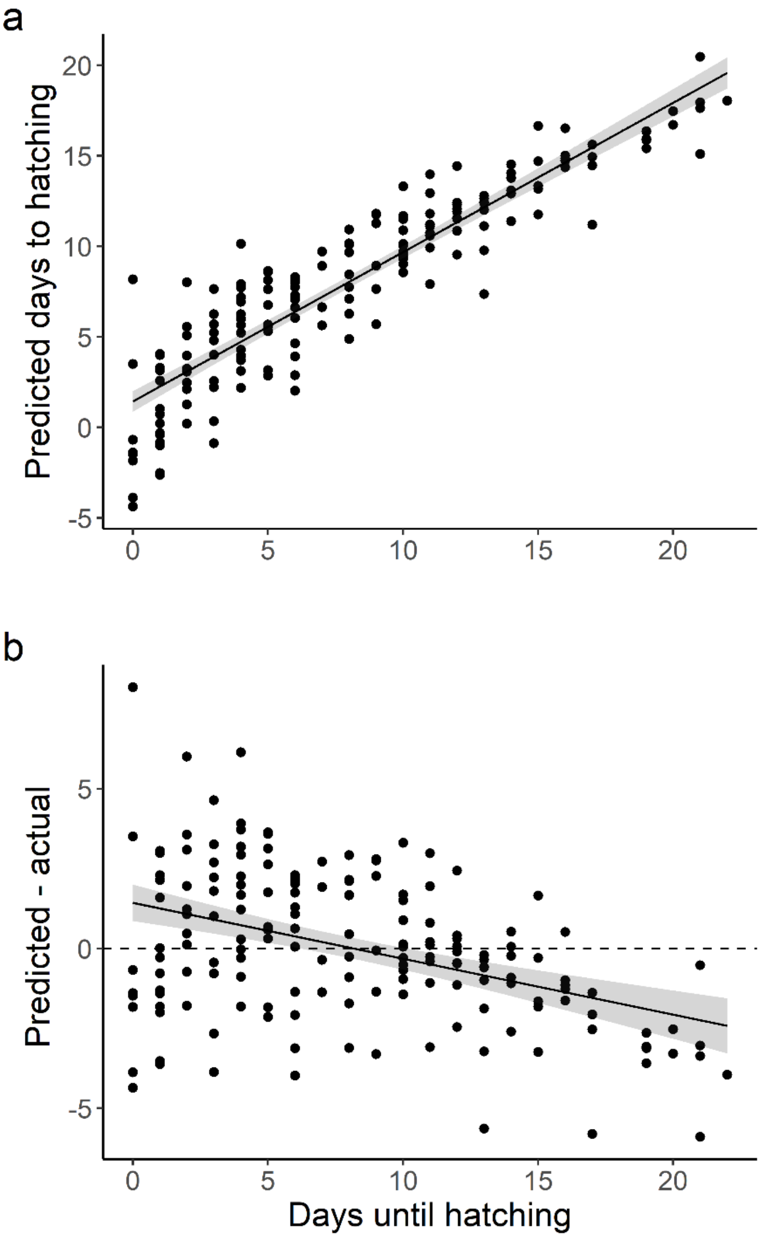


Figure 2.2 Assessing the results of our predicted hatch date equation. (a) The relationship between the predicted and the actual number of days until hatching. The closed circles show the raw data. The solid line is the prediction from a linear model; the shaded area is the 95% confidence interval. (b) The difference between the predicted and actual number of days until hatching (predicted – actual) and its relationship with the actual number of days until hatching. The solid circles show the raw differences between the predicted and actual number of days until hatching for each of the nest visits. The solid line is the prediction from a linear model (estimate $_{\text{actual days until hatch}}$ = -0.18, $F_{1,\,168}$ = 35.65, $P < 0.001$); the shaded area is the 95% confidence interval.

Predicting hatch date and first egg date for failed nests

We used the predictive equation to predict the hatch date of all the nests that failed prior to hatching. However, we were able to measure and weigh most of the failed clutches more than once before they were predated (median number of visits per unhatched nest = 2), meaning that we had multiple dates (and weights) from which we could calculate the predicted hatch day. For clutches that were weighed more than once, we decided to use the weight from the first time that they were measured. This is because some of the other failed clutches were only weighed once before they were predated. Finally, from the predicted hatch dates for failed nests, we back calculated to obtain a predicted FED for use in our models. For successful nests, we obtained FEDs by back calculating from the true hatch date.

Flight initiation distance

In order to investigate the influence of walkers on incubating common sandpipers, we recorded the distance at which adults left the nest on approach by an observer (i.e. a potential predator), hereafter ‘flight initiation distance’ (FID). On our regular visits to nests during incubation, the nest site was watched until the moment the adult bird was seen leaving. The distance between the approaching observer and the nest was measured to the nearest metre from the location from which the bird was first seen moving. For most nests we were able to watch the incubating adult leave the nest, but for those with high nest cover we watched for movement in the vegetation. This might have biased our measurements of FIDs, but because we could often see the vegetation move, any effect was likely to be minimal. If the moment at which the bird left the nest was missed, we didn’t record any distance. Where possible, we varied the direction of approach on each visit for two reasons: (1) in order to avoid the incubating individuals becoming habituated, and (2) to avoid creating an obvious path to the nest through the vegetation. In some cases, this was not possible because of the nest site, i.e. extremely dense vegetation and trees.

Downloading public rights of way and road maps

In order to determine the effects of disturbance on hatching success, we investigated the distance of nests from the nearest footpath. However, many of the public rights of way are joined together by roads. Therefore, we decided to obtain data on the distance of each nest from the nearest footpath or road. This was used as a proxy for disturbance at each nest. Shapefiles of all the public footpaths in the study site have been made accessible through an Open Government Licence and were downloaded via https://www.rowmaps.com/datasets/CU/. A shapefile of all the roads in the study site was accessed through the Ordnance Survey Open Access database (https://www.ordnancesurvey.co.uk/opendatadownload/products.html). We combined the footpath and road shapefiles and calculated the distance of each nest from the nearest footpath or road, hereafter referred to as 'distance from footpath'.

Rainfall data

In order to investigate the effects of rainfall on chick survival, we downloaded rainfall data for the study site using the 'raincpc' package in R (Gogeti 2014, Team 2020). This provides daily observation-based rainfall at a 50km resolution globally from the Climate Prediction Centre. Chicks are most vulnerable to weather in the week following hatching (Schekkerman *et al.* 2001, Gach *et al.* 2018); therefore, for each nest that successfully hatched, we investigated the effect of rainfall during the seven days following hatching, including the day of hatching itself (eight days in total). For this period for each successfully hatched nest, we obtained the total amount of rainfall, hereafter 'total rainfall', the number of days with any rainfall, hereafter 'rainfall days', and the number of days with >30mm rainfall, hereafter 'heavy rainfall days'. 30mm was chosen to represent heavy rainfall because it was two standard deviations above the daily mean breeding season rainfall across the three years combined.

Statistical analyses

All analyses were conducted in the R environment (Team 2020). As explained in Chapter 4, there were no effects of geolocators on hatching and fledging success, and so differences between adults with and without geolocators are not examined here. All explanatory variables were checked for collinearity prior to analysis, with correlations low enough to have independent effects in the models ($r < 0.5$); continuous variables were scaled and centred (Schielzeth 2010). All models were initially fitted with male and female identity as crossed random effects, but this sometimes resulted in convergence warnings. Male identity was therefore used as the sole random effect in all models unless otherwise stated. Once the terms in the full models had been decided, we fitted every possible combination of models using the 'MuMIn' package (Barton 2020). If there were multiple models within two AICc units (2AICc) of the best-fitting model, then these were averaged, and the full averaged model was used for plotting. We present all models within 2AICc of the best-fitting model and their marginal and conditional R^2 values for mixed effects models (Nakagawa *et al.* 2017). In cases where there was only one best-fitting model, this was used for plotting. Models were checked for overdispersion and validated by plotting the predicted versus fitted values and the distributions of the residuals.

Hatching success

We used generalised linear mixed effects models (GLMMs) to investigate the factors affecting the hatching success of common sandpiper nests. Hatching success was a binary variable based on whether at least one egg successfully hatched. We fitted a model with hatching success as the response variable and a binomial error distribution in the 'lme4' package (Bates *et al.* 2015). We included distance from footpath, nest cover and distance from the river as continuous explanatory variables. We also included interactions between distance from footpath and nest cover, and between distance from footpath and distance from the river. The former interaction was included in order to investigate whether nest cover mediated the impact of human approach and predation rates. The latter was included because proximity to the river may affect predation which could in turn interact with the effects of walkers. We also decided to include FED as both a linear and quadratic term after preliminary analyses revealed a possible change in its relationship with hatching success throughout the breeding season. We initially fitted year as a three-level categorical variable, in order to control for effects between years; however, this caused model convergence issues. A generalised linear model (GLM) comparing hatching success across the three different years revealed no significant differences and, therefore, we decided to exclude year from subsequent analyses ($Z_{2018,\ 2019} = 0.08, -0.75$; all $P > 0.4$).

Even with male identity fitted as random effect term, there was still the possibility of pseudoreplication due to unringed birds. In this analysis, there were eight nests with unringed male birds across all years of the study period: two in 2017, one in 2018 and five in 2019. In order to avoid pseudoreplication of unringed birds returning in 2018 or 2019, we removed the nests of all the unringed 2017 and 2018 birds from subsequent analyses (remaining nests = 68). The unringed 2019 birds were considered as separate individuals for all subsequent analyses as these nests overlapped in time and there is little evidence of bigamy in common sandpipers (Mee 2001).

Humans approaching the nest

In order to investigate the influence of walkers on common sandpipers, we fitted two models focussed on the factors affecting, and the effect of, FID. The first investigated the factors that affect the FID of a bird upon approach by a human approaching the nest, i.e. a potential predator. The second investigated the effect of FID and nest cover on hatching success. FID was excluded from the original model of hatching success above because it would have considerably reduced sample size.

Flight initiation distance

In order to investigate the factors that affect birds' responses to humans being close to, and approaching, the nest, we used a GLMM fitted with a Poisson error distribution and FID as the response variable. We fitted distance from footpath, nest cover and the number of days until hatching as explanatory variables. We also fitted the interaction between distance from footpath and nest cover, and that between distance from footpath and the number of days until hatching. We included the number of days until hatching because adults might become more attentive in the latter stages of incubation, as by that stage they have invested more in their clutch (Montgomerie & Weatherhead 1988, De Jong *et al.* 2013).

We fitted male and female identity as crossed random effects. In this dataset we had several unringed adults in 2018 and 2019. Therefore, the nests of all unringed males and females in 2018 were removed ($n_{males} = 1$, $n_{females} = 3$) and all the unringed birds in 2019 were considered as separate individuals in the analyses as their nests were active simultaneously ($n_{males} = 3$, $n_{females} = 4$). This resulted in a dataset comprising 138 flushing events from 43 different nests.

Hatching success and flight initiation distance

In order to investigate the potential for human presence to affect hatching success, we obtained the mean FID for every nest in our dataset. Then, we fitted a GLM with hatching success as the binary response variable and a binomial error distribution. The explanatory variables fitted were the mean FID, nest cover and the interaction between them.

Fledging success

To investigate the factors affecting fledging success once a nest had hatched (n = 38), we fitted separate models for each of the three different rainfall measures described above (total rainfall, rainfall days and heavy rainfall days). Fledging success was a binary variable based on whether at least one chick successfully fledged. All models were fitted with the same basic structure: one of the three rainfall measures, year as a three-level categorical variable, FED and FED^2. Year was included to account for inter-annual variation in rainfall.

There was only one unringed male in this dataset (from 2018), which we removed to avoid pseudoreplication. With male identity as the only random intercept term, the models were singular. In order to determine whether this was producing inflated effects sizes, we fitted GLMs (thereby not accounting for any pseudoreplication) using the same explanatory variables and the model outputs were almost identical. We present the model outputs from those including the random intercept term.

Results

Hatching success

Hatching success was positively correlated with distance from footpath and with distance from rivers (Table 2.2). The effect of distance from footpath was mediated by distance from the river, however, with nests close to the river being far less affected by footpaths. Nests that were far from the river had increased hatching success as they got further away from public footpaths (Figure 2.3). The amount of nest cover was positively correlated with hatching success, with less visible nests more likely to hatch (Table 2.2). Finally, there was a quadratic relationship between first egg date (FED) and hatching success showing that early and late nests were less likely to hatch than those laid in the middle of the breeding season (Figure 2.4).

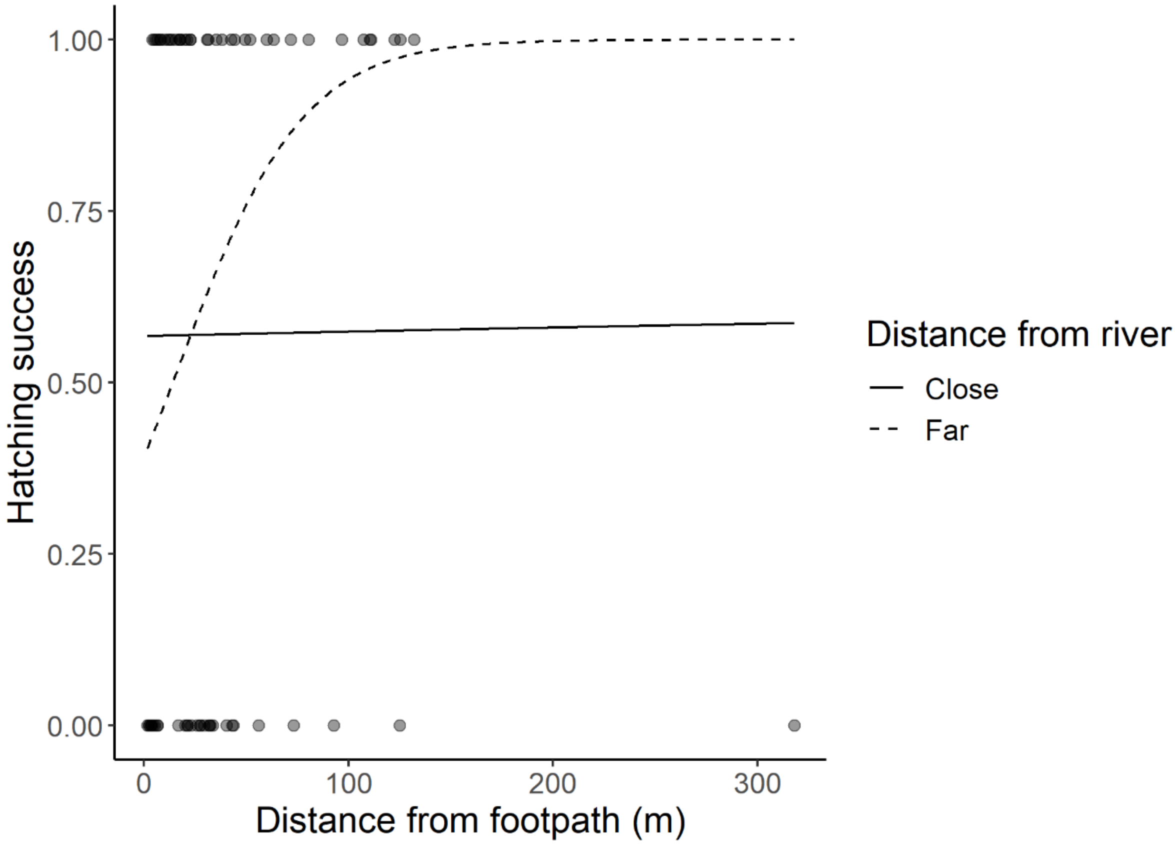


Figure 2.3 The relationship between hatching success and distance from footpath when the nest is either close to or far from the river. Distances from the river represent values half a standard deviation below (17m) and above (66m) the mean distance from the river (41m). Half a standard deviation was used to represent distance from the river because its distribution was Poisson shaped and, therefore, one standard deviation below the mean (as used for plotting below) resulted in negative distances from the river. Closed circles show the raw data and are transparent to show overlapping points (n = 68); the solid lines are predictions from a GLMM, plotted for the mean value of all other variables.

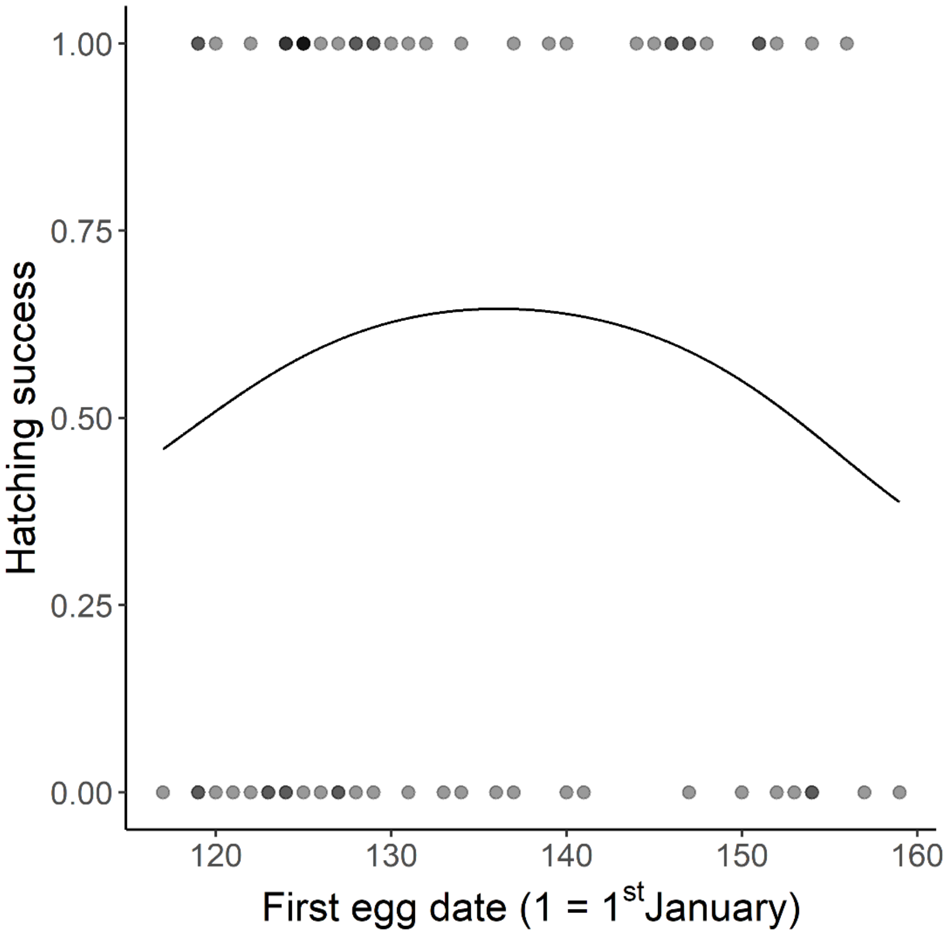


Figure 2.4 The relationship between hatching success and first egg date. Closed circles show the raw data and are transparent to show overlapping points (n = 68); the solid line is the predicted relationship from a GLMM, plotted for the mean value of all other variables.

Table 2.2 The results the GLMMs of the factors affecting hatching success. The models presented are those within 2AICc of the best-fitting model together with the null model for comparison.

	Intercept	Nest cover	Distance from the river	FED	FED^2	Distance from footpath	Distance from the river x distance from footpath	df	Log likelihood	AICc	weight	Marginal R^2	Conditional R^2
	0.35	0.53	0.64	\	\	0.75	1.56	6.00	-38.56	90.49	0.24	0.45	0.57
	0.35	\	0.74	\	\	0.88	1.73	5.00	-39.82	90.61	0.23	0.47	0.60
	0.88	0.56	0.62	\	-0.55	0.74	1.50	7.00	-37.43	90.73	0.22	0.46	0.55
	0.86	\	0.74	\	-0.52	0.89	1.70	6.00	-38.87	91.11	0.18	0.48	0.60
	1.23	0.73	0.65	0.59	-0.94	0.81	1.42	8.00	-36.67	91.78	0.13	0.43	0.62
Null model	0.15	\	\	\	\	\	\	2.00	-46.19	96.56	0.01	0.00	0.22

Humans approaching the nest

Flight initiation distance

FID was negatively correlated with distance from footpath and nest cover (Figure 2.5). FID was positively correlated with the number of days until hatching, agreeing with our predictions (Table 2.3). None of the interactions were important in the final models; nests with low vegetation cover had consistently higher FIDs than those with high cover across all distances from footpaths or roads (Figure 2.5).

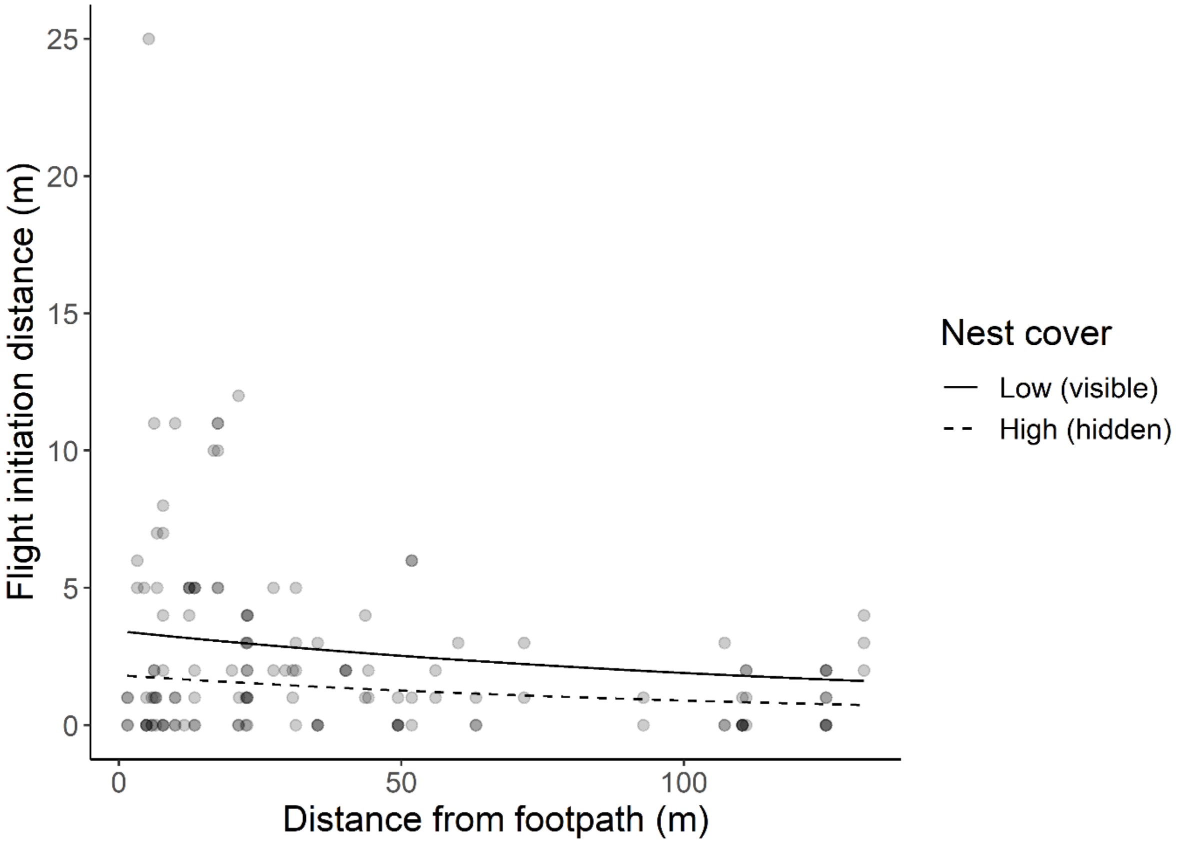


Figure 2.5 The relationship between flight initiation distance and distance from footpath at low and high levels of nest cover. The amount of nest cover is one standard deviation below (18% cover) and above (88% cover) the mean (53% cover). Closed circles show the raw data and are transparent to show overlapping points ($n_{\text{flushing events}}$ = 138, n_{nests} = 43); solid lines show the predicted results from a GLMM, plotted for the mean value of all other variables.

Table 2.3 The results of the GLMMs of the factors affecting flight initiation distance. The models presented are those within 2AICc of the best-fitting model together with the null model for comparison.

	Intercept	Nest cover	Distance from footpath	Days to hatch	Nest cover x distance from footpath	Distance from footpath x days to hatch	df	Log likelihood	AICc	Weight	Marginal R^2	Conditional R^2
	0.63	-0.33	-0.30	0.14	\	\	6.00	-292.24	597.12	0.40	0.29	0.69
	0.61	-0.32	-0.31	0.11	\	-0.09	7.00	-291.61	598.08	0.25	0.30	0.68
	0.66	-0.34	-0.31	0.14	-0.11	\	7.00	-291.85	598.55	0.19	0.33	0.70
	0.64	-0.39	\	0.14	\	\	5.00	-294.26	598.98	0.16	0.18	0.66
Null model	0.64	\	\	\	\	\	3.00	-302.38	610.93	0.00	0.00	0.69

Table 2.4 The results of the GLMs of effect of flight initiation distance on hatching success. The models presented are those within 2AICc of the best-fitting model together with the null model for comparison.

	Intercept	Nest cover	FID	Nest cover x FID	df	Log likelihood	AICc	Weight	R^2
	0.39	0.51	-1.91	-1.48	4.00	-22.16	53.38	0.53	0.27
	0.54	\	-1.18	\	2.00	-25.32	54.95	0.24	0.15
	0.55	0.54	-0.90	\	3.00	-24.25	55.12	0.22	0.19
Null model	0.42	\	\	\	1.00	-28.86	59.81	0.02	0.00

Hatching success and flight initiation distance

Hatching success was negatively correlated with FID and nest cover. Furthermore, the interaction between them revealed that FID was less important for nests with low cover (visible nests; Figure 2.6,Table 2.4).

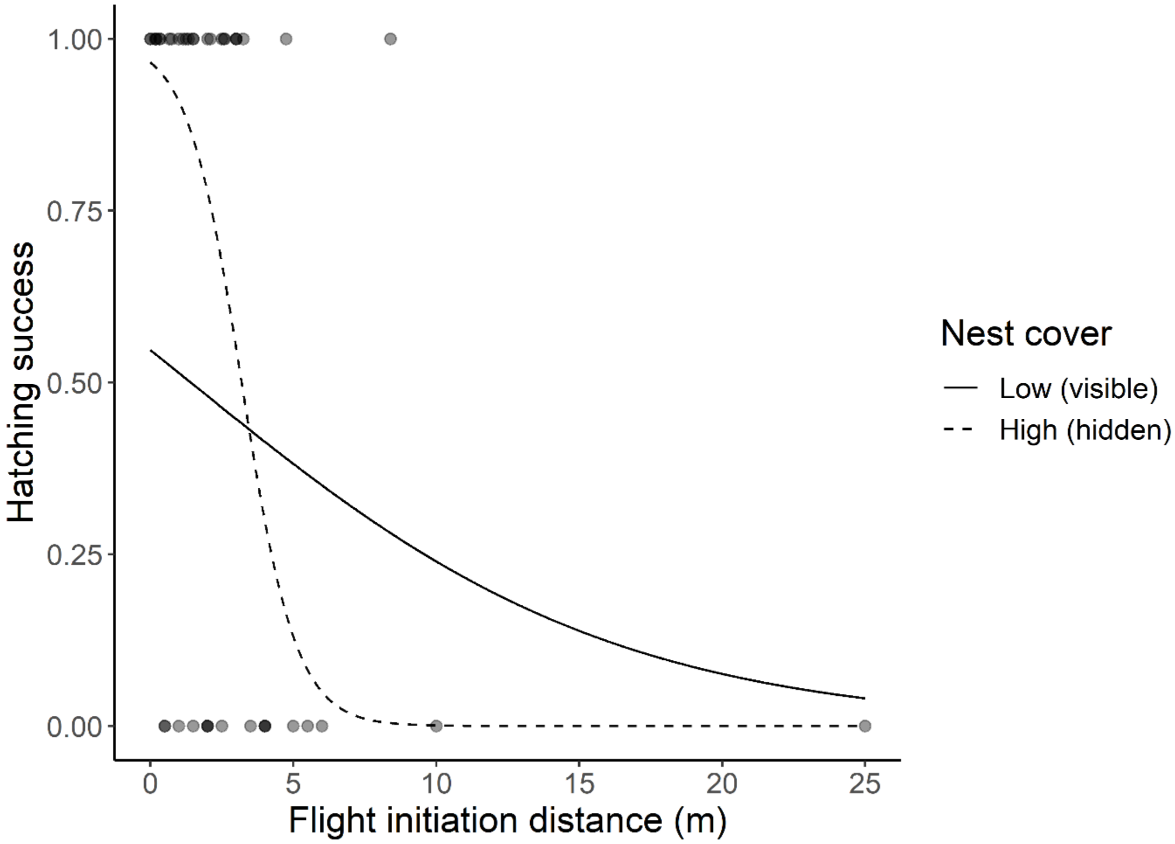


Figure 2.6 Relationship between hatching success and FID at low and high levels of nest cover. Nest cover values were one standard deviation below (18% cover) and above (88% cover) the mean (53% cover). Closed circles show the raw data and are transparent to show overlapping points (n = 44); solid lines are the predictions from a GLM, plotted for the mean value of all other variables.

Fledging success

Fledging success was negatively correlated with the total amount of rainfall (Figure 2.7a, Table 2.5) and with the number of heavy rainfall days (Figure 2.7b, Table 2.6) in the week after hatching. Fledging success was not correlated with the number of rainfall days; only year was retained in the best-fitting model set (Table 2.7).

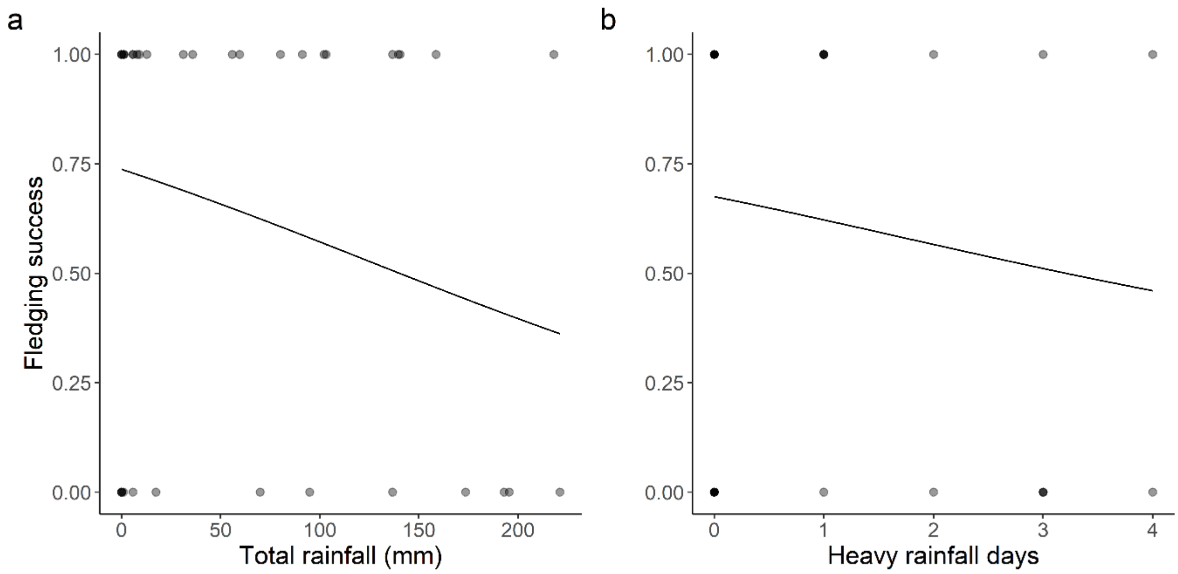


Figure 2.7 The relationship between fledging success and (a) total rainfall, and (b) the number of heavy rainfall days, on the day of and in the week after hatching. Closed circles are the raw data and are transparent to show overlapping points (n = 37); solid lines are the predicted relationships from GLMMs, plotted for the mean value of all other variables.

Table 2.5 The results of the GLMMs of the effect of total rainfall on fledging success. The models presented are those within 2AICc of the best-fitting model together with the null model for comparison.

Intercept	FED	FED^2	Total rainfall	Year	Total rainfall x year	df	Log likelihood	AICc	Weight	Marginal R^2	Conditional R^2
0.95	\	\	-1.28	+	\	5.00	-18.52	48.97	0.38	0.45	0.45
0.00	\	\	\	+	\	4.00	-20.73	50.71	0.16	0.30	0.30
0.50	\	\	\	\	\	2.00	-24.54	53.43	0.04	0.00	0.00

Table 2.6 The results of the GLMMs of the effect of heavy rainfall days on fledging success. The models presented are those within 2AICc of the best-fitting model together with the null model for comparison.

Intercept	FED	FED^2	Heavy rainfall days	Year	df	Log likelihood	AICc	Weight	Marginal R^2	Conditional R^2
0.00	\	\	\	+	4.00	-20.73	50.71	0.25	0.30	0.30
0.65	\	\	-0.80	+	5.00	-19.40	50.74	0.24	0.38	0.38
0.50	\	\	\	\	2.00	-24.54	53.43	0.06	0.00	0.00

Table 2.7 The results of the GLMMs of the effect of rainfall days on fledging success. The models presented are those within 2AICc of the best-fitting model together with the null model for comparison.

Intercept	FED	FED^2	Rainfall days	Year	df	Log likelihood	AICc	Weight	Marginal R^2	Conditional R^2
0.00	\	\	\	+	4.00	-20.73	50.71	0.36	0.30	0.30
0.50	\	\	\	\	2.00	-24.54	53.43	0.09	0.00	0.00

Discussion

Our results show that the adults of nests close to footpaths have lower hatching success and larger FIDs than those far away from footpaths. This suggests that humans approaching, and being close to, a nest can have a negative impact on reproductive success in common sandpipers; human-related disturbance has been shown to have negative effects for several other species (Langston *et al.* 2007, Geffroy *et al.* 2015). The effect of disturbance and how it interacts with predation appears to vary between species (Lafferty 2001a, Lafferty 2001b, Lord *et al.* 2001, Baudains & Lloyd 2007), and this is likely to depend on behavioural traits such as boldness (Cooper *et al.* 2015). For example, species that become habituated to human presence might benefit from increased disturbance through reduced predator abundance (Richardson *et al.* 2009, Geffroy *et al.* 2015, Syrová *et al.* 2020). Interestingly, the negative correlation between FID and distance from footpaths suggests that common sandpipers have become sensitised to humans approaching the nest, as has been suggested in another population (Yalden 1992). Further, our results showing that FID was negatively correlated with hatching success suggest that this could be an important mechanism driving the effect of disturbance. Large FIDs are likely to mean that adults spend less time incubating and have lower nest attentiveness, which can reduce hatching success through its effect on embryo development and by increasing the susceptibility of a nest to predation (Westmoreland & Best 1985, Lord *et al.* 2001, Verhulst *et al.* 2001, Frid & Dill 2002). Large FIDs could also make the nests easier to find by giving the predator an area in which to search (Burrell & Colwell 2012, Cooper *et al.* 2015). Indeed, we found it easier to find nests when the incubating adults flushed from large distances. On the other hand, a low FID is likely to increase the risk of the incubating bird being predated and therefore represents a trade-off between adult and clutch survival (Gómez-Serrano & López-López 2014). Our results suggest that birds with higher nest attentiveness (i.e. low FIDs) have increased hatching success. Further work carrying out predator surveys and monitoring incubation schedules in areas with varying disturbance levels could help to unpick the interacting effects of predation and disturbance.

The amount of nest cover was positively correlated with hatching success and negatively correlated with FID. Increased cover is likely to benefit the nest in multiple ways (but see Gómez-Serrano & López-López 2014). Firstly, it will reduce the visibility of the incubating adult and eggs to potential predators (Troscianko *et al.* 2016, Laidlaw *et al.* 2020). Secondly, in our study, incubating adults on well-covered nests are less likely to flush, which our results suggest would increase hatching success, potentially through reduced visibility to predators (Burrell & Colwell 2012, Cooper *et al.* 2015). The benefit of increased vegetation cover through its effect on FID could depend on the most abundant predators. For example, birds that do not flush readily on nests with large amounts of vegetation are likely to be well hidden from visual predators such as corvids, which might take cues from the movement of incubating adults. However, these individuals may be more vulnerable to mammalian predators that primarily use olfactory mechanisms to find their prey (Burrell & Colwell 2012, De Jong *et al.* 2013). Perhaps counterintuitively, our results show that if adults flush from over four metres away, hatching success is lower for well-hidden nests than for more visible nests. In theory, one might expect hidden nests to have higher hatching success than visible nests, regardless of FID (Bowman & Harris 1980). In our case, it might be that adults flushing from hidden nests are more visible to predators as they leave, because they have to escape through large amounts of vegetation (Burrell & Colwell 2012), although the opposite relationship has been found for European nightjars (*Caprimulgus europaeus*; Langston *et al.* 2007. We would need experimental manipulation of vegetation cover at nest sites to understand its influence on FIDs and hatching success, as their relative importance are likely to change throughout the breeding season due to vegetation growth (Laidlaw *et al.* 2020).

Our results show that proximity to the river negatively affects hatching success, which could be because of the prevalence of American mink and Eurasian otter in our study site; these are generalist predators that regularly use the riverbanks. While they may be unlikely to regularly encounter common sandpiper nests (*S.P. Sharp, pers. Comm.*), it could be that predators on the riverbanks cause incubating adults to flush more easily, thereby making them more visible (Díaz *et al.* 2013). Alternatively, our distance from the river metric may have been correlated with habitat fragmentation around the nest site. The rivers in our study site are lined with narrow wooded strips which are in turn surrounded by farmland. Common sandpipers rarely nest in open fields (*Pers. Obs.,* Cramp *et al.* 1983), preferentially using the narrow strips of denser vegetation along the river. Therefore, the nests that were further from the river were also in larger areas of natural woodland. Narrow wooded strips surrounded by farmland can have increased numbers of predators (Saracco & Collazo 1999), meaning that predation could also be higher (Andrén *et al.* 1985; but see Fahrig 2017). Several studies have suggested that this is driven by an increased number of predators, which are at higher densities in farmland landscapes, foraging more frequently within neighbouring woodland (Andrén & Anglestam 1988, Paton 1994, Saracco & Collazo 1999).

More work is needed to identify the predators associated with predation events throughout the site, for example by using remote cameras.

We found that hatching success was relatively unaffected by distance from the footpath when the nest was close to the river, which could have been driven by the relative importance of different predators between these areas. It could be that proximity to the river increases predation from mammals which use olfactory cues to find nests, whereas nests that are far from the river are more susceptible to predators using visual cues such as corvids (Chalfoun *et al.* 2002). The nests that are more susceptible to visual predators may be at increased risk from disturbance, as being flushed from the nest alerts these predators to the nest's location (Burrell & Colwell 2012, De Jong *et al.* 2013). Even if we are unsure of the reason for the importance of this interaction, our results suggest that unfragmented natural habitats and greater distance from human disturbance increase hatching success.

Our hatching success models could have been affected by biases arising from the stage at which nests were found and because of nests that failed prior to being found. As already discussed, common sandpiper nests are particularly inconspicuous during egg laying meaning that we could have missed nests if they were predated early in the nesting cycle or in the case of replacement nests after failure (Verhoeven *et al.* 2020). Finding nests at late stages of incubation means that the probability of eggs surviving until hatching is greater than if they were found during the early stages of incubation (Mayfield 1975, Shaffer 2004). This could have biased our models and led to spurious correlations being found between hatching success and first egg date, for example. Rerunning our models using Mayfield analyses could account for these biases by considering the number of days that nests in our population had been exposed to predation (Mayfield 1975, Shaffer 2004).

Fledging success was negatively correlated with total rainfall and heavy rainfall days in the week following hatching, but not with the number of rainfall days. This suggests that common sandpiper chicks are affected by extreme rainfall events, rather than persistent light rain. Heavy rainfall has been shown to reduce chick survival, particularly for the youngest and those in the worst body condition (Gach *et al.* 2018). Young chicks are dependent on adult brooding to maintain their body temperature (Beintema & Visser 1989), but during brooding, the chicks are unable to forage and may therefore fail to meet their daily energy requirements (Schekkerman *et al.* 2001). Once chicks get older, the relative proportion of their energy budget required for thermoregulation decreases substantially, meaning that they may be less susceptible to poor weather (Klaassen *et al.* 1989, Schekkerman *et al.* 2001, Gach *et al.* 2018). This reliance on adults could leave young chicks particularly susceptible to human disturbance if, for example, it coincides with periods of heavy rainfall which forces them to hide away from their parents (Verhulst *et al.* 2001). Unfortunately, we were unable to test the effect of disturbance on fledging success because we did not have any estimates of the number of walkers using different parts of each territory. Common sandpiper territories range from 200-500m in length (Holland *et al.* 1982) and, therefore, chicks may be able to avoid highly disturbed areas (Finney *et al.* 2005, Pearce-Higgins *et al.* 2007). However, studies of other species have suggested that disturbance could still impact chicks through its effects on foraging (Lord *et al.* 1997, Frid & Dill 2002), although this might vary with disturbance level and food availability (Leseberg *et al.* 2000, Baudains & Lloyd 2007).

Finally, hatching and fledging success show differing trends throughout the season. Early and late nests had a lower probability of hatching than those laid in the middle of the season. Although many studies report increased hatching success for individuals breeding earlier in the year (Hochachka 1990, Verhulst *et al.* 1995, Norris *et al.* 2004, Morrison *et al.* 2019), early nests might have reduced vegetation cover compared to later nests (Laidlaw *et al.* 2020) or might be more vulnerable to bad early season weather conditions which are likely to be more volatile than in late spring (Newton 2010). Large amounts of rainfall increase water levels and could lead to nests being flooded, but within the three-year study period we know of only one nest that failed due to flooding, so this seems unlikely to be a major influence. Nests towards the latter stages of the season were also more likely to fail. This has been reported for many other species, with a variety of mechanisms suggested including age, body condition and territory quality (Verhulst & Nilsson 2008). For example, birds able to arrive early to their breeding grounds might be those in better body condition, which itself could increase reproductive success or might provide them with access to the best quality territories (Currie *et al.* 2000, Jonzén *et al.* 2007, Verhulst & Nilsson 2008). Late arriving birds therefore only have access to the worst quality sites. In many other species, arrival and first egg date are correlated with age, meaning that older birds have higher reproductive success than younger individuals (Daunt *et al.* 1999, Verhulst & Nilsson 2008). Interestingly, FED was not correlated with fledging success for common sandpipers. This suggests that other factors might reduce the importance of predation on chicks throughout the season. For example, there was considerably more vegetation cover towards the latter parts of the breeding season than during the early stages, which could provide cover for vulnerable chicks and reduce the chances of predation (Bowman & Harris 1980, Angelstam

1986, Gregg *et al.* 1994, Lee *et al.* 2006). Further, predation may have affected the total number of chicks fledging, rather than our binary measure of fledging success, which could be crucial for population trends through its effects on productivity and recruitment.

Together, our results have important implications for the conservation of common sandpipers, as they suggest that higher levels of human activity could affect breeding birds. This is especially relevant in the UK, where there are high densities of people using the extensive network of public footpaths. This means that increasing the amounts of natural undisturbed habitat is likely to be important for this species (Arlettaz *et al.* 2011). Furthermore, our results suggest that incubating adults do not become habituated to human disturbance, and that this might significantly reduce hatching success. We were unable to test for the impacts of disturbance on common sandpiper chicks, but studies of other species have shown that this is likely to be important and therefore requires further work, especially in any interaction with extreme weather events (Frid & Dill 2002).

Chapter 3 The ecology and behaviour of common sandpipers in winter

Introduction

Understanding the causes of recent declines in migratory bird populations requires knowledge of their behaviour and ecology. However, the majority of studies have focussed on the breeding season and for many species we know little about other stages of the lifecycle (Sheehan & Sanderson 2012, Vickery *et al.* 2014). Studying the wintering ecology of migratory species is important because it has significant implications for individual fitness and population dynamics throughout the year (Mcnamara *et al.* 1998, Newton 2010). For example, an increasing number of studies have found that conditions on the wintering grounds can affect survival and reproductive success (Marra *et al.* 1998, Sillett & Holmes 2002, Danner *et al.* 2013). Most of this research relies on indices to infer wintering ground conditions, such as remote sensing metrics or stable isotope analyses (Bearhop *et al.* 2004, Norris *et al.* 2004, Saino *et al.* 2004). There are relatively few field-based studies of migratory birds during winter, meaning that we lack fundamental information about their ecology at this critical time of the year (Vickery *et al.* 2014, Willemoes *et al.* 2018).

The few studies that have investigated habitat use during winter have revealed intraspecific variation (Ruiz-Sánchez *et al.* 2017, Willemoes *et al.* 2018). For example, Willemoes *et al.* (2018) found that in several migratory passerines wintering in Ghana, individual home ranges and population densities differed between disturbed and undisturbed sites. These differences in wintering ecology may result in fine-scale variation in habitat use that might not be apparent when using remote sensing techniques. Therefore, it is important to investigate habitat selection during winter using field-based methods, as it might be important for understanding the factors limiting migratory bird populations (Piersma 2002). Recent research has focussed on the wintering ecology of terrestrial species (Blackburn & Cresswell 2016c, Ruiz-Sánchez *et al.* 2017, Willemoes *et al.* 2018), but less is known about wetland birds despite their recent population declines (Both *et al.* 2009, Vickery *et al.* 2014).

One potentially interesting aspect of habitat use in wading birds is water salinity, as many species use both freshwater and saline habitats. This is important because of the costs associated with salt and osmoregulation (Mahoney & Jehl Jr 1985, Piersma 1997). A build-up of salt in the body can lead to severe dehydration and reduce chick growth rates during the breeding season (Hannam *et al.* 2003). Birds using saline habitats have developed strategies to reduce salt intake and increase salt excretion, both of which can increase energy expenditure (Mahoney & Jehl 1985, Mahoney & Jehl Jr 1985, Sabat 2010). In fact, birds in saline environments have higher basal metabolic rates and overall energy consumption than those using freshwater (Gutiérrez *et al.* 2011), and these increased costs may have important consequences for migratory species. Individuals reliant on saline habitats prior to spring migration, for example, may have reduced energy intake rates which could influence migration (Piersma 2002). However, there also appear to be benefits associated with saline habitats, as some species have reduced parasite loads compared to those using freshwater sites (Figuerola 1999, Mendes *et al.* 2005, Blakey *et al.* 2006).

The population trends of many Afro-Palearctic migratory species are correlated with conditions in West Africa and the influence of these is predicted to increase because of agricultural intensification and urbanisation (Zwarts & Van Horssen 2009, Ockendon *et al.* 2012, Vickery *et al.* 2014, Willemoes *et al.* 2018). However, we know relatively little about the wintering ecology of these species (Vickery *et al.* 2014), and wintering behaviours may cause intraspecific variation in access to resources (Brown & Long 2007). Importantly, for some species we even know little about key life history traits such as return rates and winter site fidelity. This lack of basic information about the wintering ecology of migrants means that further knowledge of habitat use and territorial behaviour on the wintering grounds could benefit future conservation efforts (Sheehan & Sanderson 2012).

Common sandpipers (*Actitis hypoleucos*) are known to winter in West Africa, which we know is the wintering location of some breeding populations from the UK and Scandinavia (Chapter 5; Summers *et al.* 2019). Pearce-Higgins *et al.* (2009) suggested that wintering conditions could be one of the major causes of recent population declines and that more work focused on the non-breeding season was therefore needed. Previous studies of common sandpipers in winter suggest that they might be site faithful and have relatively high return rates to wintering sites (Sauvage *et al.* 1998). These factors are likely to be important determinants of their susceptibility to winter habitat change. They also appear to be habitat generalists, as they are found along the coast, in mangrove forests and on many inland freshwater bodies (Cramp *et al.* 1983). However, no study has formally investigated their return rates to wintering sites or the influence of water chemistry on their presence (Cramp *et al.* 1983). Furthermore, relatively little is known about their wintering behaviour, but anecdotal evidence shows that they respond to conspecifics and tape lures, which has been suggested as evidence of territoriality (Cramp *et al.* 1983, Sauvage *et al.* 1998). In order to understand more about the wintering ecology of common sandpipers, we investigate (1) return rates to the wintering grounds, (2) the influence of water chemistry on habitat use and foraging success from direct field observations, and (3) the response of individuals to conspecifics using a playback experiment. We also investigate sex differences in their wintering distributions using the stable isotope ratios of feathers and geolocator data (Chapter 5).

Methods

Ringing, return rates and sexes

Wintering ground fieldwork was carried out in Djoudj National Bird Sanctuary, Senegal (16.3600˚N, 16.2753˚W; Figure 3.1) in January and February 2018 and in January 2019. In 2018, we established a colour marked population (described in Chapter 4) which was closely monitored throughout the six-week study period in order to investigate habitat choice, foraging success and territoriality. We netted and trapped common sandpipers along the edge of freshwater and saline pools, targeting individuals on daytime feeding areas and at roost sites (Chapter 4). Almost all ringing was carried out using tape lures and specific individuals were often targeted using interactive playback methods. For two weeks in 2019, we carried out thorough daily searches of the site to resight colour marked individuals and to recover geolocators (Chapter 4).

In addition to the colour ringing and fitting of geolocators discussed in Chapter 4, we collected blood and feather samples from the individuals caught in both Senegal and in Sedbergh, Cumbria, UK (study site described in Chapter 2). Blood samples were taken for the molecular sexing of individuals; feather samples were used to carry out stable isotope analyses to investigate the wintering distributions of individuals from Cumbria. Approximately 20-50µl of blood was collected by piercing the brachial vein with a hypodermic needle and immediately transferred to a plastic vial containing 1ml of 100% ethanol using a capillary tube. We also cut an approximately 0.5 – 1cm section from the tip of a primary covert using a pair of scissors; feather samples were stored in sealed plastic sample bags.

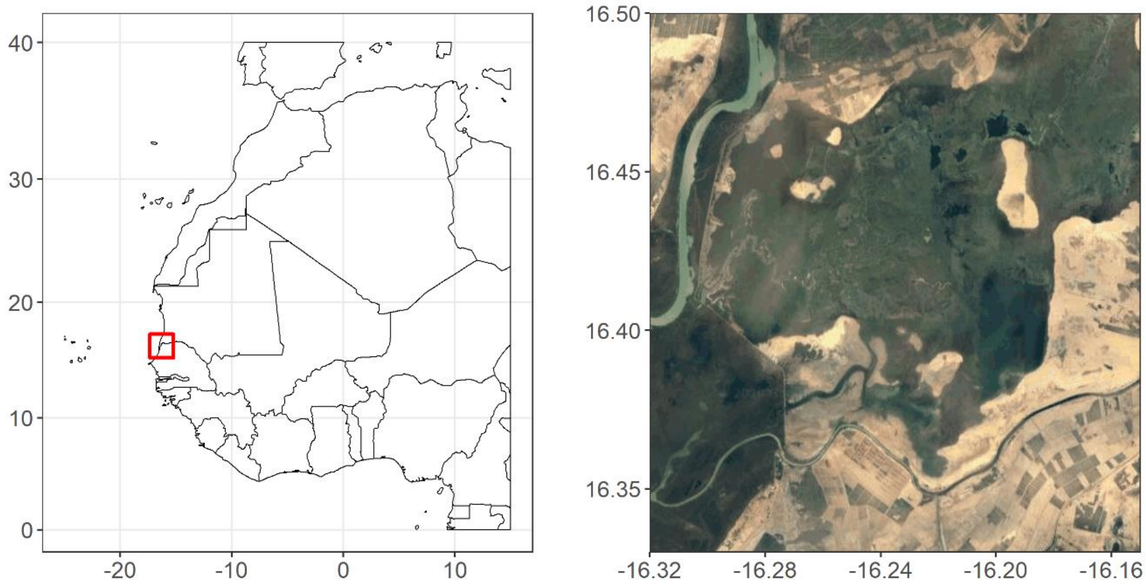


Figure 3.1 The location of Djoudj National Bird Sanctuary, Senegal. The satellite image was taken in December (year unknown) and downloaded from Google maps using the package 'ggmap' (Kahle & Wickham 2013); the conditions pictured are considerably wetter than they were when we carried out fieldwork in January and February 2018 and 2019.

Molecular sexing

Blood samples of the common sandpipers caught in Cumbria and Senegal were analysed at the NERC Biomolecular Analysis Facility (NBAF), University of Sheffield, in January and February 2020. DNA was extracted using the ammonium acetate technique (https://www.protocols.io/view/dna-extraction-using-the-ammonium-acetate-techniqu-jjwckpe?version_warning=no) and W- and Z-linked sequences were amplified using PCR with Z37B and Z002A primers. These primers have been shown to work with a wide range of different bird species (Dawson 2008, Dawson *et al.* 2015). 1µl volumes containing 10ng or more of DNA were used with each primer. PCR amplification conditions were 95˚C for 15min, followed by 35-45 cycles of 94˚C for 30s; 56˚C for 90s; 72˚C for 1 min; and 72˚C for 10min. We increased the PCR volumes (to 2 or 4µl) and the number of cycles if initial runs failed to amplify. PCR products were loaded on a 96-capillary ABI 3730 DNA analyser and genotypes assigned using GeneMapper software (Applied Biosystems).

Of the 105 adult common sandpipers sexed, five failed to amplify after multiple attempts. The 100 assigned genotypes were verified using fourteen known-sex individuals, as determined by catching gravid females and assuming their partners were male; there were no contradictory results between the molecular sexing and field-based methods. Furthermore, there were no cases of same-sex pairs being assigned to any of the nests found during the breeding season. The results of the molecular sexing suggested that male and female common sandpipers may be segregated during winter (see results). Therefore, to investigate this we used the stable isotope ratios of feathers (see below) and the geolocator data from individuals tagged in Cumbria (Chapter 5). Using the geolocator data, we plotted the mean location of individuals during their wintering period (as described and used in Chapter 5).

Stable Isotopes

In order to investigate the wintering locations of common sandpipers from the UK, we analysed the Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) isotope ratios of feathers ($n = 72$). The $\delta^{13}C$ and $\delta^{15}N$ content of the feathers were determined using continuous flow analysis by EA-IRMS at the Lancaster University Stable Isotope Analysis Facility. The feathers were washed in 1:1, methanol:dichloromethane solution and left to soak for four hours. Each feather was then rinsed using a fresh mix of the same solution. Both of these solvents are degreasers and the latter performs in a similar way to the more commonly used chloroform. Each feather was dried and then cut into fine strips (*circa* 1mm), transferred to tin capsules (which act as a catalyst to improve combustion) and weighed; samples weighed between 0.2 and 1.4 mg. The samples in the tin capsules were combusted using a Vario PROcube Elemental Analyser to convert the Carbon and Nitrogen into CO_2 and N_2, respectively. These gases were then transferred to an Isoprime 100 Isotope Ratio Mass Spectrometer to analyse their isotope ratios.

Standards of known isotope ratio were run alongside all samples in order to calibrate the reported numbers to the δ values on the appropriate scale: $\delta^{13}C$ ‰VPDB, $\delta^{15}N$ ‰Air. For carbon, the calibration standards used were IAEA CH6 and LEC-Acetanilide; the first is an international standard, the second is traceable to international standards. For nitrogen, the calibration standards were IAEA 600 and USGS 41, both international standards. All analyses were also run with a laboratory standard of known isotope ratio, USGS 14. These were run at the start, middle and end of the analyses to ensure that the isotope values did not drift over the course of the analysis run. Following analyses, nitrogen isotopic values were corrected for peak height following amplitude check using international standard USGS 14. We compared the $\delta^{13}C$ and $\delta^{15}N$ isotopes between females and males using t-tests for unequal variances.

Habitat choice

For five weeks in 2018, water bodies at Djoudj were visited regularly to look for common sandpipers and resight colour ringed individuals. Each visit to a water body lasted 10 minutes, during which the banks were surveyed using a Leica telescope 25-50x magnification. The entire bank of large water bodies was not always visible from a single vantage point; in these cases, the water body was observed from different points along the bank in order to get a clear view of all suitable common sandpiper habitat. Each watch of the same water body from different points were considered separate 'watching locations'; each watching location was visited between two and eight times. The proportion of times a common sandpiper was seen during watches from the same watching location was analysed in order to investigate the factors affecting their presence or absence. The presence or absence of a common sandpiper during a watch was noted and the water chemistry from the nearest point on the water body was examined; salinity (ppt) was measured using a VWR EC300 unit, and electrical conductivity (mS), temperature (°C) and pH were measured with a Hanna HI-98129 combined probe.

Each time a common sandpiper was seen, a foraging success watch was attempted. Individuals were watched from between 25 and 100m away, for a maximum of 10 minutes (range: 30 seconds to 10 minutes) through the telescope. Each peck by the focal bird was counted using a tally counter and the number of successful attempts recorded; a peck was counted only if the outcome was certain and successful pecks were determined by watching for swallowing or beak snapping. The watch ended if the bird was lost from sight or if it had been watched for 10 minutes. The same water chemistry measurements as above were taken after each foraging success watch from where the individual spent most of its time during the session.

All analyses were carried out in the R environment (Team 2020). The proportion of times a common sandpiper was seen during repeat visits to the same watching location ($n_{\text{watching locations}} = 50$, $n_{\text{visits}} = 146$) was analysed using a generalised linear mixed effects model (GLMM; Bates *et al.* 2015), to investigate how water chemistry affected presence or absence. We fitted the proportion of times a common sandpiper was seen when visiting a watching location as the response variable in a model with a binomial error distribution. We fitted the mean salinity, conductivity and pH across all visits to a water body as explanatory variables, as these were thought to be potentially important factors affecting the presence of common sandpipers. We also fitted water temperature as an explanatory variable to control for potential changes due to sampling time. All explanatory variables were centred and standardised prior to analyses. We fitted water body as a random intercept to control for repeated measures from the same water body at different watching locations.

Foraging success

Foraging success watches (*n* = 59) were carried out at thirteen different water bodies and for eighteen different individuals. The influence of water chemistry on the proportion of successful foraging attempts, hereafter 'foraging success', was analysed using a GLMM. We fitted the proportion of successful pecks as the response variable in a model with a binomial error distribution. We fitted salinity, conductivity, pH, day of the year, water temperature and time of day as explanatory variables; all were centred and standardised prior to analysis. Day of the year was included in order to control for birds potentially feeding more intensively as spring migration approached. In order to control for repeated watches of the same individuals and from the same water body, we fitted individual identity and water body identity as crossed random intercept terms. A number of foraging success measurements involved unringed individuals. During our surveys in 2018, colour ringed individuals were always seen within the same 1km area. We therefore considered all sightings of unringed birds within 1.5km of each other as involving the same individual; otherwise these birds were treated as different individuals ($n_{\text{colour ringed}} = 9$, $n_{\text{unringed}} = 6$).

For both the analyses of habitat choice and foraging success, collinearity between explanatory variables was assessed using correlational plots and variance inflation factors (VIFs). Salinity and conductivity were highly correlated (for both datasets, $r > 0.9$) and so only salinity was retained in subsequent analyses because we were more interested in its effect due to the challenge it can pose to wading birds. Time of day and water temperature were also highly correlated ($r_{\text{habitat choice}} > 0.7$; $r_{\text{foraging success}} > 0.6$) and so only water temperature was included. All other correlations in both datasets were low enough to have independent effects in the models ($r < 0.5$) and the VIFs were low (< 2). The explanatory variables for the analysis of the factors affecting the presence or absence of common sandpipers were therefore salinity, pH and water temperature. The explanatory variables for the analysis of the factors affecting foraging success were therefore salinity, pH, day of the year and water temperature. In both models, all two-way interactions were included as different aspects of water chemistry may interact with one another. We fitted all possible models and those within two AICc units (2AICc) of the best-fitting model are presented here (Barton 2020); R^2 values for each model were also obtained (Nakagawa *et al.* 2013). We averaged the models within 2AICc of the best-fitting model and used the estimates of this for plotting. All models were validated using a binned plot of the residuals versus predicted values and an index plot of residuals.

Response to conspecifics in winter

We used playback experiments to investigate the response of focal individuals to the simulated presence of a conspecific. We compared the responses of individuals in winter to those of individuals during the breeding season, during which birds are likely to be territorial (Holland *et al.* 1982, Cramp *et al.* 1983), to infer whether common sandpipers may be territorial during the winter. We carried out two playback experiments, the first in Djoudj National Bird Sanctuary and the second in the Cumbria study site.

Playback file preparation

Common sandpipers have a number of different vocalisations including a 'long call' and a single note alarm call (Cramp *et al.* 1983). The first is often considered a territorial call as it is usually heard early in the breeding season when birds are arriving and establishing territories, but could also be used in mate attraction (Dougall *et al.* 2010). The second call they give when a potential predator is near the nest or chicks (Cramp *et al.* 1983). To carry out our playback trials, we downloaded five recordings of single individuals performing long calls from the xeno-canto website (https://www.xeno-canto.org/) which is an online repository for bird sounds. All recordings originated from countries within northern Europe (three from the UK and two from Sweden), to minimise the potential effects of regional variation in call structure. The idea was that the recordings would stimulate natural territorial responses but were from birds that the focal individual were unlikely to have been in contact with. Finally, we only used recordings which had an 'A' grade quality rating.

Recordings were edited using RavenLite 2.0 software to isolate a 17-20 second section in which the long call was clearly audible above background noise or other bird species and performed without interruption by conspecifics. The 17-20 second window was the longest duration of vocalisation we could obtain from the recordings that met the above criteria. In order to reduce background noise, usually flowing water, all lower frequency sounds were removed from each recording (below 1.50kHz). The lowest frequency of the long call of common sandpipers is 3.5kHz (*Pers. Obs.*). Each 20 second section was repeated to produce a track lasting five minutes in length.

Playback trials

In Senegal, playback trials were performed whenever a common sandpiper was found on a water body. This usually occurred after a foraging success watch was carried out (described above). In the UK, playback trials were carried out by targeting known pairs at established territories during egg laying and incubation. In all cases, the pair were identified from their colour rings and their nest had already been found. The playback trials were loud enough to be overheard by individuals in neighbouring territories. Therefore, we avoided carrying out playback trials at neighbouring territories on the same day in the UK, or at locations within earshot in Senegal.

We started playback trials once a common sandpiper had been seen nearby. In most cases the individual could be seen foraging at the edge of the river (UK) or pool (Senegal). In some cases, the individual had flown past and landed just out of sight, but if it was near enough to hear the call, the trial was carried out regardless. We used a FoxPro Inferno speaker with remote control so that we could start the call once we had retreated to approximately 50m away from the speaker. The distance that the observer stood from the speaker varied between locations because of the terrain, but in no cases did we observe behaviours typical of disturbed individuals before the playback trial started (e.g. 'head-bobbing'). One of the five playback tracks was chosen using a random number generator and the volume of the speaker was set to maximum, which was consistent with the volume of a normal common sandpiper territorial call.

A playback trial began at the point that the observer started the call and ended when the focal individual had returned to 'normal' behaviour (defined below). The observer spoke quietly into a voice recorder to record the behaviours of common sandpipers during a playback trial. From these audio files, we obtained measurements for several variables to investigate the level of territorial response. The 'time to respond' was the amount of time in seconds that it took an individual to first respond to the call. A response to the tape was defined as any alarm or long call directed at the speaker, a movement towards the speaker or any wing display. When defending territories in the breeding season, individuals are often seen raising one or both wings in response to an intrusion (Holland *et al.* 1982, Cramp *et al.* 1983). Flying or walking directly towards the speaker were considered responses to the tape but getting closer to the tape whilst foraging was not. We also measured how long it took for the focal individual to 'return to normal'. We considered an individual to have returned to normal behaviour in the following circumstances: if the bird flew a considerable distance away from the speaker (e.g. it landed the other side of the river or pool) and stopped calling, or if it flew out of sight and stopped calling, or if it started foraging continuously. During the trial we also recorded whether the individual performed an alarm and/or long call in order to investigate the type of response to the playback. We believe that a greater response to conspecific would involve a shorter time to respond and a longer time to return to normal. For the playback trials in Senegal we were also interested in whether the level of response was related to the quality of habitat that the individuals were defending. Therefore, following a successful playback trial in Senegal, we took the same water chemistry measurements as described above from the water body that the focal individual was using prior to disturbance.

We carried out tests to investigate how the time to respond and the time to return to normal (1) differed between Senegal and the UK, (2) changed over time, and (3) were affected by water chemistry. We compared the time to respond and the time to return to normal between Senegal and the UK using Mann-Whitney U-tests because the data were non-normally distributed ($n_{Senegal} = 14$, $n_{UK} = 15$). We assessed whether the time to respond and the time to return to normal were correlated with the day of the year (as a Julian date) using Spearman’s rank correlation tests. We compared the frequency with which long calls and alarm calls were given between Senegal and the UK using binomial proportions tests. Finally, we used generalised linear models (GLMs) to investigate the effect of water chemistry in Senegal on the time to respond and the time to return to normal, separately ($n_{respond} = 14$, $n_{normal} = 13$). Time to respond and time to return to normal were fitted as response variables in two separate models; we fitted salinity and pH (both centred and standardised prior to analysis) and the interaction between the two as explanatory variables. We fitted these models with a ‘quasipoisson’ error distribution to account for overdispersion and used the full model for plotting the results.

Results

Ringing, return rates and sexes

In Senegal in 2018 we ringed twenty-one birds ($n_{geolocator} = 10$, $n_{colour\ ring} = 11$), seven of which were ringed at roost sites (two were fitted with a geolocator and five with rings only). As discussed in Chapter 4, eight of the ten geolocator-tagged birds were resighted in 2019. The two remaining birds were caught at evening roost sites and their daytime feeding areas were unknown, so it is possible that they were present outside of the survey area. Four of the six birds (67%) in Senegal that were colour ringed at their daytime feeding areas but not tagged returned in 2019. The return rate in 2019 for birds that were not caught at roost sites in

2018 was therefore 86% (12/14). On several occasions in 2019, we attempted catches at the roost sites we had found in 2018 but had no success in recapturing individuals. In 2019, we caught and sampled an additional seven unringed birds ($n_{\text{total ringed}}$ = 28). Of the 28 Senegalese birds that were sexed, four failed to amplify with either of the primers; the remaining 24 Senegalese birds were all male.

Large scale wintering distributions

Male and female common sandpipers from the UK did not have significantly different $\delta^{13}C$ isotope ratios (T_{29} = -0.14, P = 0.89) or $\delta^{15}N$ isotope ratios (T_{30} = -0.11, P = 0.91; Figure 3.2, n_{female} = 18, n_{male} = 17). Furthermore, there was considerable overlap in the mean wintering ground locations as determined by geolocators of females and males (Figure 3.3).

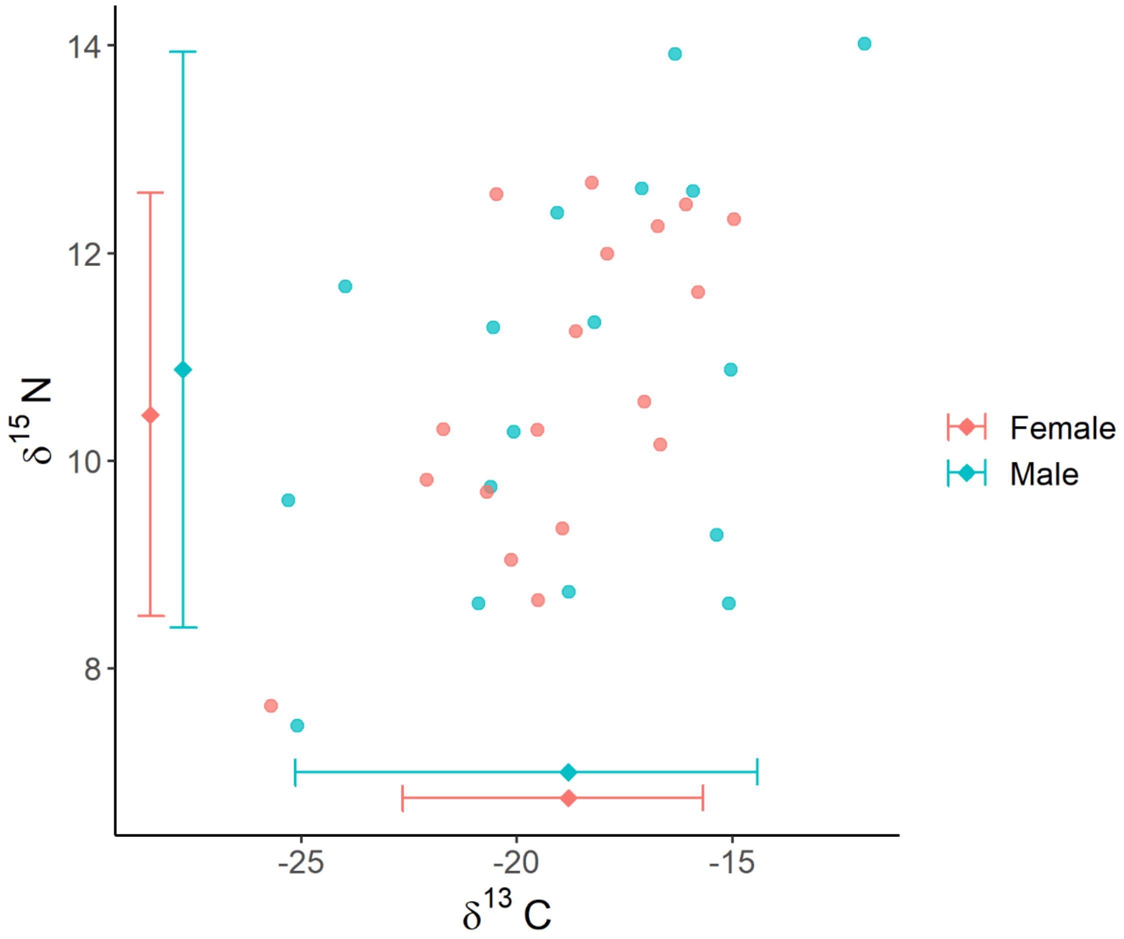


Figure 3.2 The relationship between $\delta^{13}C$ and $\delta^{15}N$ isotope ratios from the feathers of male and female common sandpipers caught in the UK. Closed circles are the raw data; the solid lines and diamonds represent the 95% quantiles and median of the distributions for females and males, respectively.

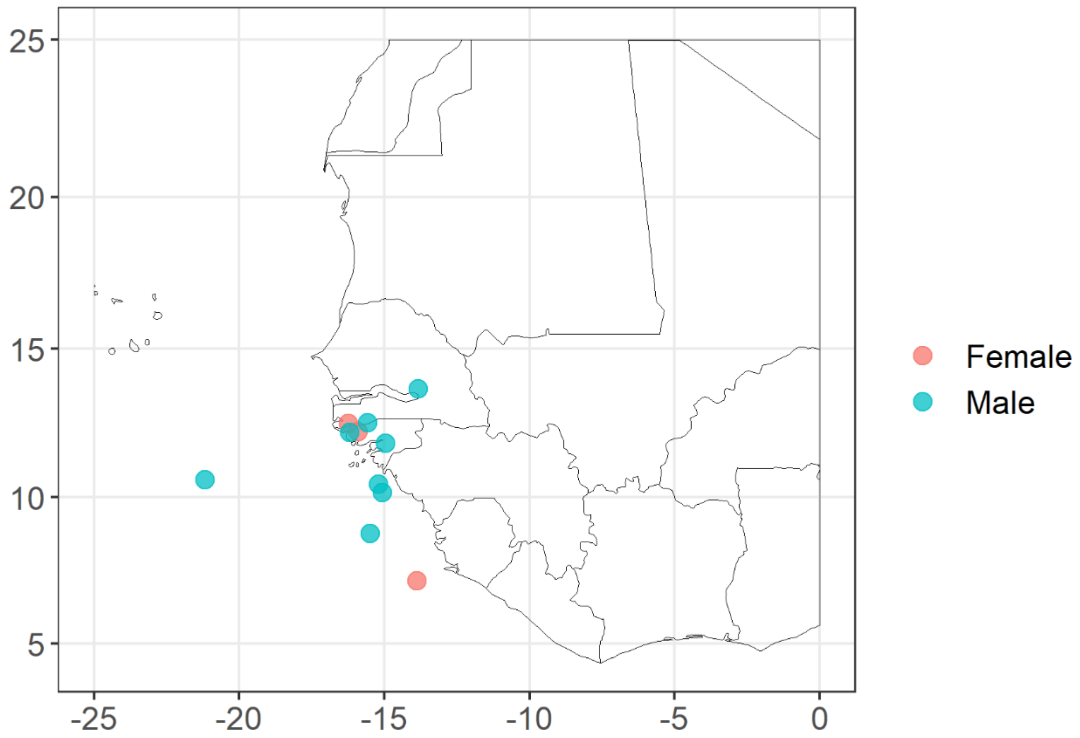


Figure 3.3 Mean wintering regions of male (n = 8) and female (n= 3) common sandpipers as determined by geolocators attached to common sandpipers in Cumbria, UK.

Habitat choice and foraging success

Common sandpiper presence

Average salinity was lower in pools where common sandpipers were seen than in those where they were not (seen: 16.5 ppt ± 19.0 SD, not seen: 38.9 ppt ± 28.0 SD), whereas mean pH showed the opposite relationship (seen: 8.6 ± 0.5 SD, not seen: 8.2 ± 0.5 SD). The proportion of visits during which a common sandpiper was spotted was negatively correlated with salinity but positively correlated with pH; the interaction between the two was such that when pH was high, the effect of salinity was minimal (Table 3.1, Figure 3.4).

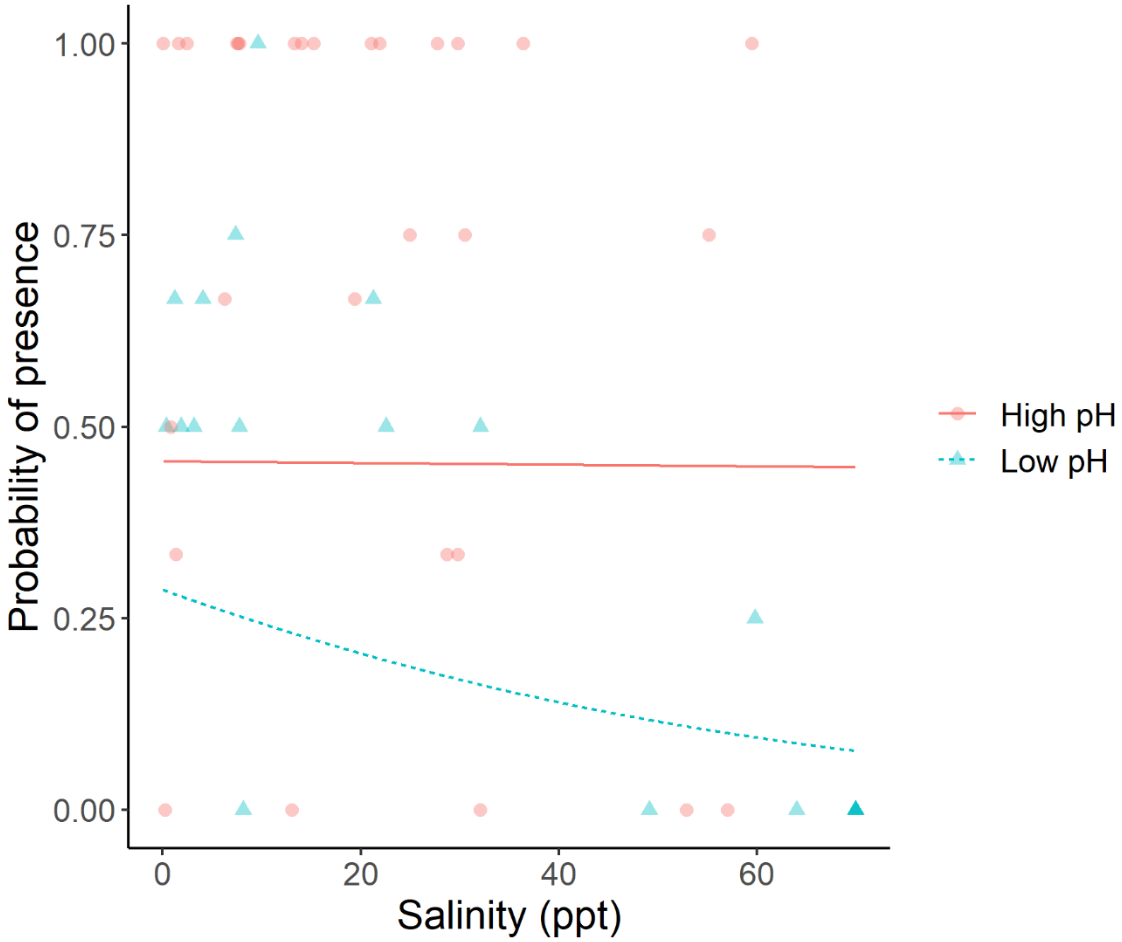


Figure 3.4 The relationship between the probability of a common sandpiper being present on a water body and salinity at high (9) and low (8) pH. High and low pH values are calculated as one standard deviation higher and lower than the mean. The lines show the predicted relationships from a GLMM, plotted for the mean value of all other variables; the solid circles and triangles show the raw data higher and lower than the mean, respectively.

Foraging success

Salinity and pH were negatively correlated with foraging success. Both temperature and day of the year were positively correlated with foraging success and retained in the best-fitting model set. Although several interactions were retained, these had very small effect sizes and were therefore unlikely to be biologically meaningful (Table 3.2). The low marginal and conditional R^2 values of all models suggest that factors other than those in the model may have an important impact on common sandpiper foraging success (Table 3.2, Figure 3.5).

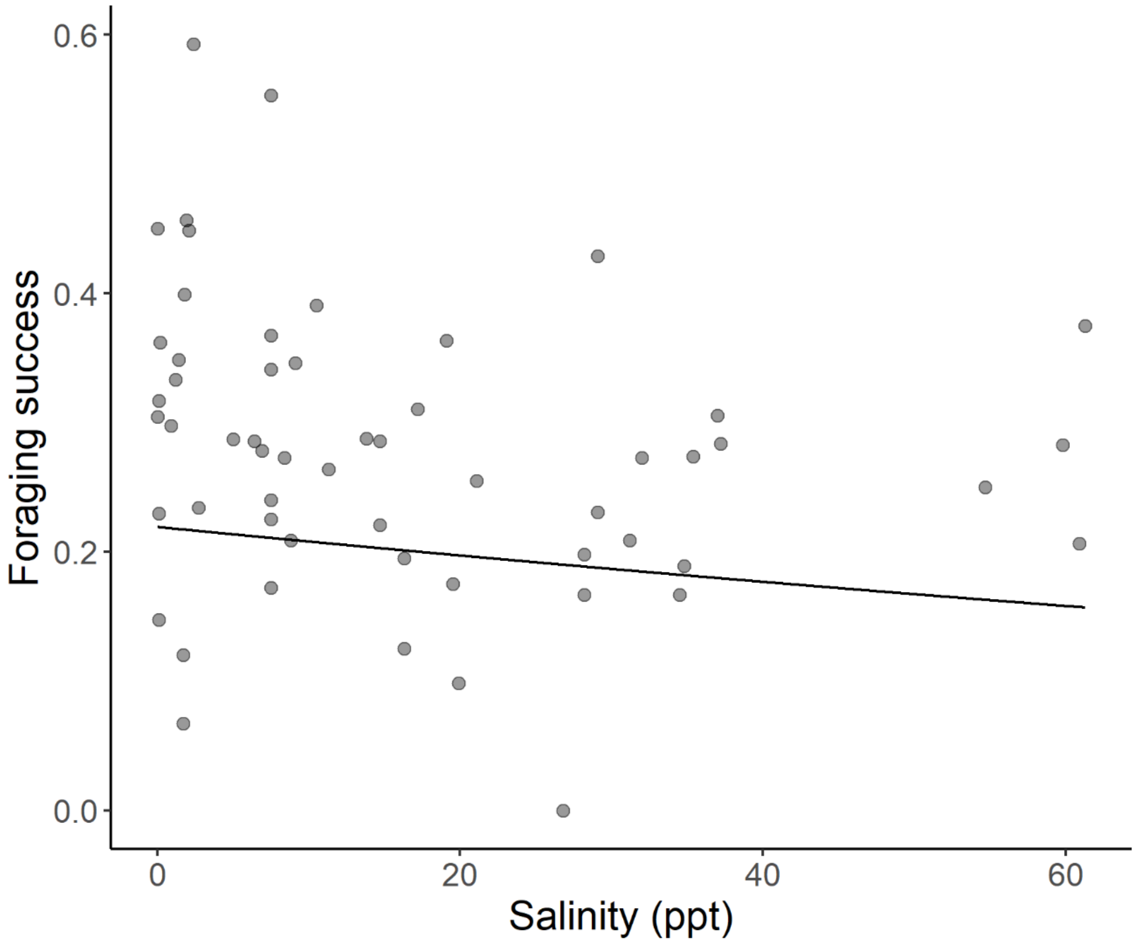


Figure 3.5 The relationship between the proportion of successful foraging attempts and salinity. Closed circles are the raw data and the solid line shows the predicted relationship from a GLMM, plotted for the mean value of all other variables.

Table 3.1 The models within 2AICc of the best fitting model of the factors affecting the presence or absence of common sandpipers at a water body. Only one model was contained in the top model set. The null model is shown for comparison.

Intercept	pH	Salinity	Water temperature	pH x salinity	pH x water temperature	Salinity x water temperature	Log Likelihood	AICc	weight	Marginal R^2	Conditional R^2
-0.75	0.56	-0.56	\	0.53	\	\	-47.36	106.08	0.46	0.73	0.73
-0.47	\	\	\	\	\	\	-55.96	116.18	0.00	0.00	0.00

Table 3.2 The factors affecting common sandpiper foraging success. The interaction between Julian sate and pH, pH and salinity and salinity and water temperature have been removed from the table because they did not appear within the models within 2AICc of the best fitting model. The null model is shown for comparison.

Intercept	Julian date	pH	Salinity	Water temperature	Julian date x salinity	Julian date x water temperature	Log Likelihood	AICc	weight	Marginal R^2	Conditional R^2
-1.39	0.11	\	-0.13	0.10	\	\	-162.52	338.76	0.09	0.23	0.77
-1.37	0.10	-0.07	-0.12	0.13	\	\	-161.34	339.02	0.08	0.31	0.74
-1.37	\	\	\	0.11	\	\	-165.53	339.84	0.05	0.13	0.72
-1.36	\	-0.08	\	0.15	\	\	-164.36	339.93	0.05	0.21	0.70
-1.43	0.13	\	-0.19	0.09	0.07	\	-162.11	340.55	0.04	0.24	0.77
-1.38	\	\	-0.07	0.12	\	\	-164.68	340.56	0.04	0.17	0.72
-1.38	0.11	\	-0.14	0.10	\	-0.03	-162.17	340.67	0.03	0.22	0.79
-1.37	\	-0.08	-0.07	0.15	\	\	-163.51	340.73	0.03	0.27	0.70
-1.37	0.06	\	\	0.10	\	\	-164.77	340.75	0.03	0.14	0.75
-1.35	\	\	\	\	\	\	-169.93	346.32	0.00	0.00	0.73

Response to conspecifics in winter

The time taken for common sandpipers to respond to a playback trial was not significantly different between the UK and Senegal (W = 88, p = 0.46; Figure 3.6a). The time to respond was not correlated with day of the year in Senegal (ρ = 0.1, P = 0.74) or in the UK (ρ = 0.46, P = 0.082; Figure 3.6b).

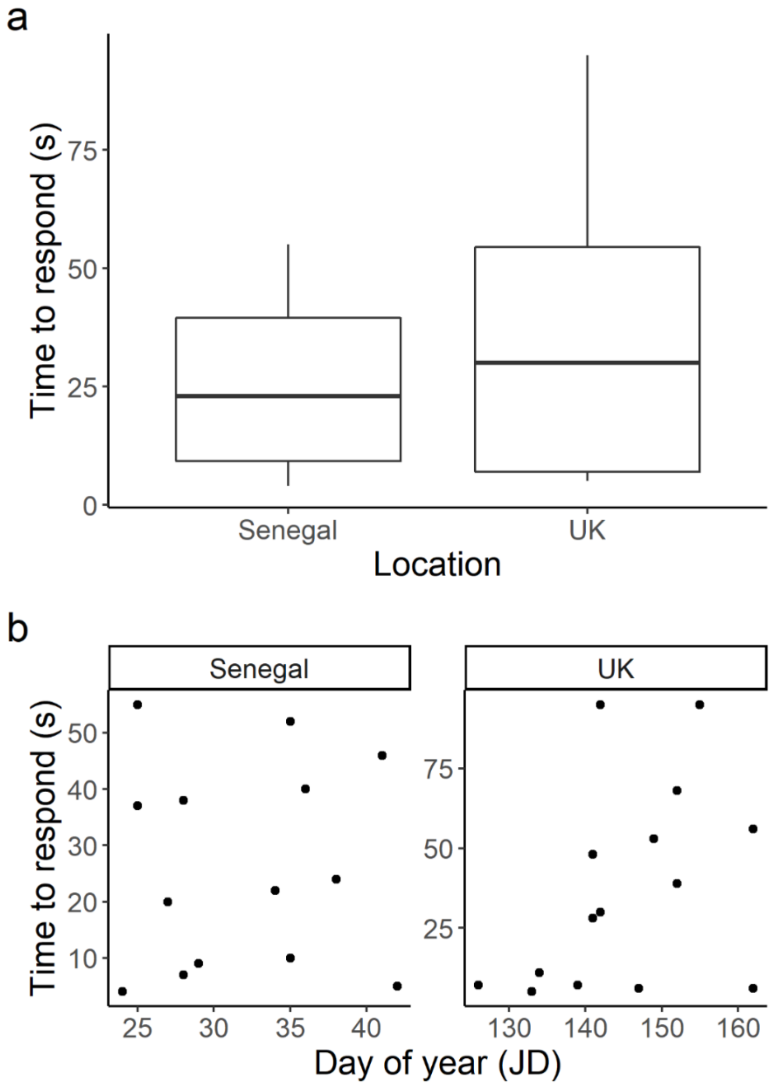


Figure 3.6 The time taken for common sandpipers to respond to playback trials in (a) Senegal versus the UK, and (b) over time. In (a) the solid line corresponds to the 50th percentile, the boxes to the 25th and 75th percentiles, the whiskers to 1.5 times the interquartile range and the solid circles show any points beyond these. Solid circles in (b) show the raw data.

The time taken for common sandpipers to return to normal after a playback trial was not significantly different between Senegal and the UK (W = 69, P = 0.30; Figure 3.7a). The time taken to return to normal was not correlated with day of the year in either Senegal (ρ = -0.16, P = 0.59) or the UK (ρ = -0.17, P = 0.55; Figure 3.7b).

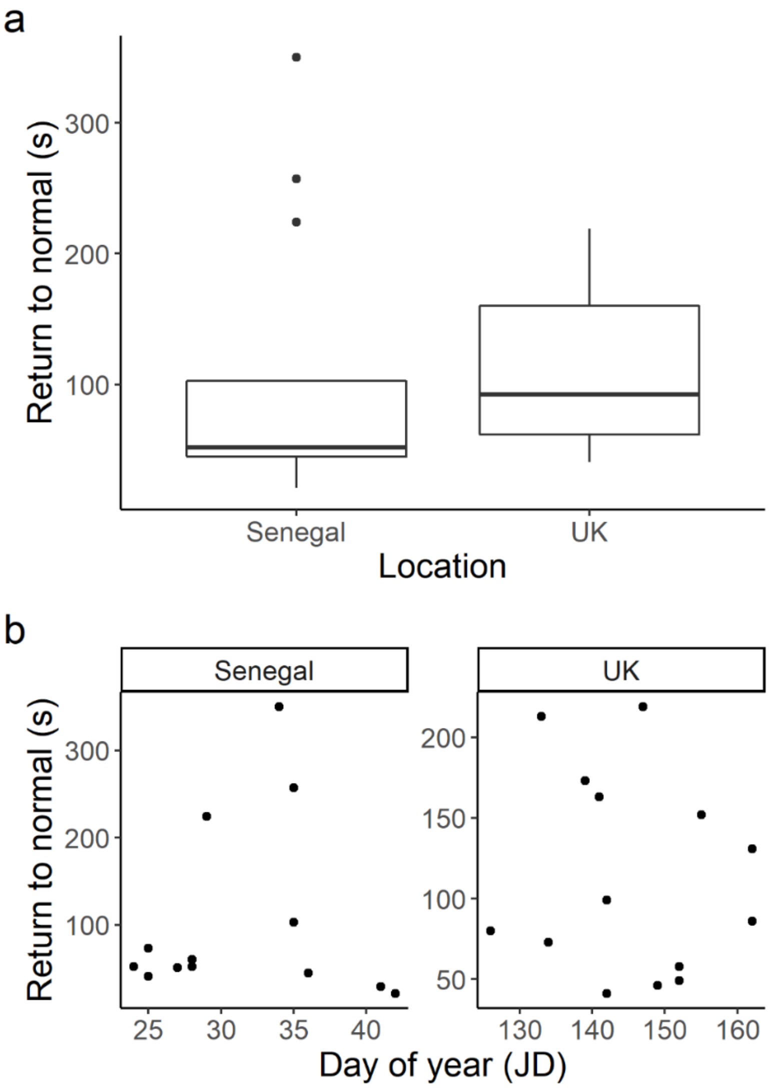


Figure 3.7 The time taken for common sandpipers to return to normal behaviour after a playback trial in (a) Senegal versus the UK, and (b) over time. In (a) the solid line corresponds to the 50th percentile, the boxes to the 25th and 75th percentiles, the whiskers to 1.5 times the interquartile range and the solid circles show any points beyond these. Solid circles in (b) show the raw data.

In Senegal, common sandpipers were significantly less likely to long call than in the UK ($Prop_{Senegal}$ = 29% 4/14, $Prop_{UK}$ = 80% 12/15, χ^2 = 5.80, P = 0.02). Birds in Senegal were not more likely to alarm call than those in the UK ($Prop_{Senegal}$ = 93% 13/14, $Prop_{UK}$ = 60% 9/15, χ^2 = 2.66, P = 0.10).

The amount of time a common sandpiper took to respond to a playback trial was slightly negatively correlated with pH and with the interaction between pH and salinity (Table 3.3a). This was such that at high pH levels, the time to respond was negatively correlated with salinity, but at low pH levels, the time to respond was positively correlated with salinity (Figure 3.8a). The time taken for individuals to return to normal was not significantly correlated with either pH or salinity (Table 3.3b, Figure 3.8b).

Table 3.3 Results of the GLMs of the effect of water quality on (a) the time to respond and (b) the time taken to return to normal.

(a) Time to respond	Variable	Estimate	Standard Error	T-value	P-value
	Intercept	3.12	0.20	15.4	/
	Salinity	-0.14	0.24	-0.59	0.57
	pH	-0.78	0.39	-2.01	0.07
	Salinity x pH	-1.34	0.61	-2.22	0.05
(b) Return to normal					
	Intercept	4.43	0.28	16.0	/
	Salinity	-0.54	0.39	-1.40	0.20
	pH	-0.12	0.72	-0.17	0.87
	Salinity x pH	0.58	1.03	0.56	0.59

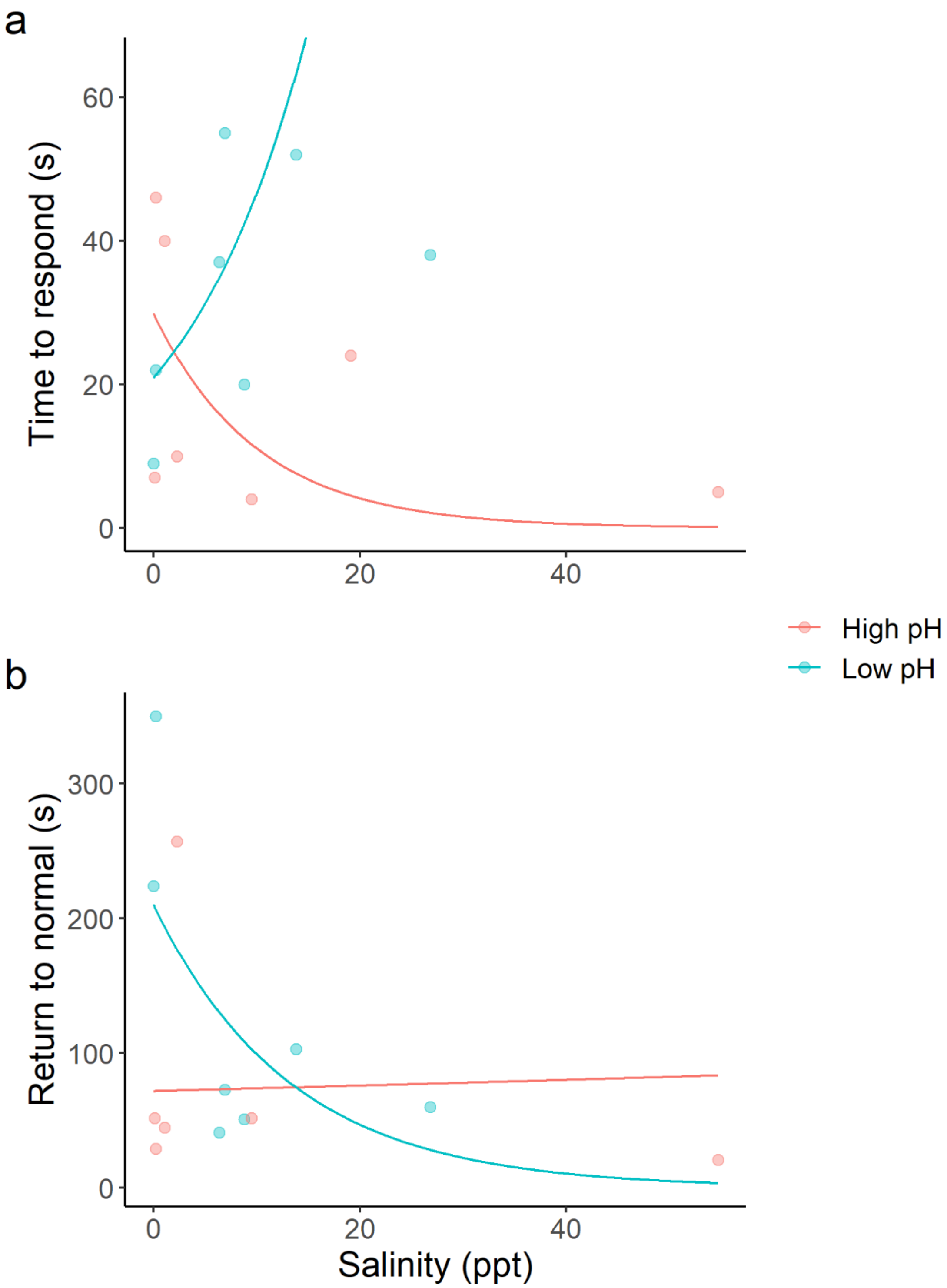


Figure 3.8 The relationship between salinity and (a) the time taken to respond, and (b) the time taken to return to normal at high and low levels of pH. High and low pH levels correspond to values one standard deviation higher (9) and lower (8) than the mean. Solid circles show the raw data, coloured by whether they were higher or lower than the mean pH value. Solid lines are the predictions from GLMs.

Discussion

Return rates

We found that common sandpipers had a high return rate to their wintering grounds, which corroborates previous observations (Cramp *et al.* 1983, Sauvage *et al.* 1998). There is substantial anecdotal evidence that winter site fidelity is common among migratory birds, with an increasing number of studies finding this for particular species (Cramp *et al.* 1983, Blackburn & Cresswell 2016a, Gill *et al.* 2019). Furthermore, repeat tracking of the migration of individuals has revealed significant consistency in both non-breeding distributions and timings (Conklin *et al.* 2013, Gill *et al.* 2014). These findings are likely to have important implications for conservation, as they suggest that individuals might be relatively inflexible in their migratory behaviour and so high-density wintering sites must be protected.

Wintering segregation of common sandpipers

Sexual segregation of migratory species on the wintering grounds can occur at large spatial scales because of physiological traits (e.g. bigger birds flying to more distant wintering grounds; Myers 1981, Gill *et al.* 1995, Mathot *et al.* 2007) or at fine scales because of different behavioural traits and foraging ability (e.g. individuals with longer bills foraging in different habitats to those with shorter bills; Catry *et al.* 2012, Alves *et al.* 2013, Duijns *et al.* 2014). Therefore, us only catching males in Djoudj could have been because females are segregated from males during winter. During the 2018 field season we caught most of the birds that we targeted, meaning that we were unlikely to have missed females had they been present. Indeed, Holland (2018) found that among museum specimens, the proportion of female birds was higher in southern wintering grounds than those further north. Although not conclusive, it could mean that a lower proportion of female common sandpipers use northerly wintering sites than males. However, our geolocator and stable isotope results suggest that female and male common sandpipers do not segregate across large spatial scales during winter, even though all birds caught at Djoudj were male. The considerable overlap in feather stable isotope ratios suggests that females and males from the UK are likely to forage in similar habitats during winter, unlike for some other species (Alves *et al.* 2013b, Gherardi-Fuentes *et al.* 2020). This could mean that using tape lures to catch individuals in Senegal biased our sample towards male birds. It is interesting that no females responded to tape lures given that some of our successful playback experiments in the UK were carried out on pairs, suggesting that females are territorial during the breeding season. Other wader species appear not to be territorial in winter, although often these species form flocks, which has not been observed in common sandpipers (Cramp *et al.* 1983, Colwell 2000). It is unclear how common it is for only one sex to defend a non-breeding territory, with the other not exhibiting any territorial behaviours. In other species, both females and males can be territorial during winter, defending them in pairs or as single birds (Colwell 2000, Hau *et al.* 2004, Crowther *et al.* 2018). Furthermore, it is surprising that we only caught males despite netting at several roost sites, where one might expect both sexes to congregate (Kristin *et al.* 2001, Mainwaring 2011).

It is also possible that segregation between the sexes during winter could arise from differences in habitat use due to size or dominance, which are not discernible using stable isotopes or from geolocator data because of their coarse resolution (Hallworth *et al.* 2013, Rakhimberdiev *et al.* 2016). Several studies have shown that sexual size dimorphism can result in sexually-segregated non-breeding distributions at both large and fine spatial scales (Myers 1981, Alves *et al.* 2013b, Nebel *et al.* 2013). Our results show that common sandpipers are unlikely to segregate across large spatial scales but cannot determine whether they do so at fine scales. In waders, variation at a fine spatial scale could be driven by food accessibility due to sex differences in bill size and morphology (Rubega 1996, Le V. Dit Durell 2000, Alves *et al.* 2013b, Duijns *et al.* 2014). Additionally, dominant birds may be able to defend high quality territories and habitats, thereby excluding less dominant individuals (Cresswell 1994, Catry *et al.* 2012). In Senegal, we were unable to reach large areas of potentially high-quality habitat, which could have mainly been populated by the larger females. Further ringing at a greater range of sites is needed to determine whether both sexes use Djoudj in winter. This is important to determine because non-breeding sexual segregation could have significant implications for conservation action (Catry *et al.* 2006).

Habitat choice and foraging success

The proportion of times a common sandpiper was seen at a site was negatively correlated with salinity. Other studies have found that birds suffer physiological and behavioural stresses when ingesting food from saline environments (Mahoney & Jehl 1985, Mahoney & Jehl Jr 1985, Nyström & Pehrsson 1988), and that although many wading bird species use these habitats, they may have relatively low avian diversity and abundance (Warnock *et al.* 2002). Many bird species have salt glands to help with osmoregulation, including common sandpipers, but the mechanism of salt extraction is energetically costly (Rubega & Robinson 1997). It is therefore possible that individuals avoid saline environments when foraging (Nyström & Pehrsson 1988), especially if ingesting salt also increases basal metabolic rate and overall energy expenditure (Gutiérrez *et al.* 2011). Furthermore, we found that foraging success declined marginally with salinity, indicating that there may be direct costs of water salinity for common sandpipers, unlike for at least some other species (Blakey *et al.* 2006). This could be, for example, because saline water can increase invertebrate mortality and reduce their reproductive output and abundance (Kefford *et al.* 2005, Kefford *et al.* 2007, Carver *et al.* 2009, Zalizniak *et al.* 2009), meaning that there may be fewer available for foraging birds. Additionally, birds may spend more time on salt avoidance and excretion behaviours than actively foraging, thereby reducing the proportion of successful attempts (Mahoney & Jehl 1985, Gutiérrez *et al.* 2011, Rocha *et al.* 2016). Further work could focus on determining the abundance of invertebrates in the various habitats throughout Djoudj, as work on other waders has revealed fine-scale habitat selection based on invertebrate availability (Colwell & Landrum 1993).

It appears that the effect of salinity on the probability of common sandpiper presence may be buffered by pH. Molluscs and crustaceans may be able to survive in highly saline environments if pH levels are also high. This is because pH could buffer the negative effects of low salinity on exoskeleton formation (Havas & Advokaat 1995, Lien *et al.* 1996, Zalizniak *et al.* 2009), although it might be dependent on the ionic composition of the water rather than salinity itself (Zalizniak *et al.* 2006). Common sandpipers feed on a large range of invertebrate species and crustaceans are likely to be considered high-quality prey items (Yalden 1986, Arcas 2004). It is possible that pools with high pH levels increase the survival of these prey items and, therefore, are considered suitable habitat by common sandpipers regardless of salinity concentrations.

If common sandpipers and other species face costs when using saline environments, the highly saline waters in Djoudj National Bird Sanctuary could impose limitations on northward migration (Piersma 1997, Piersma 2002, Gutiérrez *et al.* 2011). Many of the water bodies in the park are formed during the June to October rains and continuously evaporate throughout the year, becoming progressively more saline. This means that conditions for migratory species become worse as they are preparing for their northward migration, which is likely to be a key lifecycle bottleneck (Piersma 2002, Lok *et al.* 2015, Zwarts *et al.* 2015, Loonstra *et al.* 2019). However, the park officials in Djoudj can control the amount of freshwater available within its boundaries by opening sluice gates to the River Senegal and so these costs could potentially be mitigated through careful landscape management.

Response to conspecifics

Our results suggest that male common sandpipers respond to conspecifics in winter in a similar way to birds during the breeding season. This could reflect several different behaviours, including social behaviours like courtship and flocking or aggressive behaviours like territoriality (Cramp *et al.* 1983). In the absence of knowledge regarding the specific functions of common sandpiper calls in different contexts, it is difficult to draw conclusions about the meaning of their responses to conspecifics in winter. During the breeding season in the UK, territorial behaviour makes sense as individuals mate guard and defend resources for their chicks; interactions between individuals have normally been considered aggressive and used as evidence of territoriality (Dougall *et al.* 2010). Therefore, given the similarity of individual responses to tape lures in the UK and Senegal, it could be that common sandpipers are also territorial during winter, as has been previously suggested (Cramp *et al.* 1983). Non-breeding territoriality is a facultative behaviour in other species and might depend on lifecycle stage, with wintering territoriality being more common than during migration periods (Colwell 2000). Anecdotal evidence suggests that, during winter, common sandpipers only flock for roosting (Cramp *et al.* 1983), and we never observed flocks in Senegal. However, we occasionally saw pairs foraging together, meaning that the apparently aggressive interactions between individuals could also have reflected courtship behaviours. Indeed, it has been suggested that some individuals might form pairs during winter (Mee 2001). To determine the function of common sandpiper calls and the nature of interactions between individuals, we would need to investigate the responses of both males and females to conspecifics in different contexts.

Common sandpipers used different vocalisations in the UK and Senegal, which could suggest that responses reflect different behaviours. In the UK, interactions between conspecifics are thought to be territorial, to protect foraging habitats and refuge sites for chicks, rather than for foraging adults. This is because individuals from different pairs are regularly observed foraging together in fields bordering the river but are territorial when at the water's edge (Dougall *et al.* 2010). In the UK, the playback trials were all carried out prior to eggs hatching and still provoked long call responses. This could mean that in the UK, the long call responses, and the territories themselves, are important for mate guarding and protecting nesting habitat. In Senegal, however, in the absence of chicks, mates or nesting habitat to protect, it is unclear whether the responses reflected social behaviours or aggressive behaviours to defend food resources or to protect refuge sites to reduce predation (Davies 1976, Myers 1980, Cuadrado 1997).

Our results suggest that in winter, the magnitude of response might be linked to habitat quality. As discussed in the previous section, highly saline water is likely to impose energetic costs on foraging birds and, as such, might be considered poor quality habitat (Nyström & Pehrsson 1988, Gutiérrez *et al.* 2011), although its effect might be buffered by pH (Zalizniak *et al.* 2009). pH again appeared to buffer the effect of salinity on their responses, primarily the time to respond, reinforcing the idea that high salinity and low pH environments might be poor quality habitat for common sandpipers. While these interactions between responses to playback and water chemistry should be regarded with caution due to small sample sizes, our results suggest that common sandpiper responses to conspecifics might vary depending on territory quality, as has been found in other species (Fedy & Stutchbury 2005, Ruiz-Sánchez *et al.* 2017, Willemoes *et al.* 2018). More work is needed to determine the effect of habitat quality on responses, particularly if this can be linked to food abundance and quality, and whether this could influence intraspecific variation in survival or migratory performance.

Conclusion

Many African countries are experiencing significant landscape changes, through agricultural intensification and urbanisation, potentially affecting millions of migratory birds (Vickery *et al.* 2014, Willemoes *et al.* 2018). However, we know relatively little about the wintering ecology of many species and this is likely to play an important role in their susceptibility to habitat change. Further, winter conditions are likely to have significant knock-on effects throughout the lifecycle and, while using indirect measures to investigate their effects can provide extremely valuable insight, they could also miss key intraspecific information (Ruiz-Sánchez *et al.* 2017, Willemoes *et al.* 2018). Therefore, more field-based studies of the wintering ecology of migrants in Africa are needed, both to further our understanding of their lifecycles and to implement successful conservation measures (Vickery *et al.* 2014).

Chapter 4 The effects of geolocators on return rates, condition and breeding success in common sandpipers

Introduction

Many migratory bird species are in decline, and understanding the underlying causes is paramount for reversing these trends (Vickery *et al.* 2014, Rosenberg *et al.* 2019). Migrants are reliant on multiple, distinct geographic regions throughout their lifecycles, making them particularly susceptible to environmental change but also challenging to monitor year-round (Newton 2004, Wilcove & Wikelski 2008). For many species, we even lack fundamental information about migration routes, stopover sites and non-breeding areas. There are now a wide range of tracking devices available which are used to address these knowledge gaps, and archival light level geolocators (hereafter 'geolocators') are one-such device that can be attached to even some of the smallest species (Bridge *et al.* 2011). However, these trackers add weight, especially as a proportion of the birds' body mass, and therefore have the potential to affect the behaviour, migration and survival of the individuals carrying them (Geen *et al.* 2019).

While some reviews have concluded that the effects of geolocators on individuals are weak (Bodey *et al.* 2018, Brlik *et al.* 2019), the impact varies between species and negative effects may be underreported. Several studies have found considerable negative effects (Bridge *et al.* 2013), including reduced apparent survival (Bodey *et al.* 2018), reduced hatching success due to egg damage (Weiser *et al.* 2016), and increased stress levels (Elliott *et al.* 2012). Geolocators can influence flight behaviour by increasing drag and flight duration, and by reducing flight efficiency (Pennycuick *et al.* 2011, Chivers *et al.* 2016, Bodey *et al.* 2018), which models show can in turn reduce total migration distance (Bowlin *et al.* 2010). The effects of geolocators appear stronger for aerial foragers and small-bodied species, and those in which the weight of the tag as a proportion of body mass is greater (Costantini & Møller 2013, Weiser *et al.* 2016, Brlik *et al.* 2019; but see Tomotani *et al.* 2018). Their effects are also dependent on the attachment method, with, for example, differences between the effects reported for back, leg-loop and leg-mounted geolocators (Bowlin *et al.* 2010, Costantini & Møller 2013, Blackburn *et al.* 2016, Bodey *et al.* 2018, Tomotani *et al.* 2018).

Wader populations across the globe are in decline and the need to understand their migration behaviour is therefore great (Group 2003). Geolocators and other devices are increasingly being used on these species, often mounted to colour rings or leg flags (Clark *et* *al.* 2010). Other mounting methods have been used, such as backpacks or leg-loop harnesses, but they can increase the risk of predation (Chan *et al.* 2015) and might cause problems because waders undergo large changes in body mass before and during migration (Clark *et al.* 2010). Conventional guidelines suggest that tag weights should not exceed 3% of the total body mass, but these are being revised as more information on the impacts of tags becomes available (Kenward 2000, Weiser *et al.* 2016). A recent meta-analysis on waders found little overall effect of geolocator attachment, but that there were significant effects on the smallest species and especially when tags weighed more than 2.5% of the individual's mass (Weiser *et al.* 2016). Tracking devices may have unintended consequences on behaviour and reproductive success, and continuous monitoring of individuals is needed to understand fully their effects (Weiser *et al.* 2016, Smith *et al.* 2018).

Here, we report the effects of carrying geolocators on common sandpipers (*Actitis hypoleucos*), a relatively small wading bird species (40-60g) whose migration routes are poorly documented. We attached geolocators to leg flags on common sandpipers in the UK and in Senegal, and investigated their effects on (1) return rate, (2) return date, (3) body condition and (4) reproductive success.

Methods

Catching birds and fitting geolocators

All UK fieldwork was carried out in the River Lune catchment within a 6.5km radius of Sedbergh, Cumbria, UK (54.3236˚N, 2.5282˚W), in the breeding seasons of 2017 and 2018. This individually marked study population of 23-24 pairs was monitored closely from April to July each year. At the start of the season, surveys of each territory were carried out 2-3 days per week in order to record the timing and identity of returning individuals. At least 80% of the nests in the population were found (n = 24-27 in each year including replacement nests following failure) and monitored through to hatching or failure; chicks were then monitored until fledging or failure. In those territories where birds returned but no nests were found, we assumed failure before discovery but could identify the breeding pair from other attempts in the same territory that year. Almost all unmarked adults were caught each year and fitted with a British Trust for Ornithology (BTO) metal ring on their right tarsus, a yellow colour ring engraved with two unique black characters on their left tarsus, and a plain red colour ring on their right tibia. We targeted individuals on their breeding territories by setting mist nets across rivers or by using wire mesh walk-in nest traps. Parents share incubation duties and, in most cases, one individual sits on the nest overnight and in the morning before switching with its partner for the afternoon (Mee 2001). This meant that we could target specific individuals during different parts of the day. We avoided nest trapping within the first week of incubation to limit the chances of desertion. Following capture and ringing, we measured the following biometrics before releasing the bird: tarsus length (± 0.1mm using Vernier callipers) and body mass (± 0.1g using an electronic weighing scale).

We also caught common sandpipers on their wintering grounds in Djoudj National Bird Sanctuary, Senegal, a 160km^2 area (16.3600˚N, 16.2753˚W), in January 2018 and January 2019. This landscape consists of a mosaic of freshwater and saline pools surrounded by an arid, sandy landscape with small shrubs. We caught individuals here by setting nets over, or close to, these water bodies and using tape lures. We also used drop traps and whoosh nets placed at the water's edge. Birds were ringed with the same colour scheme as those in the UK. For two weeks in January 2019, we carried out thorough daily searches of the site to look for returning individuals and to recapture individuals carrying geolocators.

We fitted geolocators to 22 individuals in the UK and 10 individuals in Senegal in 2017 and 2018, respectively. The control samples of birds with colour rings but no geolocators were 28 individuals in the UK and 6 individuals in Senegal. All geolocators were glued to leg flags made from red Darvic using epoxy resin, with a 3.3mm internal diameter and flag area of 10mm high by 15mm long. These were fitted on the right tibia in place of the red colour ring and only deployed on individuals weighing over 45g (mean body mass of birds with geolocators = 49.7g, mean body mass of birds without geolocators = 50.7g). In the UK, we deployed Lotek MK5040 geolocators (dimensions: length = 13mm, width = 8mm and depth = 6mm), which weighed 1.1g in total (including the glue and leg flag; Figure 4.1). Individuals were targeted for fitting and recovering geolocators from the second week of incubation, with the latest tags being deployed on the day of hatching. In Senegal, we used Migrate Technology Intigeo geolocators (dimensions: length = 15mm, width = 6mm and depth = 6mm), weighing 1g in total. The geolocator and attachment method never exceeded 2.6% of the individual's total body mass in either site. All birds tagged in the UK were observed at least weekly throughout the breeding season; tagged birds in Senegal remained site faithful and were observed opportunistically at least once but usually weekly for up to five weeks following capture. On recapture in 2018 (UK) and 2019 (Senegal), all birds were checked for injuries and biometrics taken. In order to avoid excessive disturbance of untagged individuals, we did not target them in their return years (2018 in the UK and 2019 in Senegal). Therefore, recaptures of these individuals were coincidental, but their biometrics were taken for the analyses of change in body condition.

In the UK, we initially fitted birds with geolocators mounted parallel to the leg. Early on during the study, two individuals carrying parallel mounted geolocators were seen limping. We managed to recapture one of these birds, remove the tag and then remount it perpendicular to the leg. This individual was never observed limping after the change in tag orientation, and all birds were fitted with perpendicularly mounted tags from then on. This resulted in ten birds carrying parallel mounted geolocators and twelve carrying perpendicularly mounted geolocators, allowing us to compare the effects of mounting orientation on individuals (Figure 4.1). In Senegal, all ten individuals carried perpendicularly mounted geolocators and none were seen limping during subsequent monitoring.

Figure 4.1 Common sandpipers carrying geolocators mounted parallel (left panel) and perpendicularly (right panel) to the leg. The bird in the left panel was tagged with a Lotek MK5040 geolocator in the UK; the bird in the right panel was tagged with a Migrate Technology Intigeo geolocator in Senegal.

Analyses

We investigated the effects of geolocators on common sandpipers by comparing their return rates, return dates, changes in body condition and reproductive success with those of individuals fitted with metal and colour rings only. In the UK, we compared return rates using binomial proportions tests; the date individuals were first seen in the study site (converted to the day of the year i.e. Julian date) using a t-test for unequal variances (with tags n = 13, without tags n = 14); and changes in body condition using a Mann-Whitney U-test (with tags n = 11, without tags n = 5). We created an index of body condition using a linear model regressing body mass against tarsus length from measurements of the birds caught in both 2017 and 2018 (Schulte-Hostedde *et al.* 2005). We took the residual deviation of each individual from the fitted line as an index of its condition relative to the other birds in the population. We did this separately for the birds tagged in the UK and Senegal because we were unsure of the breeding origin of the Senegalese individuals and size can vary with latitude. The predicted mass of individual i given its tarsus length x_i is

$$\hat{y}_i = a * x_i + b,$$

where $a * x + b$ is the regression equation. The body condition is the residual error e_i and corresponds to the variation not explained by the equation, i.e. the difference between the actual mass y_i and the predicted mass $\hat{y}_i$,

$$e_i = y_i - \hat{y}_i.$$

This index corrects for any variation in body size between individuals or due to sex (Schulte-Hostedde *et al.* 2005). The index from 2017 was subtracted from the index in 2018, providing the change in body condition for each individual between the two years.

Finally, we compared two components of breeding success, hatching success and fledging success, between nests with at least one adult carrying a geolocator and nests at which both adults had rings only; we did this for both 2017 and 2018 using Fisher's exact tests. These were binary variables, so hatching and fledging were successful if at least one egg hatched or at least one chick fledged, respectively. Five nests had both adults with a geolocator and seven had only one, although the adults at two other nests had geolocators fitted on the day of hatching and so are only included in the comparison of fledging success for that year. After removing second breeding attempts to avoid pseudoreplication, there were six nests at which both adults had rings only. Each nest was visited once every four to five days and hatching success determined by visiting the nest every day in the latter stages of incubation. Territories that successfully hatched young were visited once every five days until the adults were no longer seen alarm calling or until the chicks were seen flying. On several occasions, we observed chicks flying when 17 days old ('day 17'); we therefore took this to be the minimum age of fledging. When adults or chicks were seen during the last visit to a territory prior to day 17, but not after, we counted the chicks as having successfully fledged. If no adults were seen alarm calling on two consecutive visits to the territory before day 17, we concluded that the chicks had failed. For the two measures of reproductive success in 2017, most data came from first observed breeding attempts; however, in cases where geolocators were fitted after the first clutch had failed (n = 3), we included second breeding attempts instead. For the return year, 2018, we only included first breeding attempts for all birds. We also compared the effects of parallel versus perpendicularly mounted tags on all the variables mentioned above.

For the birds tagged and resighted in Senegal, we compared their raw return rates with those fitted with metal and colour rings only. We did not carry out any analyses due to small sample sizes. We were unable to recapture many colour ringed birds because of the targeted nature of our ringing, and we therefore present mean change in the body condition of tagged birds only. Finally, we were not in Senegal for the arrival of common sandpipers to the wintering grounds and so could not determine return dates.

Results

Thirteen of the twenty-two birds tagged with geolocators in the UK in 2017 were resighted in 2018 (Table 4.1a). One of these was identified at the start of the season but not seen again within the study site, and another had lost its geolocator (see below). All eleven of the remaining individuals were caught and the geolocator removed.

The first returning bird observed in the study site, on the 11th April 2018, was carrying a geolocator. There were no significant differences between the return rates or return dates of birds with a geolocator and those without (Table 4.1a). Furthermore, there were no significant differences in hatching success or fledging success between birds with and without geolocators in either 2017 or 2018, although sample sizes were small (Table 4.1a). Similarly, there were no significant differences in any of these variables between birds with parallel and perpendicularly mounted geolocators (Table 4.1b). Carrying a geolocator caused a small decrease in body condition, whereas birds carrying only rings had a slight increase, but this difference was not significant (Table 4.1a). The pattern of change in condition differed between mounting orientations, but again there was no significant difference (Table 4.1b).

Eight of the ten birds (80%) fitted with geolocators in Senegal in 2018 were resighted in 2019. The two remaining birds were originally trapped at evening roost sites and their daytime feeding areas were unknown, so it is possible that they were present outside of the survey area. Four of the six birds (67%) in Senegal that were colour ringed but not tagged returned in 2019. The mean change in body condition for birds carrying geolocators was -0.44; range = -2.02 to 2.61, n = 4).

Table 4.1 The effects of (a) carrying a geolocator compared with colour rings only and (b) carrying a geolocator mounted parallel or perpendicularly to the leg on: return rate, return date, change in body condition and hatching and fledging success in the year of attachment and year of recapture. The raw proportions and the standard errors (se) are in brackets. OR is the Odds Ratio statistic from the Fisher’s exact test.

a	No Geolocator	Geolocator	Test Statistic	P value
Return rate	54% (15/28)	59% (13/22)	χ^2 = 0.011[2]	0.918
Return timing	118.86 (+/- 2.11se)	118.39 (+/- 2.19se)	T = 0.153	0.880
Δ Body condition[1]	0.64 (+/- 1.20se)	-0.29 (+/- 0.81se)	W = 30	0.827
Hatching success 2017	67% (4/6)	67% (8/12)	OR = 1	1.000
Fledging success 2017	25% (1/4)	36% (5/14)	OR = 0.616	1.000
Hatching success 2018	43% (3/7)	43% (3/7)	OR = 1	1.000
Fledging success 2018	14% (1/7)	43% (3/7)	OR = 1.810	1.000

b	Parallel	Perpendicular	Test Statistic	P value
Return rate	70% (7/10)	50% (6/12)	χ^2 = 0.265[3]	0.607
Return timing	121.29 (+/- 3.53se)	115.00 (+/- 3.81se)	T = 1.247	0.239
Δ Body condition[1]	-1.33 (+/- 1.07se)	0.58 (+/- 0.98se)	W = 10	0.429
Hatching success 2017	71% (5/7)	75% (3/5)	OR = 0.627	1.000
Fledging success 2017	0% (0/4)	43% (3/7)	OR = Inf	0.236
Hatching success 2018	33% (1/3)	50% (2/4)	OR = 1.810	1.000
Fledging success 2018	33% (1/3)	50% (2/4)	OR = 1.810	1.000

[1] Change in body condition is calculated as the difference in an index of mass relative to tarsus length between 2018 and 2017, see methods.

[2] Confidence interval for the difference of proportions = -0.37, 0.26

[3] Confidence interval for the difference of proportions = -0.29, 0.69

Other effects

Although there were no detectable effects of geolocators on the measures described above, a small number of individuals tagged in the UK did suffer injuries. Two of the seven birds (29%) carrying parallel mounted geolocators that returned in 2018 had bruising on their tarsus, apparently caused by the geolocator hitting the lower leg whilst the bird was walking; this may also explain the limping reported in two such birds in 2017, as described above. One of the bruised individuals was recaptured again in 2018, by which time the leg had healed fully. In five cases in total (38%), individuals had a slightly swollen tibia or had lost some skin underneath the leg flag. This occurred irrespective of tag orientation and appeared to be caused by the internal diameter being marginally too small for the individual, although no rubbing was noted and all flags rotated freely at the time of fitting. For one of these birds carrying a parallel mounted geolocator, the swelling seemed to have reduced blood flow to the tarsus. This bird was first observed in the study site on the 11th May 2018, carrying the geolocator but placing no weight on that leg. We attempted but failed to catch it several times before finally succeeding on the 8th June 2018, by which time the bird had lost its lower leg and the geolocator. The wound had already healed, indicating that it had not fallen off during capture. After this bird was released, we watched it return to its nest and incubate the eggs, and we observed it foraging several times over the subsequent weeks. The nest was predated on the 3rd July 2018 and the bird was not recorded in 2019. To summarise, of the thirteen birds tagged with geolocators in the UK, eight (62%) had an injury on either the tibia, tarsus or both; only two of these prevented the geolocator from spinning freely on the leg, with the others suffering only minor bruising. In Senegal, no injuries were seen for any of the tagged birds.

Discussion

In our study, the injuries caused to the birds' legs appeared to be the biggest consequence of carrying a geolocator. These issues were probably due to a combination of geolocator size and weight, and the short tibias of common sandpipers. Mounting long geolocators parallel to the leg on species with short tibias is likely to impede leg movement while walking, as has been found in other wader species (Weiser *et al.* 2016). Furthermore, the weight of these relatively long tags, coupled with the internal diameter of the ring, is likely to have caused the swollen tibias and, in one case, limb loss. Senegalese birds were never observed to be limping and none of the returning birds had issues with swelling under the rings. These individuals were carrying thinner and lighter tags than those tagged in the UK. The only other study to attach geolocators to common sandpipers using leg flags did not report any adverse effects, but used tags similar in size and weight to those we deployed in Senegal (Summers *et al.* 2019). Given the prevalence of tracking studies carried out on many different species, it is surprising that no others that we know of have reported tags causing limb loss. Limb loss from metal ringing has occurred very occasionally and so it is possible that such injuries might occur due to unusual combinations of factors (Calvo & Furness 1992, Murray & Fuller 2000); its incidence is perhaps increased by the added weight associated with geolocators. Care should be taken when considering tracking studies on small species, especially when mounting them to leg flags. Removing the middle section of the flag carrying the geolocator to reduce the surface area in contact with the leg may help, but alternatives to leg mounting should also be considered. However, it is important to note that other methods may also have negative effects (Bowlin *et al.* 2010, Clark *et al.* 2010, Costantini & Møller 2013).

The leg injuries that geolocators caused highlight the need for complete transparency when reporting the effects of tagging birds (Geen *et al.* 2019). In our case, reporting only return rates and measures of reproductive success would have suggested that geolocators had no effect at all. Indeed, several other studies have found that the effects of geolocators might not be immediately obvious when presenting only return rates and reproductive success (Elliott *et al.* 2012, Chivers *et al.* 2016, Smith *et al.* 2018, Tomotani *et al.* 2018). Weiser *et al.* (2016) found negative effects of carrying geolocators for species similar in size to common sandpipers, such as the *articola* subspecies of Dunlin *Calidris alpina*. They suggested that geolocators would have an effect when they approached 2.5% of total body mass. In some cases, the proportion of body mass for our birds was very close to this threshold, which could have resulted in the injuries we saw to some of them. However, the body mass of birds that suffered injuries was on average slightly higher than that of uninjured birds (Mondain-Monval & Sharp, *unpublished data)*. Regardless of any threshold, studies should try to minimise the total weight attached to the bird, perhaps by excluding colour rings when fitting geolocators to small species (Costantini & Møller 2013, Weiser *et al.* 2016, Tomotani *et al.* 2018, Brlik *et al.* 2019).

Despite the injuries we observed and our relatively small sample sizes, it seems that most birds from both the UK and Senegal were not severely affected by the geolocators. There were no significant differences between the return rates, return dates or breeding success of common sandpipers fitted with and without tags. Furthermore, return rates (with a tag = 59%, without a tag = 54%) are consistent with those previously reported, although are at the lower end of the range (59-94%, Holland 2018; 52-81%, Méndez *et al.* 2018). This is consistent with findings that the effects of geolocators are relatively weak (Brlik *et al.* 2019). We did, however, find that birds carrying parallel mounted geolocators returned in slightly worse body condition than those with perpendicularly mounted tags, although not significantly so; birds carrying parallel mounted tags were also more likely to suffer bruising. Weiser *et al.* (2016) found parallel mounted tags to be worse for return rates than perpendicularly mounted tags, suggesting that they might negatively affect body condition, and mounting tags in this orientation should perhaps be avoided with short-legged species.

Our results, like those of others, appear to show weak effects of geolocators on individuals, suggesting that tagging could have little overall impact (Weiser *et al.* 2016, Brlik *et al.* 2019). However, there appear to be complex interactions between tag weight, dimensions and attachment methods (Bowlin *et al.* 2010, Weiser *et al.* 2016, Tomotani *et al.* 2018, Brlik *et al.* 2019), and this highlights the need for transparency when reporting on tracking studies. Furthermore, it is important to consider that tracking methods could influence individuals in ways that are not apparent based solely on demographic parameters, such as changes in flight or foraging behaviour (Elliott *et al.* 2012, Chivers *et al.* 2016, Smith *et al.* 2018). Unfortunately, our ability to understand the true effects of tagging, i.e. the differences between tracked and untracked birds, is limited by our inability to follow unmarked individuals year-round. It is also important to note that for many studies, including our own, there could be biologically important effects of tagging, but that the power needed to detect them is greater than sample sizes usually allow.

Chapter 5 Migration routes, connectivity and wind assistance in the common sandpiper

Introduction

Recent declines in migratory bird populations are well-documented, with climate change and habitat degradation often suggested as important drivers (Vickery *et al.* 2014, Rosenberg *et al.* 2019). Migratory species are particularly susceptible to these changes because they use multiple distinct sites throughout their lifecycle (Wilcove & Wikelski 2008, Patchett *et al.* 2018). However, understanding their impact is challenging because of global variation in the rates of temperature and habitat change. This means that the effects on species might differ between lifecycle stages and could vary depending on migratory strategies. For example, studies have revealed more negative population trends for long-distance migrants than short-distance migrants, and also for birds wintering in more humid bioclimatic zones (Ockendon *et al.* 2012, Morrison *et al.* 2013). The combination of environmental change and variation in their ecology make the conservation of migratory species difficult, as the measures needed are unlikely to be the same across the entire flyway (Wilcove & Wikelski 2008). Therefore, understanding the species-level mechanisms driving the effects of, and responses to, environmental change is paramount for successful conservation action (Vickery *et al.* 2014, Alves *et al.* 2019).

Migratory connectivity, the amount of mixing between populations during the lifecycle, is likely to have important implications for population trends (Webster *et al.* 2002). Populations that mix considerably throughout their lifecycles are likely to be buffered from environmental change, with the opposite true for those that remain segregated (Finch *et al.* 2017, Patchett *et al.* 2018). This is because even large amounts of habitat or climatic change will only affect a relatively small proportion of any individual population (Taylor & Norris 2010, Finch *et al.* 2017). The amount of mixing between populations is positively correlated with population trends for some species, although its effects might be overwhelmed by the impact of human-induced habitat degradation for others (Patchett *et al.* 2018). Additionally, other traits such as migration distance are important for population trends. For example, long-distance migrants are more likely to encounter degraded habitats than short-distance migrants because they cover a greater range of sites during their migration (Jones & Cresswell 2010, Morrison *et al.* 2013, Patchett *et al.* 2018, Anderson *et al.* 2019). The migratory behaviours of a species are likely to be important determinants of its ability to respond to environmental change; documenting and understanding them at a species level is therefore vital for conservation.

Population-level migratory patterns are also affected by environmental factors, with the effects of wind receiving much recent attention (Liechti 2006, Shamoun-Baranes *et al.* 2010a, Shamoun-Baranes *et al.* 2017, La Sorte *et al.* 2019, Norevik *et al.* 2020). These are particularly important to understand given that climate change is predicted to increase the frequency and strength of winds in some regions (Cohen *et al.* 2014, Taylor *et al.* 2017). Wind patterns have been suggested as important determinants of migration routes (Erni *et al.* 2005, Klaassen *et al.* 2010, Shamoun-Baranes *et al.* 2017) and migratory behaviour (Shamoun-Baranes *et al.* 2010b, Norevik *et al.* 2020). Birds avoid migrating in adverse wind conditions (Anderson *et al.* 2019, Brust *et al.* 2019), which are likely to have a significant effect on mortality rate (Newton 2006, Kranstauber *et al.* 2015, Loonstra *et al.* 2019). However, individuals also use favourable wind conditions to reduce the energetic costs of migration (Newton 2010, Kranstauber *et al.* 2015, Shamoun-Baranes *et al.* 2017). The influence of wind is likely to differ between spring and autumn migration because of the selection pressures associated with synchronising reproduction with the timing of spring (Mcnamara *et al.* 1998, Conklin *et al.* 2013, Nilsson *et al.* 2013). Given that climate change is predicted to affect prevailing wind conditions in spring and autumn differently (La Sorte & Fink 2017, La Sorte *et al.* 2019), it is important to understand the relative importance of these on migratory individuals throughout their lifecycles.

Here, we investigate migration in the common sandpiper (*Actitis hypoleucos*), a wading bird that breeds across Europe and Asia and winters throughout Africa, southern Asia and Australia (Cramp *et al.* 1983). This species has recently undergone considerable declines throughout Britain and Continental Europe (Ockendon *et al.* 2012, Vickery *et al.* 2014). A study of two British populations found that declines in an English population were correlated with the effects of the North Atlantic Oscillation (NAO), but this was not the case in a Scottish population which remained stable over the study period (Pearce-Higgins *et al.* 2009). This suggests that declines are unlikely to be due entirely to changes in large-scale climatic conditions, prompting calls for a focus on determining their migration routes and wintering grounds, and documenting landscape and weather changes therein (Pearce-Higgins *et al.* 2009).

Recent work fitting geolocators to common sandpipers in Scotland showed that most birds wintered in West Africa, using the Iberian Peninsula and France as stopover sites in both autumn and spring (Summers *et al.* 2019). This study found little evidence that population changes were due to long-term shifts in weather on the wintering grounds (Summers *et al.* 2019). However, the population trends of common sandpipers, as with those of many other migratory species, differ between Scotland and England (Baillie *et al.* 2010, Morrison *et al.* 2013, Harris *et al.* 2020b), and we do not know whether the migration routes and wintering sites of different populations overlap. Indeed, segregation between Scottish and English populations on migration and over winter could lead to divergent population trends (Taylor & Norris 2010, Finch *et al.* 2017). Furthermore, the common sandpiper has a large breeding and wintering range; it is unclear whether there is longitudinal segregation in migration routes as has often been suggested for other species (Cramp *et al.* 1983). Investigating the breeding distributions of birds wintering in West Africa could help to identify larger-scale migration corridors, which is important considering the recent population declines across Europe (Vickery *et al.* 2014). Determining the amount of mixing between populations during migration and over winter, and the main migration corridors, could be key for the conservation of common sandpipers.

We were interested in understanding the amount of overlap in the distributions of English and Scottish populations during migration and winter. Further, most of the birds that were tracked by Summers *et al.* (2019) wintered in West Africa but it is unclear whether West Africa also hosts more easterly-breeding populations (Cramp *et al.* 1983). Finally, Summers *et al.* (2019) found that wind could have influenced the migration of some individuals; we therefore investigate whether birds actively select migration routes based on prevailing wind conditions. Specifically, we use the geolocator data from common sandpipers tagged in Scotland by Summers *et al.* (2019) and combine it with data from birds that we tagged in England and Senegal, to determine (1) the wintering distribution and migration routes of common sandpipers breeding in England, (2) the breeding locations and migration routes of birds wintering in Senegal, (3) the amount of overlap in the distribution of different populations during migration and on the wintering grounds, and (4) whether birds use wind to assist their migration.

Methods

Capturing and tagging

Common sandpipers were caught and tagged within a 6.5km radius of Sedbergh, Cumbria, UK (54.3236˚N, 2.5282˚W), hereafter ‘Cumbria’, and Djoudj National Bird Sanctuary, Senegal (16.3600˚N, 16.2753˚W), hereafter ‘Senegal’. The breeding population in Cumbria nests along rivers, whose banks consist of a mixture of deciduous woodland and farmland. Here, birds were targeted on their breeding territories and caught using mist nets set across rivers or wire mesh walk-in traps placed over nests. Individuals from the wintering population in Senegal were found on isolated saline and freshwater pools created by the rains in June to October and the River Senegal. Birds were targeted with tape lures using mist nets, walk-in traps and whoosh nets.

All individuals that were caught for tagging were fitted with a metal British Trust for Ornithology (BTO) ring on their right tarsus and a yellow ring engraved with two black characters on their left tarsus. Two types of geolocator were used in this study. These were mounted on a red leg flag on the right tibia. In Cumbria in 2017, twenty-two Lotek MK5040 tags were deployed; these weighed 1.1g including the attachment method. In Senegal in 2018, ten Migrate Technology Intigeo geolocators were deployed, weighing 1g in total. The geolocator never exceeded 2.6% of the individual’s total body weight in either population (Chapter 4). Although some of the birds suffered from minor injuries caused by the geolocators, they were unlikely to have affected the migration of recaptured individuals (Chapter 4). The common sandpipers in Scotland were captured and tagged using the methods described in Summers *et al.* (2019). They tagged birds at two separate breeding populations approximately 140 km apart, one on the River Spey, hereafter ‘Speyside’ (57.3500˚N, 3.5333˚W), and one on a Lake in north Sutherland, hereafter ‘Sutherland’ (58.5167˚N, 4.3333˚W).

Geolocator data analysis (Cumbria and Senegal)

Geolocator data were analysed in R using the package ‘GeoLight’ and following the method outlined in Lisovski *et al.* (2012a), (Team 2020). This uses the threshold method for the identification of twilights; a twilight event takes place once light exceeds or goes below a predetermined threshold and provides daily location estimates (Lisovski *et al.* 2019). We used a threshold value of 3 for the Lotek tags and a value of 0.5 for the Migrate Technology tags; the rest of the analyses were identical. The calibration of geolocator data can be done either by using an individual’s known location or using the Hill-Ekstrom calibration method

(Lisovski *et al.* 2012b). Some common sandpipers in Cumbria nested on riverbanks which were heavily vegetated, thereby shading the geolocator at dawn and dusk. Similarly, some of the wintering sites that the Senegalese birds used were also heavily vegetated. This shading can lead to erroneous sunrise and sunset times, resulting in imprecise location estimates (Lisovski *et al.* 2012b) and meaning that using a bird's breeding or wintering territory for calibration purposes sometimes results in infeasible stopover locations and wintering sites. Therefore, for each individual we ran the analyses using both the known location and Hill-Ekstrom calibration methods and compared the geographic positions and stopover sites generated. For the Cumbria birds, we used the calibration method which produced the most accurate breeding location; for the Senegalese birds, we used the calibration method which produced the most accurate wintering location.

We extracted timings of departure and arrival from breeding and wintering sites using the 'ChangeLight' function (Lisovski *et al.* 2012a). We used movement probabilities between 0.97 and 0.98 and minimum stopover durations of one to two days. These values were changed for some birds because the shading during breeding and wintering resulted in multiple, shifting locations during times in which we knew the birds were stationary. We combined stopover locations that were between two and five hundred kilometres from each other. Again, this merging value was chosen based on the results that provided the most accurate breeding locations for birds in Cumbria, or wintering locations for those in Senegal. A distance filter prevented birds moving at more than 75km per hour (Lisovski *et al.* 2019).

Common sandpipers are thought to be territorial during winter (Cramp *et al.* 1983; Chapter 4) and are unlikely to migrate around the equinoxes; we therefore removed all position data ten days either side of the autumn and spring equinoxes. For several birds, the analysis of stationary periods identified latitudinal shifts of over several hundred kilometres during the wintering period around the time of the equinoxes, with no concurrent changes in longitude. Latitudinal estimates during the time surrounding the equinoxes is not possible with geolocator data (Lisovski *et al.* 2019) and common sandpipers are likely to maintain the same territory throughout their non-breeding period, as suggested by the raw light data and from our work on the wintering grounds in Senegal (Chapter 4). As such, we averaged all the location estimates across the entire non-breeding season in Africa to obtain a single wintering location for use in plots and for the analysis of wind assistance (see below). The arrival and departure date to and from the wintering location was used for identifying autumn, spring and wintering periods. For the kernel density analyses (see below), the raw positional data were used and so no assumptions about the wintering locations of individuals were made. Positional data were twice smoothed for plotting purposes, kernel density estimation and the analysis of wind assistance.

Geolocator data analysis (Scotland)

In order to understand the differences in migration routes and wintering locations between birds tagged in Cumbria, Senegal and Scotland, we used the data from Summers *et al.* (2019). To ensure that the results of the geolocator analyses were comparable between birds tagged in each location, we reanalysed the data in Summers *et al.* (2019) using the methods described above (using a light threshold value of 3). In order to validate our methods, we compared the results of our analyses of the geolocator data from Scottish birds to those of Summers *et al.* (2019). For each Scottish bird we compared the timing of the departure from the breeding grounds, arrival to the wintering grounds, departure from the wintering grounds and arrival to the breeding grounds. The results from the two analyses were strongly correlated, validating our analyses (Pearson correlations, $r_{\text{breeding departure}} = 0.90$, $P_{\text{breeding departure}} < 0.005$; $r_{\text{winter arrival}} = 0.98$, $P_{\text{winter arrival}} < 0.005$; $r_{\text{winter departure}} = 0.91$, $P_{\text{winter departure}} < 0.005$; $r_{\text{breeding arrival}} = 0.71$, $P_{\text{breeding arrival}} = 0.05$).

Breeding locations of Senegal-tagged birds

Preliminary analyses of the geolocator data from common sandpipers tagged in Senegal showed that they bred in areas with 24-hour daylight. Traditional methods of geolocation using sunrise and sunset times cannot obtain location estimates in the high arctic with 24-hour daylight. In order to determine the breeding locations of these birds, we used the 'PolarGeolocation' package (Lisovski 2018). We followed the workflow outlined in Lisovski (2018) and used the most likely breeding location for plotting purposes and for the analysis of wind assistance (see below).

Migratory connectivity (kernel density and overlap)

To identify the overlap in the stopover sites and wintering distributions of common sandpipers from the different tagging locations, we analysed kernel densities using the package 'adehabitatHR' (Calenge 2019). For each individual in our dataset, we separated positions from the breeding grounds, during the autumn (southbound) and spring (northbound) migration periods and during the wintering period. However, because of shading to the geolocators at dawn and dusk on the breeding grounds, there was some error surrounding the positions of breeding locations. Therefore, we assumed that birds had reached the breeding grounds after crossing certain latitudes, depending on their tagging location. For Cumbria, this threshold was 50 degrees latitude, for the two Scottish populations it was 52 degrees latitude and for the Senegalese birds it was 57 degrees latitude. We excluded positions that were above these thresholds for the analyses of overlap during the autumn and spring migration periods.

For each season we obtained the 75% utilisation distribution of the stationary periods of all individuals from each tagging location in order to identify overlap in distributions between individuals from different populations. This provided an estimate of the areas used as stopovers and wintering location for birds from each of the tagging locations. We then determined the amount of overlap between individuals from different tagging locations during autumn, spring and winter by calculating the proportion of the 75% kernel density estimate for each tagging location that was found in the kernels of the other locations (Calenge 2019).

Migratory connectivity during winter

In order to determine the amount of mixing between individuals from the same breeding populations on the wintering grounds, we performed Mantel correlation tests. These were used to determine whether the distances between individuals on their breeding and wintering grounds are correlated (i.e. whether birds that breed close together also winter close together), using a scale ranging between -1 and 1. Low Mantel coefficients indicate a high degree of mixing, high coefficients indicate low mixing (Ambrosini *et al.* 2009). We did this for individuals from the two Scottish populations and Cumbria, but excluded the individuals tagged in Senegal because of the small sample size and uncertain spatial structure between individuals on their wintering grounds.

Analysis of wind assistance

To understand whether birds used wind to support their migratory journeys, we compared the wind costs (as determined by the speed and direction of wind, described below) experienced by migrating birds to those of randomly simulated migrations. This was to determine whether birds were actively using wind to support their migration, or whether they were migrating irrespective of wind conditions. We used the package 'rWind' to obtain daily gridded (0.5-degree resolution) wind direction and speed data at surface level (10m; Fernández-López & Schliep 2018). For the autumn and spring migration periods of each individual in our dataset separately, we obtained the daily wind conditions across the entire Afro-Palearctic flyway at a 0.5-degree spatial resolution. We calculated the mean daily wind direction and speed values to obtain a gridded map of the average conditions across the entire flyway for the autumn and spring migration periods of each individual tracked with a geolocator (Figure 5.2). We then calculated the transition probabilities between every cell in the flyway, with movement into oncoming winds allowed, but incurring a greater cost penalty than tailwinds (Fernández-López & Schliep 2018).

Observed birds

For each spring and autumn track of an individual, we calculated the cost of moving between sequential positions based on the transition probabilities using the 'costDistance' function from the package 'gdistance' (Van Etten 2017); this function selects the route of least cost between two points. The costs of all relocations in the migratory track were summed and divided by the total number of relocations to obtain a cost index. This equates to the average cost of movement per relocation and made migration costs comparable across tagging locations (i.e. because birds from each tagging location travelled different total distances) and between the observed and simulated birds.

Simulated birds

We simulated bird migrations to determine the wind costs associated with 'random' migration routes. For each migration of every bird tracked with a geolocator, we generated one hundred random tracks. The simulated tracks travelled between the same breeding and wintering location as the observed bird and were subject to the same wind conditions (i.e. the same transition probabilities). For the Senegalese birds which bred in areas of 24-hour daylight, the observed tracks ended prior to reaching the breeding grounds as it is not possible to determine movement and stopover locations in areas of 24-hour daylight using geolocators. This means that the tracks for the observed birds were considerably shorter than those for the simulated birds because they ended (spring migration) or started (autumn migration) when the bird crossed the arctic circle, rather than at the breeding site. This could have affected our analysis comparing observed versus simulated birds. We therefore ran all our analyses of the Senegalese birds twice, once with tracks that started and ended at the same points as the tracks of observed individuals (i.e. where the bird crossed the arctic circle) and a second time with tracks that began and ended at the breeding sites.

For autumn migration, we created a latitudinal sequence between the breeding and wintering locations in 0.5-degree increments. We then created a sequence between the breeding and wintering longitudes of the same length as the latitudinal sequence. For each latitudinal step in the data, we used the corresponding longitudinal value as the mean in a random number sampler following a normal distribution with a standard deviation of four.

We sampled one random number for each latitudinal step, thereby generating a ‘random track’. This standard deviation was chosen because it generated tracks that covered most of the observed flyway of common sandpipers from the three tagging locations (Supplementary Figure 1). As individuals approached the end point of their migration (as determined by the breeding and wintering locations of the observed birds), the standard deviation of the normal distribution was reduced. We repeated these steps in the opposite direction for spring migration. The random tracks were twice smoothed and their cost determined using the same process as above, using the wind conditions that the observed individual experienced during its real migration.

We compared the cost of autumn and spring migrations for observed and simulated individuals. For observed birds we fitted a linear model with cost index as the response variable and the migration period (autumn or spring) as the only explanatory variable. For simulated birds we fitted a linear mixed effects model (LME) from the package ‘lme4’ using the same variables but included individual identity as a random intercept to control for repeated simulated tracks for the same observed individual (Bates *et al.* 2015).

We used LMEs to test whether common sandpipers used winds to facilitate their autumn and spring migrations. For each tagging location and each migration separately, we fitted the cost index as the response variable and whether the cost was that of an observed or simulated bird (hereafter ‘bird type’) as the sole explanatory variable. We also included individual identity as a random intercept, again to control for repeated simulations for the same observed individual. Locations were defined as the tagging locations, although we grouped the two Scottish breeding populations into a single location. This is because there was little difference between the start points of individuals from these two populations and there were only two birds tagged in Speyside. We validated all models by plotting the distribution of the residuals and the expected versus fitted values.

Results

In Cumbria in 2018 we recovered eleven geolocators after resighting thirteen tagged individuals at the study site (13/22). In Senegal in 2019, we recovered four geolocators, but resighted eight tagged birds in total (8/10). There were no significant differences between the return rate, body condition or reproductive success of birds with geolocators compared with those carrying only rings (Chapter 4). Additionally, the raw light data of the birds tagged in Senegal showed light patterns indicative of incubation, meaning that they were all breeding individuals. The Scottish study retrieved ten geolocators across the two study sites (Table 5.1), but there were no comparisons with a colour ringed control group (Summers *et al.* 2019). This resulted in twenty-five tracks of autumn migration and twenty-two for spring migration, as three geolocators had failed on the wintering grounds (two from birds in Scotland and one from a bird in Cumbria).

Common sandpipers tagged with geolocators in Cumbria used similar migration routes to the Scottish birds and also wintered in West Africa (Figure 5.1). In autumn, the birds from Cumbria used southern England, northern France and the western half of the Iberian Peninsula as stopover sites, before wintering in the southern half of West Africa (all south of 18˚N). In spring, individuals also stopped in Morocco and, compared with autumn migration, used sites further inland on the Iberian Peninsula and throughout France (Figure 5.1). The four common sandpipers tagged in Senegal all bred in Scandinavia, but in different populations ranging from approximately 59˚N in southern Sweden to approximately 70˚N in Arctic Norway (Figure 5.1). In autumn, birds from Senegal used northern Europe (Denmark, the Netherlands and northern Germany), western France and the east coast of the Iberian Peninsula as stopover sites. In spring, these birds used sites similar to those used by the birds from Cumbria, although these stopover sites also extended to northern Europe (Figure 5.1).

Table 5.1 The sample sizes, tagging locations and distances between individuals at their tagging locations (Tagging max and mean dist) and destinations (Final max and mean dist). All distances are reported in kilometres.

Location	Number tagged	Tagging long	Tagging lat	Tagging max dist	Tagging mean dist	Final mean long	Final mean lat	Final max dist	Final mean dist	Migration dist
Scotland Spey.	2	-3.53	57.35	0.00	0.00	-16.05	11.09	315.01	315.01	5260.11
Scotland Suth.	8	-4.33	58.49	15.85	6.02	-15.09	17.65	2262.90	843.75	4631.36
Cumbria	11	-2.55	54.32	8.59	3.38	-15.77	11.09	888.60	360.39	4951.27
Senegal	4	-16.26	16.42	20.54	11.87	17.07	63.94	1416.59	800.90	5866.76

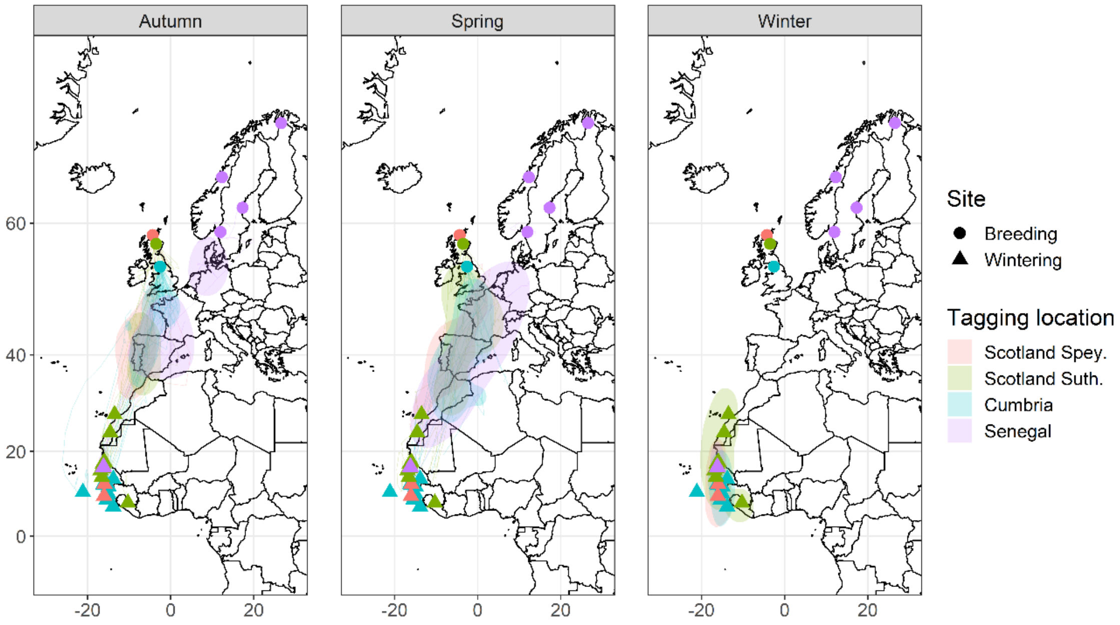


Figure 5.1 The distribution of the wintering sites of individuals from the four tagging locations and their stopover sites during autumn and spring migrations. The shaded regions represent the 75% kernel densities of the utilisation distribution of individuals from different tagging locations. Closed circles are breeding locations, closed triangles are wintering locations.

Migratory connectivity (kernel density and overlap)

The migration routes and wintering locations of birds from the three different tagging locations overlapped considerably, with the proportion of overlap between the British populations highest. The proportion of overlap between the Senegal-tagged birds and the British birds was lower in autumn than spring migration (Table 5.2). This is because the Senegal-tagged birds flew further east before crossing the Pyrenees in autumn. In spring there was more overlap between the Senegalese and British birds than in autumn, as the latter used stopover sites throughout France. In winter, there was considerable overlap in the kernel density distributions between individuals from the different tagging locations, suggesting a high level of migratory connectivity (Figure 5.1). However, the Mantel correlation coefficient was 0.26 (P = 0.001), suggesting that some of the breeding structure of common sandpipers is maintained on the wintering grounds. Indeed, the mean distances between wintering individuals from the Speyside and Cumbria populations were only 315 and 360km, respectively, whereas the mean wintering distances between the individuals from the Sutherland population was 843km (Table 5.1). However, the fact that only two birds were tagged at the Speyside population might have confounded these results.

Table 5.2 The proportion of the 75% kernel distribution of individuals from one tagging location (rows) covered by that from other tagging locations (columns) in autumn, spring and winter. The numbers in each cell correspond to the overlap in autumn, spring and winter periods, respectively.

	Scotland Spey.	Scotland Suth.	Cumbria	Senegal
Scotland Spey.	1, 1, 1	0.57, 0.67, 0.81	0.56, 0.78, 0.75	0.42, 0.83, 0.25
Scotland Suth.	0.79, 0.48, 0.36	1, 1, 1	0.66, 0.79, 0.32	0.67, 0.78, 0.11
Cumbria	0.65, 0.55, 0.87	0.57, 0.78, 0.84	1, 1, 1	0.76, 0.88, 0.23
Senegal	0.24, 0.33, 1	0.28, 0.43, 1	0.37, 0.5, 0.77	1, 1, 1

Analysis of wind assistance

For the Senegal-tagged birds, starting and ending the simulated tracks at the breeding grounds increased the raw costs of migration but not the cost indices and therefore did not affect the outcome of any of our analyses. The results of the models using the cost indices of simulated tracks to and from the breeding locations of the Senegalese birds are presented in all subsequent analyses. An example of one of the observed migratory tracks and the wind conditions the individual faced is shown in Figure 5.2.

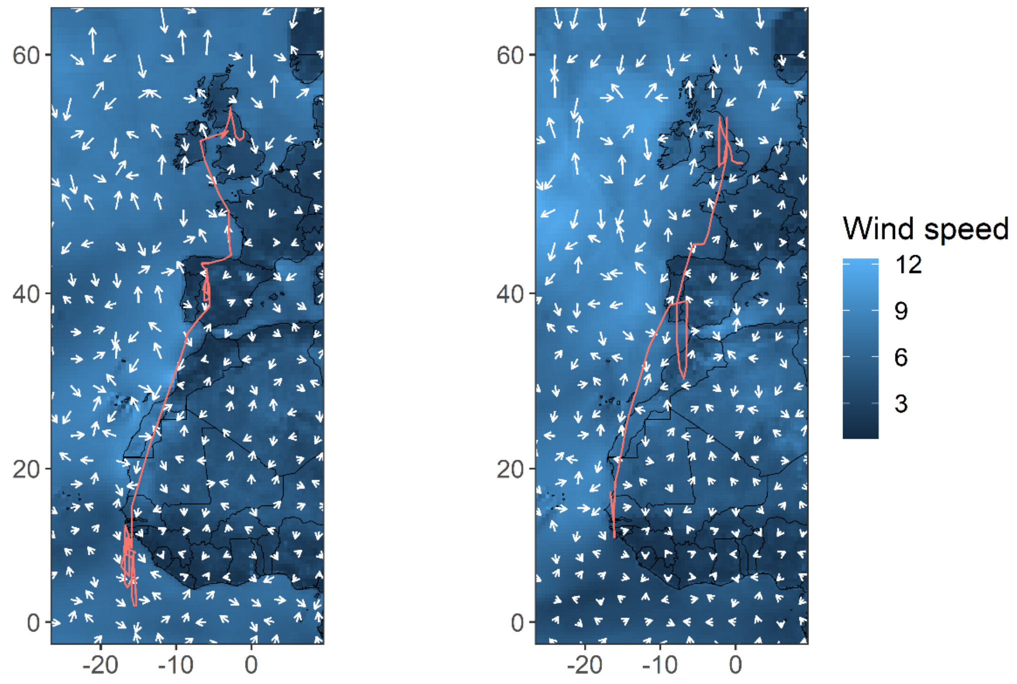


Figure 5.2 The migration of the common sandpiper "DK" tagged in Cumbria, in autumn (left) and spring (right) in relation to wind speed and direction. White arrows indicate the direction and speed of wind; the longer the arrow the greater the wind speed.

Wind costs in autumn and spring

For observed birds, the cost index of autumn migration was significantly lower than for spring migration. Conversely, for simulated birds, the cost index of autumn migration was higher than in spring (Figure 5.3, Table 5.3).

Wind assistance during migration

In autumn, the cost indices associated with the migration of observed birds were significantly lower than those of the simulated birds, suggesting that they use more favourable wind conditions than would be expected at random. In spring, the opposite was true, with the cost indices of observed birds higher than those expected at random, suggesting a lower influence of wind on migration route (Figure 5.3, Table 5.4).

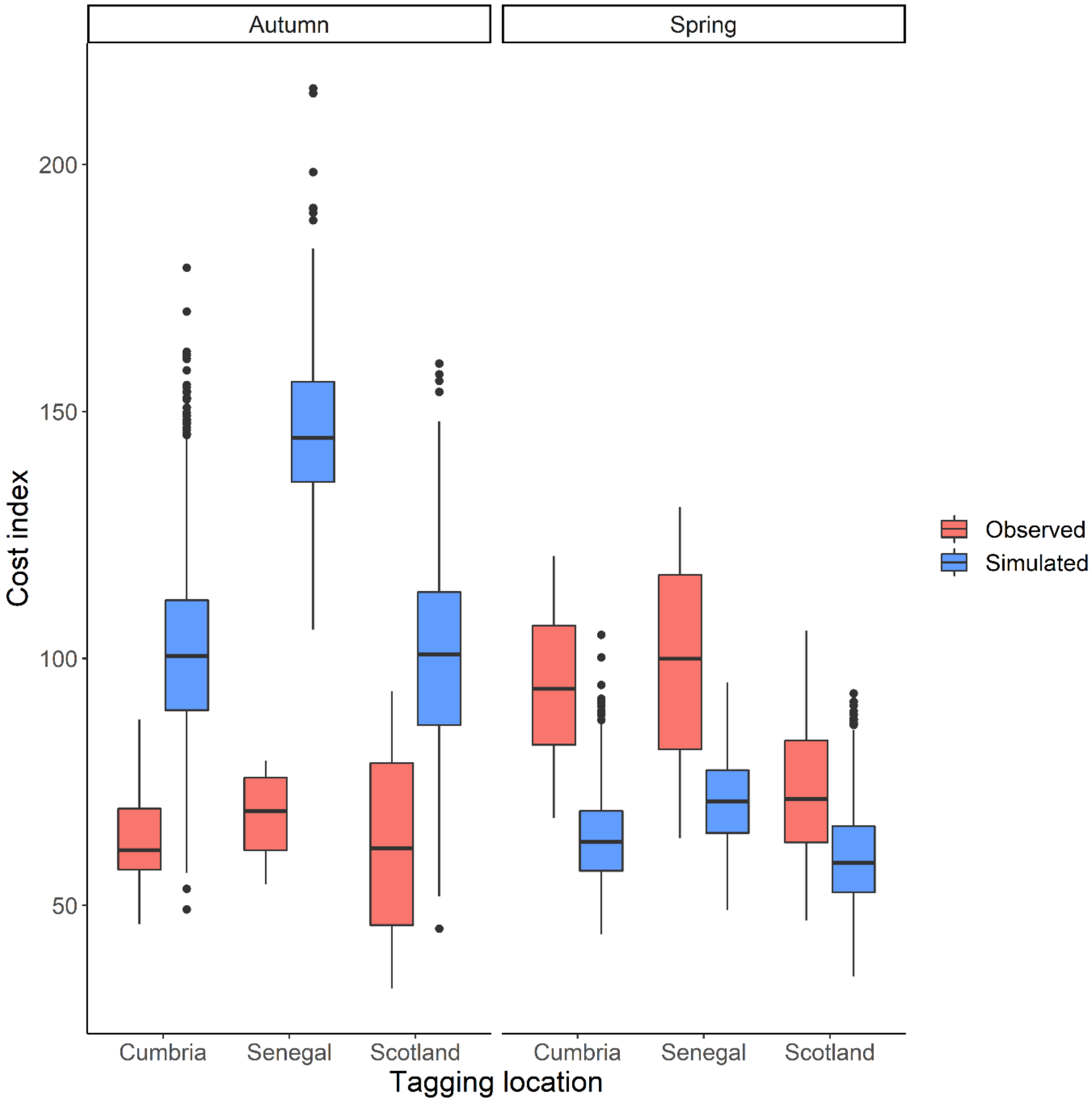


Figure 5.3 The cost index of migration of observed and simulated common sandpipers from the three tagging locations. Boxplots show the median, interquartile range, 1.5 times the interquartile range and outliers.

Table 5.3 Results of a linear model (for observed birds) and a linear mixed effects model of the difference in the cost of the autumn and spring migrations of observed and simulated birds.

Bird type	Autumn	Spring	F/T value	P value	Marginal R^2	Adjusted/Conditional R^2
Observed	63.89	87.97	19.08	<0.0001	\	0.28
Simulated	108.29	63.12	-116.53	\	0.59	0.78

Table 5.4 Results of the linear mixed effects models comparing the cost indices of observed and simulated birds from Cumbria, Senegal and Scotland in autumn and spring.

Location	Migration	Observed birds (intercept)	Simulated estimate	Standard error	T value	Marginal R^2	Conditional R^2
Cumbria	Autumn	64.15	101.74	3.87	26.32	0.04	0.49
Senegal	Autumn	67.94	146.37	4.10	35.71	0.17	0.36
Scotland	Autumn	61.98	100.25	4.33	23.13	0.04	0.51
Cumbria	Spring	93.91	63.61	2.36	-12.85	0.10	0.33
Senegal	Spring	98.53	70.80	3.54	-7.84	0.07	0.53
Scotland	Spring	74.71	59.51	2.74	-5.55	0.02	0.44

Discussion

Our study is the first to report the wintering distributions and migration routes of common sandpipers breeding in England. Our findings indicate considerable overlap in the distributions of English and Scottish birds in the non-breeding season (Summers *et al.* 2019), despite the Mantel test suggesting that some of the breeding ground structure is maintained during winter. Even with considerable overlap during the non-breeding season, greater population declines in Scotland than England could be driven by fine-scale differences in habitat selection that are not discernible using geolocator data (Baillie *et al.* 2010, Harris *et al.* 2020b). For example, the amount of anthropogenic disturbance, which has important implications for wintering migrants, varies across West Africa and could lead to localised variation in the suitability of sites (Vickery *et al.* 2014, Ruiz-Sánchez *et al.* 2017, Patchett *et al.* 2018, Willemoes *et al.* 2018). Additionally, analyses of long-term weather trends and habitat change at specific stopover and wintering sites might reveal an effect on population size, as current studies have only used large-scale climate indices (Pearce-Higgins *et al.* 2009, Summers *et al.* 2019). Our findings could mean that steeper population declines in England than Scotland are unlikely to be caused by differences in migration routes and wintering sites. Instead, it is possible that trends differ because of breeding ground conditions, perhaps through variation in productivity and recruitment rates (Dougall *et al.* 2005).

We are also the first to report the breeding distributions of common sandpipers tagged on their wintering grounds in West Africa. Our small sample of wintering birds were tagged within 20km of one another in Senegal and yet were spread across the entire length of Scandinavia during the breeding season. The breeding locations of these birds are surprising, as theory and previous research suggest longitudinal segregation in migration routes and wintering grounds for many species (Cramp *et al.* 1983, Van Bemmelen *et al.* 2019, Briedis *et al.* 2020), whereas our findings reveal an east-west migration corridor. The birds from all tagging locations wintered along the West African coast, but it is unclear where birds from the eastern parts of the Sahel breed. More work documenting the migration routes of common sandpipers breeding and wintering further east is needed, especially as recent studies of other migratory waders have revealed major differences in migration strategy between populations (Van Bemmelen *et al.* 2019).

Common sandpipers tagged in England, Scotland and Senegal had similar non-breeding distributions, which could buffer the species from habitat change (Taylor & Norris 2010, Finch *et al.* 2017). However, this overlap also means that different breeding populations will experience similar wintering conditions. In West Africa, there has been significant agricultural intensification and a reduction in the amount of mangrove forest (Vickery *et al.* 2014, Summers *et al.* 2019). Patchett *et al.* (2018) found that in the Afro-Palearctic flyway, species with high wintering ground spread are affected by habitat change in Africa, as they are more likely to encounter poor-quality habitats, and are therefore more likely to be affected by habitat degradation.

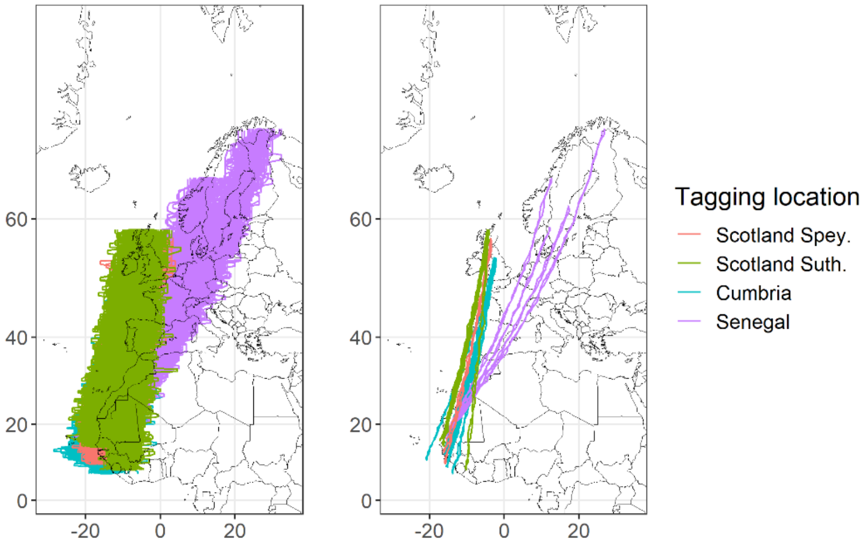
Wintering habitat change is unlikely to be solely responsible for the European decline in common sandpipers, as much of the agricultural expansion in West Africa has involved rice fields which waders can use for foraging (Elphick 2000, Wymenga & Zwarts 2010). However, it is unlikely that rice fields are equivalent to natural wetlands (Taylor & Schultz 2010, Wymenga & Zwarts 2010; but see Elphick 2000). Birds reliant on rice fields could have reduced body condition compared to those using more natural habitats, thereby affecting their ability to perform their spring migration (Duijns *et al.* 2017) or cope with adverse conditions on the breeding grounds (Morrison *et al.* 2013). Furthermore, common sandpipers may incur significant costs during their spring migration, with droughts affecting stopover sites and potentially adverse prevailing winds (Summers *et al.* 2019).

Common sandpipers appear to use wind to facilitate their migration in autumn, but in spring, appear to actively fly into adverse conditions. This is despite the wind costs of simulated migrations being significantly lower in spring than autumn, suggesting a decrease in wind speed or more tailwinds. These results are consistent with the theory that autumn migration is under lower selection pressure than spring migration (Mcnamara *et al.* 1998). In spring, early arrival to the breeding grounds is important for reproductive success (Morrison *et al.* 2019) and therefore individuals may be less inclined to wait for supportive winds or divert from the most direct route (Nilsson *et al.* 2013, Gutierrez Illan *et al.* 2017). In autumn, individuals are under reduced time pressure allowing them to wait for beneficial winds or choose migratory routes that involve more tailwinds (Nilsson *et al.* 2013, Duijns *et al.* 2017). Alternatively, it is possible that individuals are in better body condition in spring than autumn, meaning they can ignore adverse wind conditions in the former. Regardless, our results show that common sandpipers may face higher wind costs during spring migration, as also suggested by Summers *et al.* (2019), and as shown for a number of other species (Lok *et al.* 2015, Loonstra *et al.* 2019).

The wind costs associated with migration could have significant effects on population trends. This may be particularly true in spring, where our results suggest that the cost of migrating is already highest. The physiological cost of migration is likely to be high for many species, especially when making large desert or ocean crossings (Alerstam *et al.* 2003, Klaassen *et al.* 2014, Lok *et al.* 2015). Indeed, for other species, mortality is often higher during migration than in residency periods, and particularly so during spring migration (Lok *et al.* 2015, Loonstra *et al.* 2019, Robinson *et al.* 2020). This could be because of the time constraints associated with spring migration, meaning that individuals are unlikely to wait for favourable conditions (Loonstra *et al.* 2019, Robinson *et al.* 2020). If the wind costs associated with spring migrations increase due to climate change (Cohen *et al.* 2014, Taylor *et al.* 2017), then this could reduce the survival of migrating birds and have significant implications for population trends (Newton 2006, Robinson *et al.* 2020). However, this is dependent on the physiological cost of migration relative to birds' flight abilities, as tracking studies have shown that some species are able to fly non-stop between breeding and wintering regions thousands of kilometres apart (Gill *et al.* 2009, Alves *et al.* 2016). Therefore, it is possible that some species are unlikely to be affected by increases in adverse weather conditions as they have the necessary body reserves to continue migration regardless. Furthermore, wind conditions may become more favourable under climate change and particularly so in spring (La Sorte *et al.* 2019), which is where extra costs from increased headwinds are likely to have the greatest effects (Lok *et al.* 2015, Loonstra *et al.* 2019). Further research into how wind conditions shape migratory behaviours and population trends is important given the influence climate change will have on global wind patterns.

Our results are susceptible to several inaccuracies, largely due to the pitfalls of tracking migration using geolocators. Geolocators are only accurate to approximately 150km (Lisovski *et al.* 2012b, Rakhimberdiev *et al.* 2016), meaning that the observed routes of individuals that we used could be different to the true routes taken by individuals. There are further inaccuracies associated with the timings of migratory journeys, with the true date of departure lying within a few days of the date that we used. Finally, to the best of our knowledge, there are no accurate measurements of the altitude at which common sandpipers fly during migration, which could have important consequences for the wind conditions experienced (Shamoun-Baranes *et al.* 2017). These factors could have affected our measures of the wind costs during migration. Further work could therefore simulate the effects of variation in the location, timing and altitude of observed individuals on the wind costs experienced during migration. However, given the consistent wind costs across all the observed individuals relative to their simulated counterparts, we are confident in our conclusions.

Supplementary figure



Supplementary Figure 1 Tracks of the simulated bird migrations (left) and the averaged simulated tracks for each observed individual in autumn and spring (right).

Chapter 6 Flyway-level analysis reveals changes in the timing of migration in wading birds

Introduction

The effects of anthropogenic climate change on migratory bird species have received much attention, as there is a clear link to recent population declines, and changes in their phenology and distribution (Root *et al.* 2003, Visser & Both 2005, Vickery *et al.* 2014, Gill *et al.* 2019, Helm *et al.* 2019). Migratory birds are particularly susceptible to the effects of climate change, but determining the causes for their population trends is extremely difficult because changes in climate at one lifecycle stage might not reflect those occurring at others (Newton 2004, Van Gils *et al.* 2016). They travel in large numbers between ecologically distinct geographic regions, meaning that they provide valuable ecosystem services (Wilcove & Wikelski 2008, Viana *et al.* 2016a, Viana *et al.* 2016b). Further work is needed to understand the causes of change in migratory behaviour at a global scale if conservation measures are to be successful.

One particularly well-documented impact of climate change is a shift in migratory phenology (Parmesan & Yohe 2003, Lehikoinen *et al.* 2004, Gordo 2007). Most studies have focussed on changes in spring migration because its timing is thought to be under strong selection pressure due to the time constraints associated with reproduction (Mcnamara *et al.* 1998, Møller *et al.* 2008, Conklin *et al.* 2013). In general, early arrival to breeding regions is thought to be beneficial for breeding success by providing access to better territories, increasing the amount of time for reproduction and improving chick recruitment (Kokko 1999, Low *et al.* 2019, Morrison *et al.* 2019). However, while population-level timings appear to be advancing across species (Parmesan & Yohe 2003, Lehikoinen *et al.* 2004), there is growing evidence for remarkable individual consistency in the timing of spring migration (Conklin *et al.* 2013, Gill *et al.* 2014). This discrepancy suggests that population-level change may occur through generational effects rather than phenotypic plasticity (Gill *et al.* 2014).

Many birds are dependent on plant bud burst and peaks in insect abundance to feed their chicks, and time their migration accordingly (Both *et al.* 2004). Climate change has caused advances in the timing of bud burst and insect emergence due to warmer spring temperatures, but many bird species have been unable to advance their migration at the same rate (Stenseth & Mysterud 2002, Visser & Both 2005, Miller-Rushing *et al.* 2010). This mismatch is correlated with declines in reproductive success and population size (Both *et al.*

2006, Møller *et al.* 2008). Furthermore, the benefits of early arrival at breeding sites are potentially offset by the likelihood of encountering poor early season weather conditions. For example, individuals are more likely to encounter cold temperatures or even snowfall in early spring, which can increase mortality (Visser *et al.* 2015). This trade-off between the benefits of early migration and the costs of encountering bad weather is especially important given that climatic conditions are predicted to become more variable (Cohen *et al.* 2014). Indeed, there have already been contrasting phenological responses to climate change between species, as they differ in their ability to respond (Cohen *et al.* 2015, Mayor *et al.* 2017).

The consequences of climate change for the timing of autumn migration are much less clear than in spring, presumably because of the reduced time constraints associated with the former (Mcnamara *et al.* 1998, Conklin *et al.* 2013). For example, while the timing of autumn migration has become later for short-distance migrants, that of long-distance migrants has advanced (Jenni & Kery 2003). Indeed, for some species, autumn migration has advanced in line with changes to spring migration (Newson *et al.* 2016); for others, autumn migration has become later (Adamík & Pietruszková 2008). Furthermore, species follow different migratory schedules (Newton 2010, Mayor *et al.* 2017), which might cause variation in their response to climate change.

Weather plays an important role in the timing of migration. For example, many studies have shown that individuals favour tailwinds when departing for migration after stationary periods (Shamoun-Baranes *et al.* 2010b, Sergio *et al.* 2014) and adjust their flight altitude to exploit the most favourable wind conditions (Senner *et al.* 2018). However, the influence of weather is likely to differ between spring and autumn migration. Individual tracking has shown greater consistency in the timing of spring than autumn migration (Conklin *et al.* 2013). Therefore, individuals in autumn may be more likely to wait for favourable conditions (Sergio *et al.* 2014) or spend longer improving body condition prior to migration (Duijns *et al.* 2017) because they are under less time pressure (Mcnamara *et al.* 1998, Møller *et al.* 2008, Conklin *et al.* 2013). At the population level, the timing of migration is also correlated with weather conditions in different regions throughout the life cycle (Gordo 2007). Weather conditions are likely to influence the timing of population-level migration through the knock-on influence of ground conditions on individual body condition (Duijns *et al.* 2017) and the cues they can provide to birds regarding breeding site conditions (Forchhammer *et al.* 2002, Lameris *et al.* 2018). More work understanding the cross-species responses to weather conditions during migration is needed.

Phenological studies are predominantly focussed on single species at the population level, investigating the arrival of individuals to specific regions or using observatory data to study the timing of passage. While useful for understanding specific cases, and for declining species in particular, this approach may miss key information about changes occurring in different populations. For example, phenological responses vary across latitudinal gradients (Chmura *et al.* 2019), and populations may migrate at different times (Reneerkens *et al.* 2009, Chambers *et al.* 2014) or use different migration routes between years (Shamoun-Baranes *et al.* 2010b, Hooijmeijer *et al.* 2014, Hewson *et al.* 2016). Hence, even within species, different breeding populations may be segregated from one another both spatially and temporally during migration and at their wintering sites (Gilroy *et al.* 2016, Hewson *et al.* 2016, Finch *et al.* 2017). Large-scale species-level studies using citizen science datasets and radar technology have found similar patterns to those done at the population-level (Hurlbert & Liang 2012, Mayor *et al.* 2017). However, the patterns of change may differ when considering timings across a wide range of species (Zaifman *et al.* 2017, Horton *et al.* 2018, Horton *et al.* 2019a). Given the ecological importance of migratory birds (Parmesan & Yohe 2003), and that many are in severe decline (Vickery *et al.* 2014), the need to understand flyway-level changes due to global warming cannot be overemphasised (Wilcove & Wikelski 2008, Lovas-Kiss *et al.* 2019).

Most studies of phenology consider only passerine species, but other groups are also susceptible to climate change. Migratory shorebirds or wading birds (hereafter 'waders') are a group in decline and of high conservation concern (Aewa 2018). Most waders are migratory (Piersma 2003, Piersma 2007), they breed through a wide range of latitudes, and they are reliant on relatively specific and seasonal habitats (Haig *et al.* 2019), all of which increase their susceptibility to climate change (Both *et al.* 2009). Furthermore, studies of wader phenology at breeding, wintering and at passage sites have shown contrasting trends with both advances and delays to the timing of migration (Murphy-Klassen *et al.* 2005, Adamík & Pietruszková 2008, Petersen *et al.* 2012, Meltofte *et al.* 2018). Waders are therefore the ideal group in which to investigate the impact of climatic conditions on the timing of migration. Here, we use over ten years' worth of sightings from eBird, the Cornell Laboratory of Ornithology citizen science database (Sullivan *et al.* 2014), to investigate changes in the migratory phenology of waders in two major flyways. Specifically, we use a novel application of changepoint detection analysis to determine whether the phenology of migratory birds at a flyway scale has changed over time. Changepoint analysis is used to identify the point at which the statistical properties of a time series change, in this case changes in mean and variance (Killick & Eckley 2014). We then investigate whether these changes are correlated with weather conditions at breeding and wintering sites.

Methods

eBird data

Sightings of all waders species classified by Birdlife as being migratory were downloaded from the eBird citizen science database (Sullivan *et al.* 2014). Analyses were restricted to the four major families Charadriidae, Haematopodidae, Recurvirostridae and Scolopacidae, for which most data were available. The data were filtered to include only observations from 2003 to 2016. While eBird started in 2002, the database contains some historical observations which were not suitable for our analyses. Sightings were split into three major flyways based on longitude: the Nearctic Flyway (classified as 170°W to 24°W); the Afro-Palearctic Flyway (as 26°W to 90°E); and the East-Australian Flyway (as 91°E to 170°E; Colwell 2010). However, the East-Australian flyway had too few data and so we excluded it from subsequent analyses. Some species occurred in both the Nearctic and Afro-Palearctic flyways; these populations were considered separately in the analyses because there are likely to be different selection pressures operating between flyways. We also removed species that do not carry out an intercontinental migration, such as some intra-Africa migrants. Elsewhere in the methodology, ‘species’ is used to mean ‘species by flyway’.

For each day in each year, we created a mean latitudinal location for each species by averaging the latitudes of all sightings reported. Observer bias may lead to species not being reported at latitudes in which they were present. To account for this, for each day, we determined (1) the number of times a species was seen at each latitude (latitudes were considered as one-degree latitudinal bands) and (2) the total number of sightings of any wading bird species reported at any latitude. Therefore, for each day we had the number of sightings of a species in each latitudinal band and the total numbers of sightings of all species across all latitudinal bands. We then used the number of times a species was reported at each latitude as a proportion of the total number of sightings of any species seen across all latitudes to create a daily, weighted mean latitude for each species. For example, a species for which 100 sightings were reported from 35°N on a day in which 1500 sightings of waders of all species were reported across all latitudes, was given a weighting of 100/1500 for that latitude on that day. This proportion provided an index of the effort made to observe a species at a given latitude, relative to the total effort made to observe waders across all latitudes. Additionally, we removed any days on which the total number of sightings of all species within a flyway was less than five. This avoided biasing the data due to a relatively small number of observers being out on any given day (Johnston *et al.* 2019).

Changepoint analysis

We were interested in identifying changes in both spring and autumn migration. We define 'spring migration' to be the movement of individuals northwards, towards the breeding grounds, with 'autumn migration' referring to the movement south towards the non-breeding grounds. In order to determine the timing of these migrations in each year, we identified significant shifts in the mean latitude of each species. We excluded the years of data that contained fewer than three hundred days of observations for each species within each flyway separately (in the Nearctic 162 years in total from 38 different species were excluded; in the Afro-Palearctic 151 years from 26 different species), and considered each year individually. We then used changepoint detection analysis to detect these shifts.

Suppose that $\{y_t\}_{t\,=\,1,\ldots,n}$ represents our daily mean latitudinal observations of a species over a one-year period, where n is the number of observations for that year and t is the day of the year. Then, a changepoint in these data, 'τ', corresponds to a point in time such that the statistical properties of $\{y_t\}_{t\,=\,1,\ldots,\tau}$, and $\{y_t\}_{t\,=\tau+1,\ldots,n}$ differ in some way. A data set could contain multiple changepoints, which divide the data into segments; each of these segments will have some different statistical property. For example, if a data set contained changes in its mean, then each segment would have a different mean. There might be only one statistical property that changes, or there could be multiple. Supplementary Figure 1 gives an example of three types of changepoint: (a) change in mean, (b) change in variance, and (c) change in both mean and variance. For an introduction to changepoint detection in an environmental setting, see Andersen *et al.* (2009).

We used the 'changepoint' package available in R (R Core Team 2020) to implement changepoint detection. We used the Segment Neighbourhood Search algorithm (Auger & Lawrence 1989) to detect changepoints. This allowed us to restrict the number of changes detected, in each year running January through to December, to be two. These correspond to one latitudinal change for spring migration and one latitudinal change for autumn migration, splitting the data into three segments (Figure 6.1, Supplementary Figure 1). We obtained two sets of changepoint locations for each year. The first corresponded to changes in mean and the other in mean and variance combined. To obtain these, we used the 'cpt.mean' and 'cpt.meanvar' functions, respectively. Identifying changes in mean and variance simultaneously was useful because: (1) many species have wider winter range distributions and, (2) winter sighting distributions were more variable than breeding ground distributions based on visual inspection of the raw data. We did not identify changes in variance only, because bird migration is most logically defined as a shift in mean latitude over the year. We then obtained the day of the year on which the changepoints in latitude occurred for each migration. The dates identified by the two changepoint detection methods were compared with one another in order to refine our estimates of the timing of spring and autumn migrations (Figure 6.1). We did not use the changepoint estimates if the two methods identified dates that were more than fourteen days apart. After inspecting the raw data, two weeks was considered a suitable threshold to use for the removal of years. In years when the changepoints were over two weeks apart, the latitudinal data were too variable and the analyses could not reliably identify the true timing of migration. In all other cases, we used the mean of the dates identified by the two methods as the migration date in all subsequent analyses, hereafter referred to as the 'migration day'. This made for a better-defined estimate of changes in the latitudinal data for each year and a more reliable estimate of the timing of spring and autumn migration. The migration days identified were plotted against the raw latitudinal data for all species using time series plots, in order to check that they corresponded to actual shifts in latitude. In all cases there was close correspondence throughout the year.

Using changepoint analysis to identify the beginning and end of each migration, in some instances, proved problematic. This is because the entire population of a bird species does not migrate simultaneously. This manifests as a slope in the mean latitude of a species' distribution as individuals move at different times between their breeding and wintering regions, and not an abrupt shift (Figure 6.1). Changes in slope are harder to identify (Baranowski *et al.* 2019). Detecting changes in mean can be thought of as fitting a step function to the data, such that the errors between this step function and the data are minimised. As a result, if there is a slope, and not an abrupt change, the changepoint will often be placed in the centre of this slope. As such, the migration days identified using this method equate to the mid-point of migration.

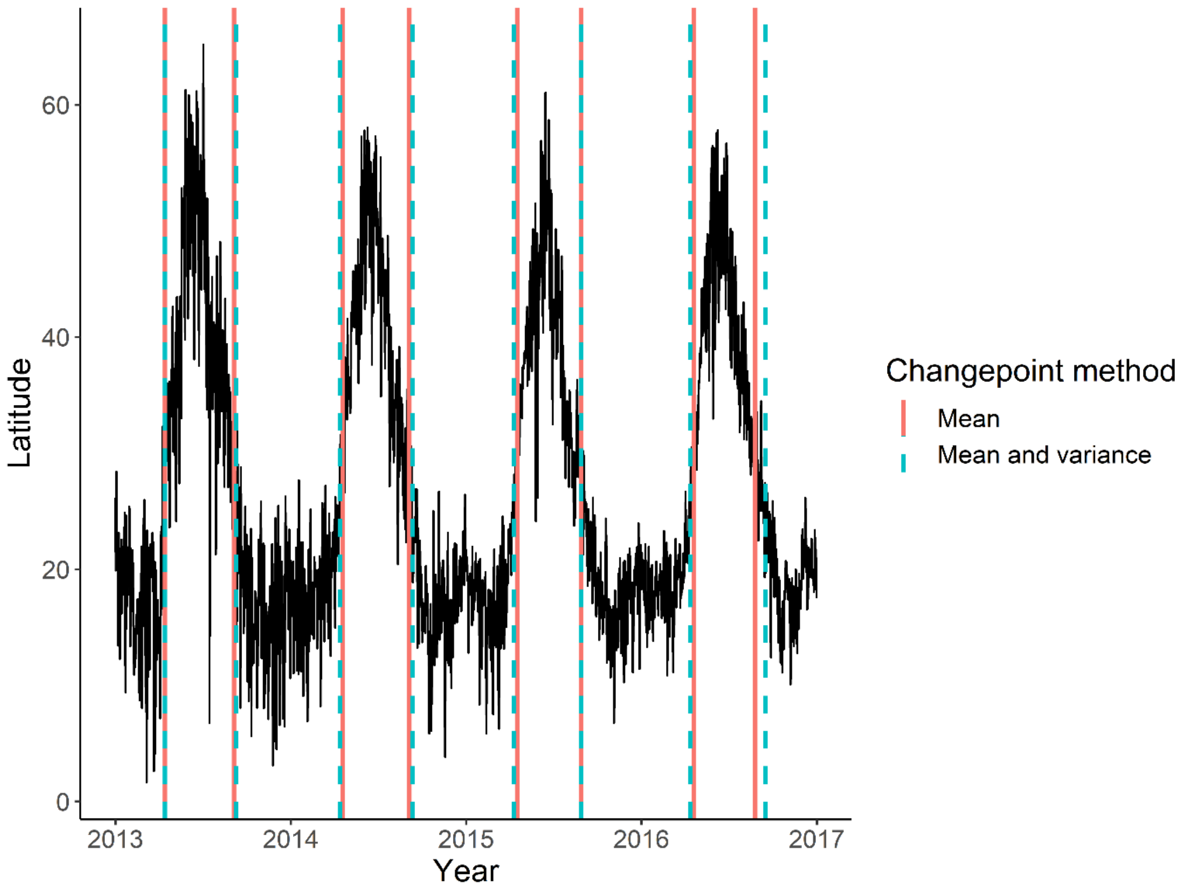


Figure 6.1 The mean latitude of common sandpipers *Actitis hypoleucos* in the Afro-Palearctic flyway between 2013 and 2017 and a comparison of the migration days identified by the two different methods of detecting changepoints, mean (red solid lines) and mean and variance combined (blue dashed lines).

Weather data

Identifying breeding and wintering regions

In order to obtain relevant weather data for each species, we needed to identify their breeding and wintering ranges. For each species, we took the means of all the migration days identified by the changepoint analysis across all years for spring and autumn migration separately. This gave a mean migration day for spring and autumn migration for each species in the study period. The latitudinal distribution of all the sightings reported between these averaged migration days was therefore an index of the breeding distribution; the latitudinal distribution of those reported before and after the average spring and autumn migration days, respectively, was an index of the wintering distribution. However, because the migration days correspond to the midpoint of migration, these sightings spanned half of the migration period also. Therefore, we excluded all the sightings falling outside of the 10th and 90th percentiles of the latitudinal distribution of sightings for each species. The remainder provided indices of the breeding and wintering distribution for each species which were then used to select relevant weather data.

Weather data download

In order to investigate the potential for seasonal change in weather to influence migration day, weather conditions were obtained from ERA-INterim reanalysis. ERA-INterim provides datasets of past climate variables that are unaffected by changes in method and uses forecast models (Dee *et al.* 2011). We obtained weather conditions for the migration days identified by the changepoint analysis in the regions defined as the breeding and wintering areas described above. Data download and processing were carried out using the Iris package in Python (Sanner 1999, Iris 2020).

For spring migration, we extracted weather data from the wintering area; for autumn, we extracted weather data from the breeding area. This allowed us to investigate if weather variables at the departure location correlated with the timing of migration. Because the migration day identified by the changepoint analysis equates to the middle of migration, individuals will migrate in the weeks before and after the day identified. We therefore retrieved weather data for the entire breeding or wintering region at noon for each day over a forty-day time window, centred on the migration day identified for each species (see below). Wader species can migrate either diurnally or nocturnally (Lank 1989), but day- and night-time weather conditions will be highly correlated in our data because our analyses are at large temporal and spatial scales. The weather variables downloaded were northward and eastward wind, and temperature for air pressures of 1000 hPa, corresponding to surface level. The weather variables were averaged over the entire breeding and wintering distribution of each species. We also considered 925, 850 and 750 hPa, corresponding roughly to 760, 1500 and 2500 metres above sea level, respectively; all were highly correlated and so only surface-level data were used. Although birds sometimes migrate at high altitudes (Senner *et al.* 2018), they are likely to take cues regarding migration from surface-level weather conditions (Åkesson *et al.* 2016). We excluded weather conditions over the oceans by applying a land mask. Although migratory birds often cross oceans on migration, they are most likely to take cues from conditions experienced where they are stationary (Åkesson *et al.* 2016).

Weather trends

For each weather variable we fitted a linear least-squares regression over the forty-day window and used the slope of that line in our models. We chose the forty-day period because we were investigating changes in migratory behaviour across large temporal and spatial scales. Furthermore, most of the individuals of a species are likely to migrate within a window of approximately this length (Newton 2010, Horton *et al.* 2019a). The rate of change in weather is likely to be important for the timing of both spring and autumn migration as individuals take cues from generally improving conditions for migration (i.e. the rate of change in weather conditions), rather than a threshold (Liechti 2006, Shamoun-Baranes *et al.* 2010a, Sapir *et al.* 2011, Åkesson *et al.* 2016). We therefore investigated whether migration was correlated with the change in northward wind, eastward wind and temperature.

Statistical analyses

We analysed the factors affecting the timing of spring and autumn migration using linear mixed effects models (LMEs). Analyses were carried out in the R environment (R Core Team 2020). Spring and autumn migration days were modelled separately because the influence of life history traits and weather are likely to differ between the two (Mcnamara *et al.* 1998, Conklin *et al.* 2013). In spring, there were fewer days on which no observations were made for a given species than in autumn, possibly because of the draw for ornithologists in seeing the first spring migrants in each year. We only included species for which at least 10 years' worth of data were available in the models, totalling twenty Nearctic species and ten Afro-Palearctic species in spring, and eighteen Nearctic and six Afro-Palearctic species in autumn (Supplementary Material Table 1).

We fitted the same explanatory variables in the models of changes in the timing of spring and autumn migration. The non-weather variables used were year (fitted as a continuous variable), flyway, the mean breeding and wintering latitude defined using the method described above, and the total number of bird observations reported on the migration day. The latter variable was included to account for the increasing number of observations made over time. The indices of breeding and wintering latitude were included to account for potential differences in the response of species to climate change across latitudinal gradients. The weather conditions included were temperature and northward and eastward wind trends. For each model we included all two-way interactions, except for those involving the number of observations. All continuous variables were centred and scaled prior to analyses (Schielzeth 2010). Species was fitted as a random effect and the models were fitted with a Gaussian error distribution. The 'lme4' package was used to fit LMEs (Bates *et al.*

2015). All possible models were fitted and those within 2 AICc of the best-fitting model were averaged for plotting (Burnham & Anderson 2002). The best-fitting models are presented in the results. Models were validated by assessing the normality of residuals and the relationship between the residuals and each explanatory variable.

Results

The migration day of waders in both spring and autumn became later over the thirteen-year study period, with changes in spring migration in the Afro-Palearctic flyway occurring the most rapidly (at approximately 0.5 days year^{-1} in the Afro-Palearctic and 0.2 days year^{-1} in the Nearctic; Figure 6.2, Figure 6.3). Spring migration was about thirty days earlier in the Afro-Palearctic than the Nearctic flyway. The migration days in autumn became later at the same rate in both flyways over the study period (approximately 0.3 days year^{-1}; Figure 6.2, Figure 6.3). Breeding and wintering latitude were important predictors in the models of both migrations. Northern breeders migrated later in spring and earlier in autumn than those breeding at more southerly latitudes, consistent with shorter breeding seasons at northerly latitudes (Figure 6.2, Figure 6.4). The timing of migration for both northern and southern breeders became later over time, but changes occurred more rapidly for the former (Figure 6.4).

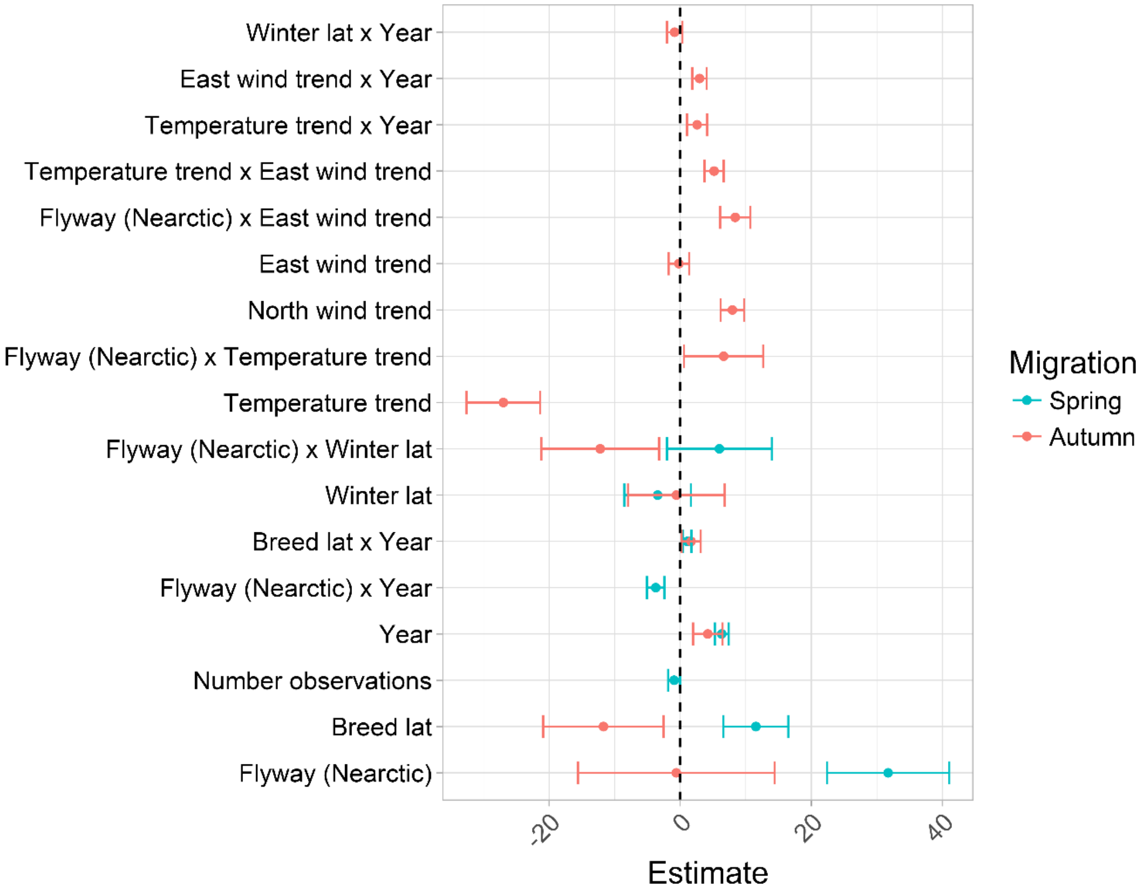


Figure 6.2 Factors affecting the spring and autumn migration day depicted as the model averaged estimates of fixed effects from the models within 2AICc of the best-fitting LME. Positive values of the estimate indicate migration getting later, negative values migration getting earlier. Only variables that were deemed important after model averaging are shown here for clarity; the full model outputs are available on request (Supplementary Tables 2 and 3). Horizontal error bars show the standard errors. If a closed circle does not appear for either spring or autumn migration this means that the variable was not present in the best-fitting model list. The intercepts of the models were 75.3 in spring and 238.8 in autumn, but were excluded for clarity. Breed lat = Breeding latitude index, Winter lat = Wintering latitude index.

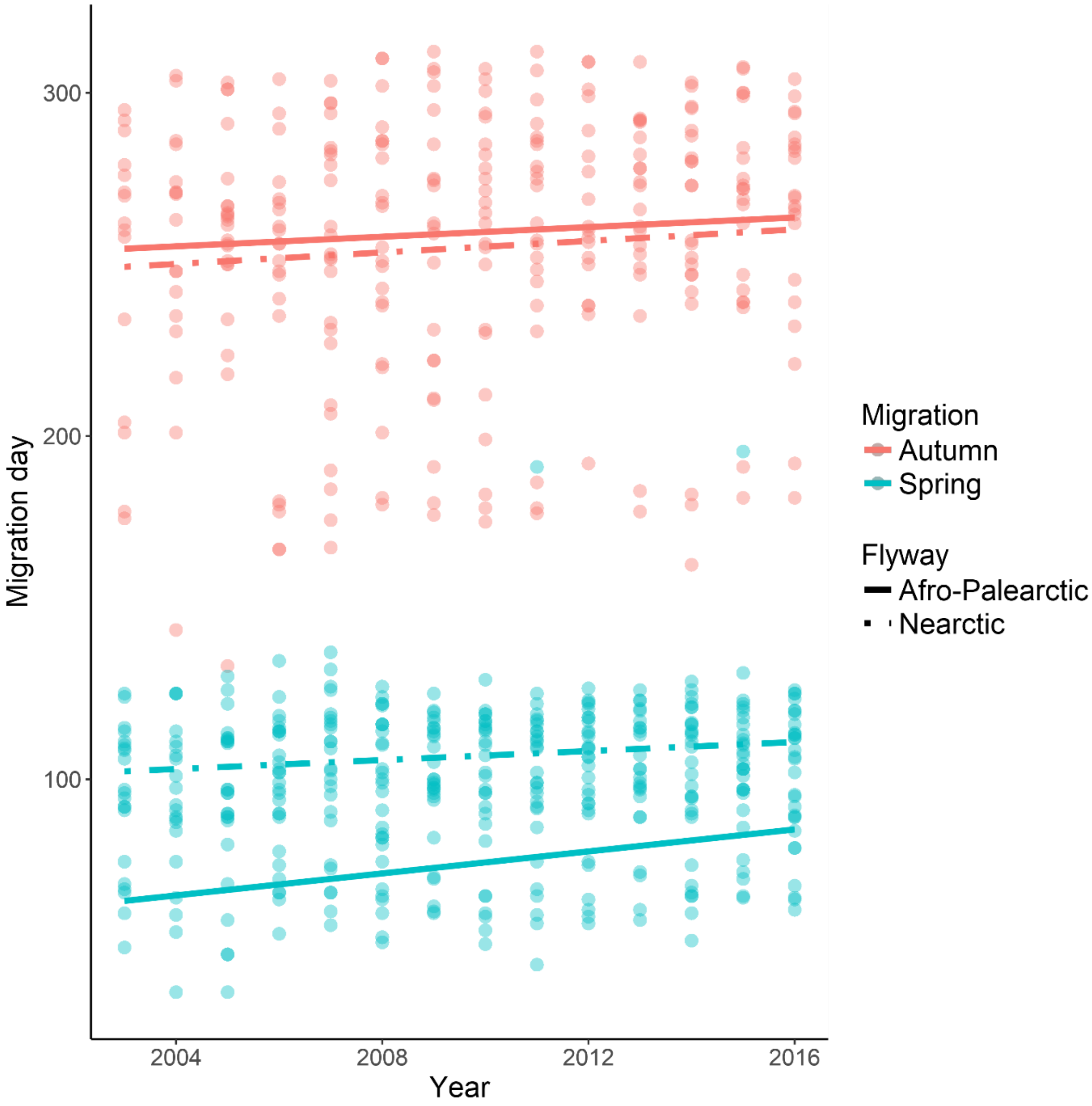


Figure 6.3 Changes in migration day over time for fifty species of wader, for both spring and autumn migration in the Afro-Palearctic and Nearctic flyways. Closed circles show the raw data, lines show the model averaged predicted relationship from the models within 2AICc of the best-fitting LMEs.

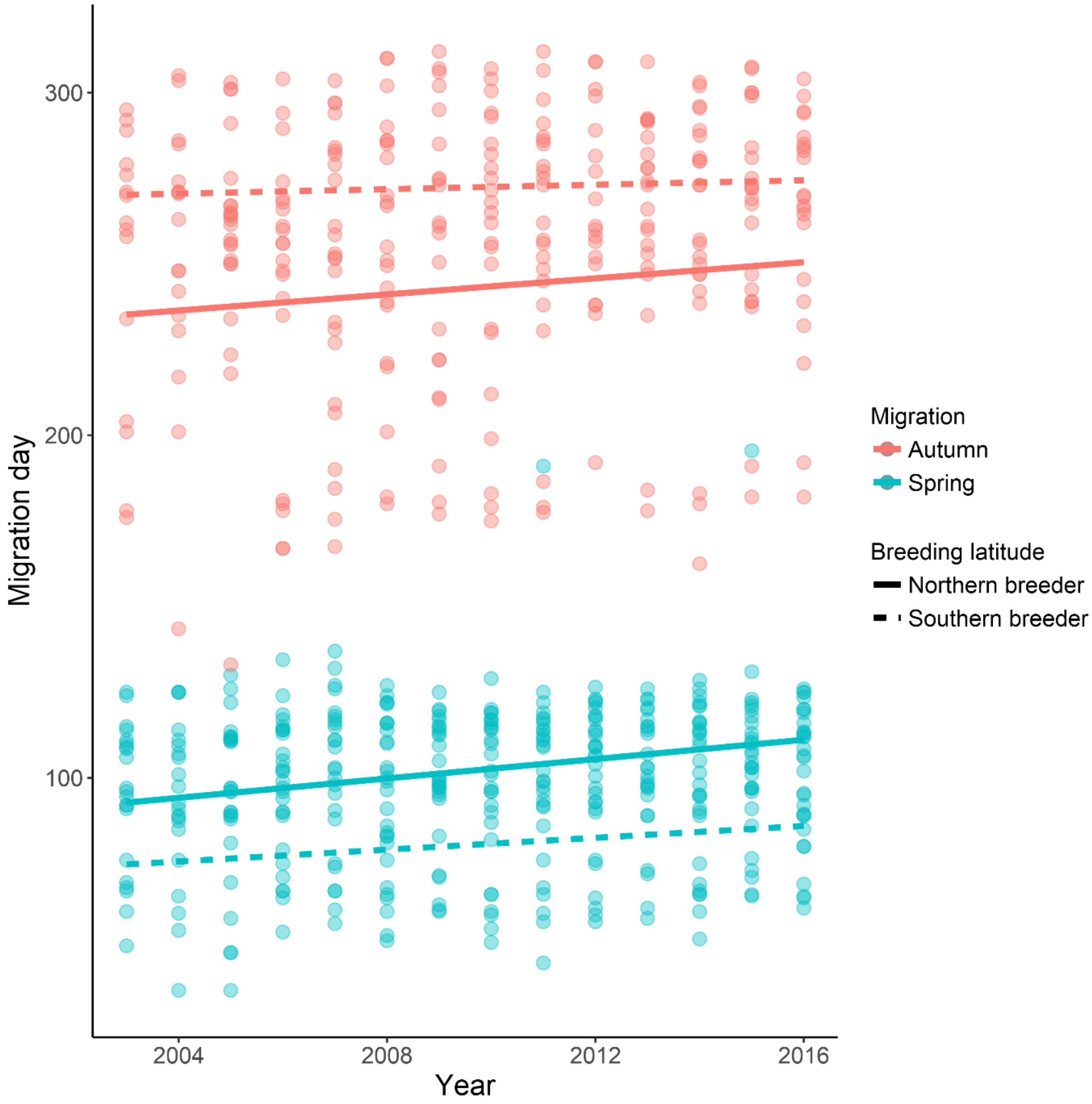


Figure 6.4 Changes in migration day over time for species breeding at northern (solid line, 58°N) and southern (dashed line, 42°N) latitudes. Closed circles show the raw data, lines show the model averaged predicted relationship from the models within 2AICc of the best-fitting LMEs.

Effects of weather

Weather variables were important correlates of autumn migration days only; in spring there were no correlations between migration days and weather (Figure 6.2). Autumn migration was earlier when temperatures became warmer more quickly (Figure 6.5). Autumn migration also occurred later when headwinds were increasing and earlier when tailwinds were increasing (Figure 6.6). Although weak, the effect of eastward wind differed between the flyways; stronger eastward winds were correlated with later migration days in the Nearctic but not the Afro-Palearctic flyway (Figure 6.2). The effects of both the temperature and eastward wind trends changed in the same way over time; migration became later over time more quickly when trends in both variables were positive than when they were negative (Figure 6.2).

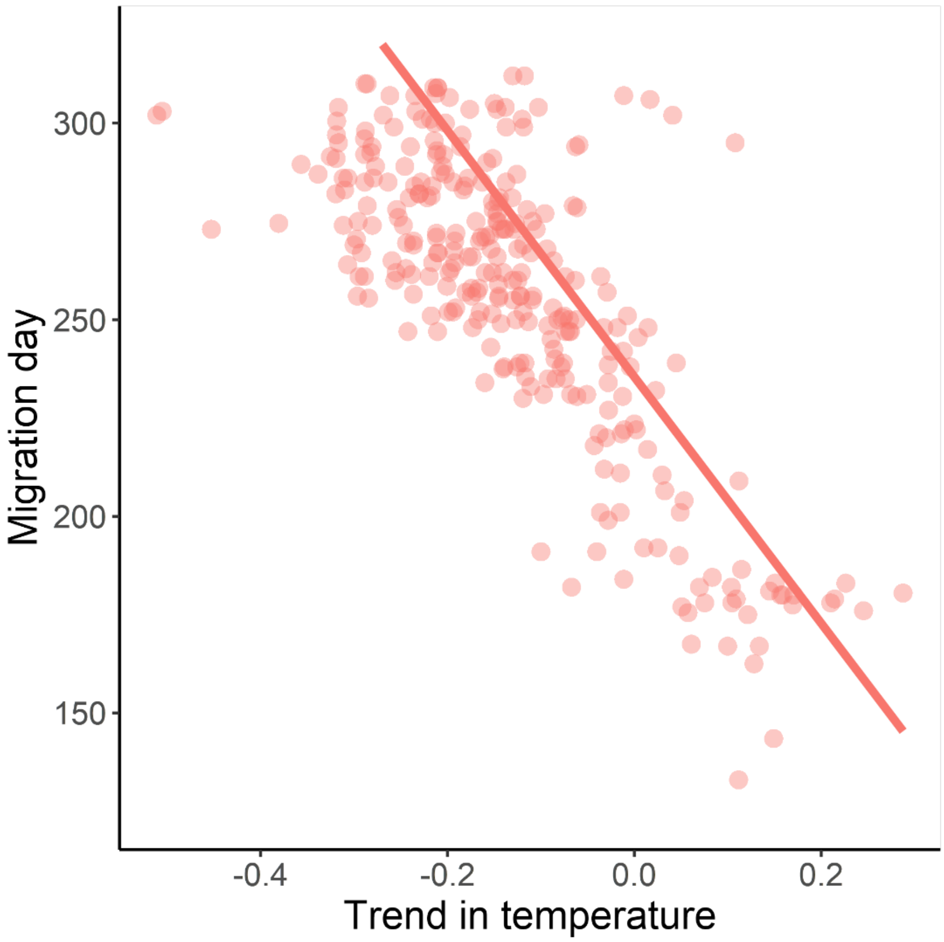


Figure 6.5 Relationship between autumn migration day and temperature trend. Closed circles show the raw data, lines are the model averaged predicted relationships from the models within 2AICc of the best-fitting LME.

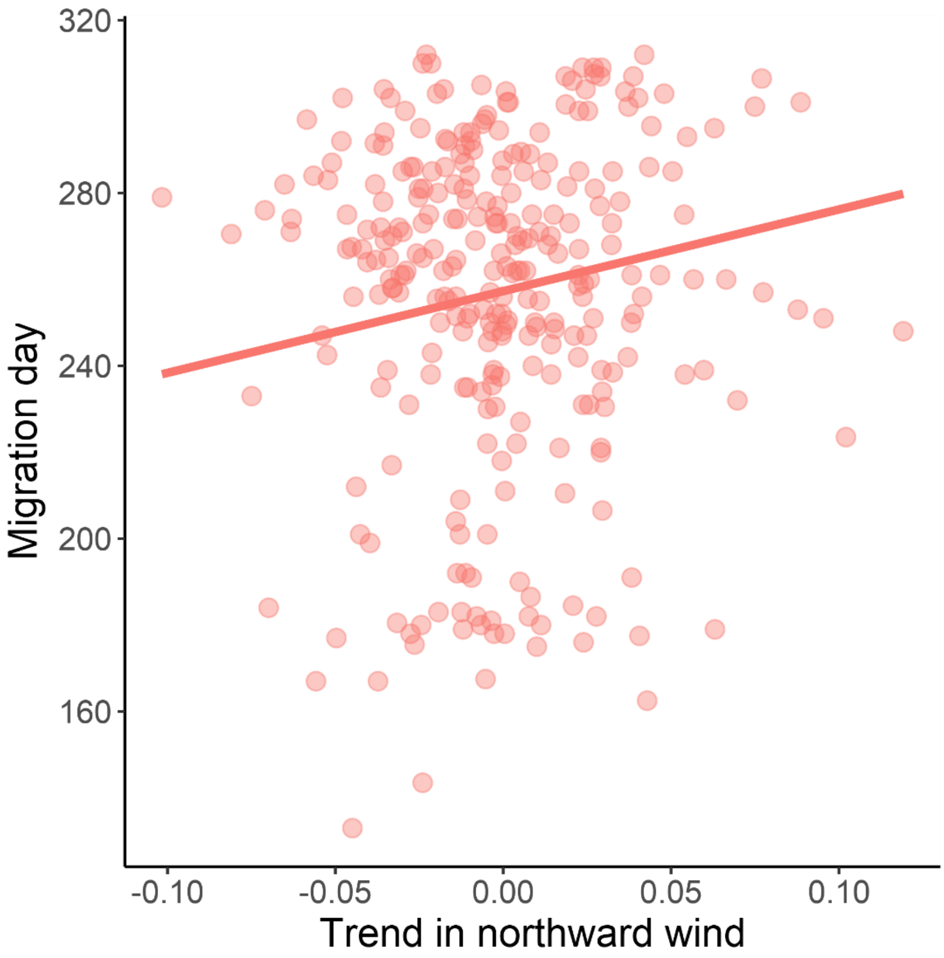


Figure 6.6 Relationship between autumn migration day and northward wind trend. Closed circles show the raw data, the line is the model averaged predicted relationship from the models within 2AICc of the best-fitting LME.

Changes in the number, timing and distribution of observations

Several factors could influence the model results. One of the major issues with the eBird dataset is that the amount of data collected has increased dramatically over time. However, in our LMEs, the number of observations made in any given year was negatively correlated with the migration day in spring and no correlation was found in autumn (Figure 6.2). It is therefore unlikely that the migration day becoming later over time was driven by changes in the number of observers.

The timing of sightings within the migration periods could influence the identification of the migration day by changepoint analysis. If sightings were reported during later stages of migration over the study period, which could happen due to the increase in observers, then the migration day might become later. To test this, we filtered the raw sightings data to include only those reported within each migration period: between March 1st and June 28th for spring and between June 28th and September 7th for autumn. These dates were chosen after visual inspection of the raw latitudinal data. Then, we fitted an LME with the day of sighting (as a Julian date) as the response variable, year as a continuous fixed effect (scaled and centred) and species as a random effect. The timing of sightings became earlier over those periods for both migrations, not later (spring model: estimate = -1.05, se = 0.01, t-value = -78.34, n = 4 306 007; autumn model: estimate = -1.80, se = 0.01, t-value = -156.5, n = 4 409 989).

Finally, changes in the latitudinal distribution of observers over time could have caused the migration days to become later. In spring, proportionally more sightings could have been reported at higher latitudes in later years because ornithologists started visiting locations further north. In autumn, proportionally more sightings from lower latitudes in later years would have the same effect. In order to test this, for each migration period annually, we split all the sightings data into ten-degree latitudinal bands covering the entire range of all species in the dataset (55°S to 85°N). We then plotted the number of sightings reported in each latitudinal band for each year. The proportion of sightings in each band did not vary substantially across years. Importantly, the proportion of sightings reported from high and low latitudes did not increase over the study period (Supplementary Figure 2).

Discussion

Our findings suggest that both spring and autumn migration have become later over time in the Nearctic and Afro-Palearctic flyways; this is in contrast with the results from many studies of population-level phenology in migratory species (Lehikoinen *et al.* 2004, Zsolt Végvári *et al.* 2010, Gunnarsson & Tómasson 2011). However, unlike many others, our study addresses changes in the phenology of migratory waders at a flyway scale. The mechanisms driving changes at local and flyway-level scales are likely to differ given that the effects of climate change vary globally. This could influence the results from population-level studies, as even those combining data from multiple populations do not account for changes occurring to areas outside of study regions (e.g. range shifts, discussed below). The only other study, to our knowledge, to investigate changes in the timing of migration at a flyway scale found contrasting results to ours (Horton *et al.* 2019a). However, our analysis is restricted to waders and uses sightings of each species rather than radar data of all species combined. Furthermore, our dataset corresponds to only the latter half of theirs, during which they found a decrease in the trend of earlier spring migration, and that autumn migration was becoming later. Our study also accounts for individuals travelling greater distances because of range shifts (see below), which can increase overall journey times (Howard *et al.* 2018) and would correspond to the timing of migration becoming later in our analyses. A study investigating arrival and departure dates of birds at sites across Australia found that the magnitude of delays across species was greater than the magnitude of advances (Chambers *et al.* 2014). This supports our findings that migration might become later over time when considering large spatial scales and cross-species trends. It also suggests that the responses to climate change, and the mechanisms driving these responses, could be highly species-specific. Understanding how individual-level mechanisms drive flyway-level responses to climate change is important for migratory bird conservation and these responses could have significant knock-on consequences (Wilcove & Wikelski 2008).

One possible explanation for our results is that migration may become later due to increases in species' ranges. Range increases could cause flyway-level migration to become later in two ways: (1) individuals migrating further distances due to the colonisation of new habitats (Howard *et al.* 2018), and (2) individuals breeding further north migrating later than those breeding at more southerly locations, as we found (see below). Studies investigating trends in migratory phenology at a population-level may still observe individuals migrating progressively earlier but miss flyway-level timings becoming later. Cross-species meta-analyses have revealed northward shifts of bird species' ranges at up to 16.9 km per decade

(Parmesan & Yohe 2003, Chen *et al.* 2011). Contractions at the warm limit of species' ranges occur at a slower rate than expansions at the cold limit (Parmesan *et al.* 1999, Virkkala & Lehikoinen 2014), thereby increasing species' global ranges. Furthermore, the flyway-level timing of species' migration could even become later without range changes, if the proportion of individuals migrating to higher latitudes increases. This would manifest as total migration time becoming later, as individuals take longer to reach their breeding sites. However, our results could also arise from differences in the rates of increase in the number of sightings reported across different latitudes. Greater rates of increase in the number of sightings reported from higher latitudes at later stages of the season over time, could cause migration to become artificially later without the true timing of migration changing. While this has been partially addressed above, modelling changes in the numbers of list submissions to eBird within each migration period over time, including interactions between month of the year and year itself, would further confirm our results.

In theory, greater warming at the poles should cause the migration of birds breeding at northerly latitudes to become earlier more rapidly than those breeding at southerly latitudes, although evidence for this is still lacking (Serreze *et al.* 2009, Chmura *et al.* 2019). Our results suggest that the flyway-level migration of northerly breeders became later over time than that of southerly breeders, a pattern which previous similar studies have not been able to investigate (Horton *et al.* 2019a). Our findings support the idea of range shifts driving the timing of migration becoming later, as it is likely that range shifts will occur more rapidly for northerly breeding species because of greater temperature increases at higher latitudes (Tingley & Huybers 2013). Further, climate change has caused warming and increased climate variability in recent decades, particularly between 20° and 50°N (Cohen *et al.* 2014). Variability in weather could increase the strength of selection on individuals, such that the only individuals able to arrive earlier are those in the best body condition. This means that while the earliest migrants may advance their migration, the timing of flyway-level migration could become later as relatively more poor-quality individuals are held-up by weather events (Shamoun-Baranes *et al.* 2010b, Duijns *et al.* 2017). Birds breeding at higher latitudes will also be exposed to weather conditions for a larger proportion of their migration, which could mean that their migration is later relative to more southerly breeders. Studies have reported that species of various taxa show contrasting phenological responses to climate change across latitudes (Chmura *et al.* 2019) and so it is likely that there are substantial differences between responses at a population and flyway level.

Birds returning later to northerly breeding sites, as we found in our analyses, may be an adaptive response to climate change if individuals are affected by the indirect effects of extreme winter warming events. These events can cause spring-like physiological responses in plants, and on return to normal winter conditions, expose them to far colder temperatures due to the lack of insulating snow (Bokhorst *et al.* 2010). This can reduce flower abundance and productivity (Semenchuk *et al.* 2013), and their effects can accumulate over several years, in some cases reducing primary productivity by more than fifty percent (Bokhorst *et al.* 2011). Extreme temperature fluctuations can also influence insect population size (Coulson *et al.* 2000) and population growth rates (Roland & Matter 2013), and lead to mismatches between invertebrates and their host plants (e.g. Boggs & Inouye 2012). Individuals returning to arctic environments affected by winter warming events could face worse conditions early in the season; more work is needed to understand how they might influence migratory birds given that they are unlikely to be able to accurately predict breeding ground conditions from their wintering region.

The influence of weather on migratory timing

Increases in headwinds were negatively correlated with autumn migration. Studies have shown that individuals will avoid headwinds during migration and wait for improved flight conditions, in order to maximise flight efficiency (Åkesson & Hedenström 2000). Crosswinds were only important in the Nearctic flyway, perhaps due to the shape of the North and South American continents. Strong eastward winds would push individuals in Central America out into the Gulf of Mexico, which could be fatal (Ward *et al.* 2018). The effects of wind conditions on migratory birds, and how these are likely to change, are incredibly complex. While autumn headwinds are projected to increase (La Sorte *et al.* 2019), crosswinds may decrease (La Sorte & Fink 2017). These changes are likely to have important effects which could differ between species depending on their size and migratory behaviour (Anderson *et al.* 2019).

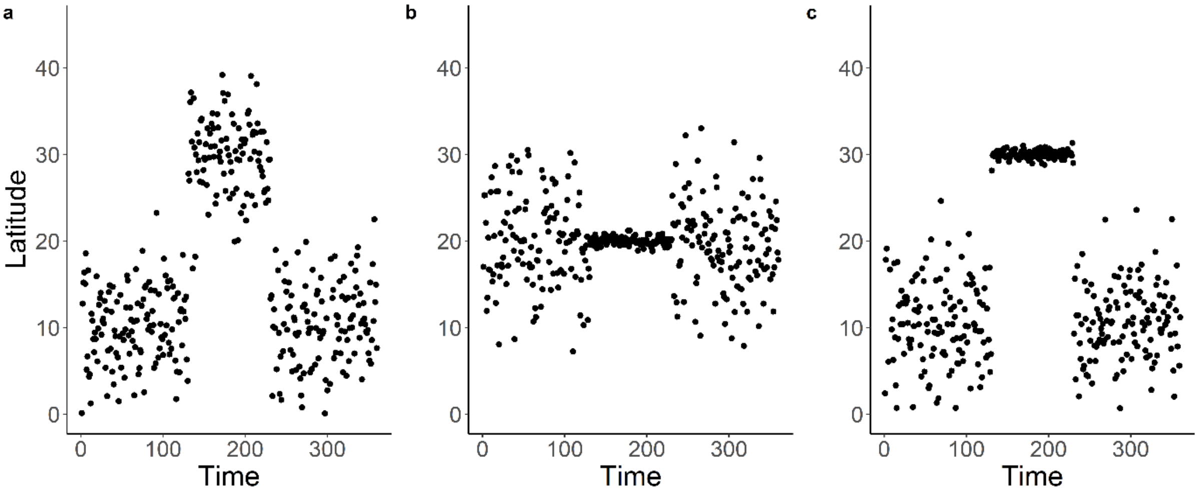
We found that warming temperatures over a forty-day window were strongly correlated with earlier autumn migration. This means that warmer temperatures in late June, through to July and August (which is the general autumn migration window for wading bird species Newton 2010), are correlated with earlier migration. Warmer temperatures during breeding are likely to be beneficial to migratory bird species as they increase insect abundance, creating a better environment for raising chicks (Townsend *et al.* 2013). Wading bird species have precocial offspring and increased insect abundance due to temperature is likely to benefit foraging success and result in faster fledging (Mcgowan *et al.* 2002). The autumn migration of birds became later at a faster rate when temperature trends were more positive, which may be due to warmer temperatures lasting later into the year, allowing individuals to lay more replacement clutches after failure (Morrison *et al.* 2019).

The lack of correlation between our weather variables and spring migration may be due to the spatial and temporal scales at which our analyses were conducted. In spring, birds are under strong selective pressure to return to the breeding grounds and, as such, have a relatively narrow window during which to migrate (Mcnamara *et al.* 1998). This could mean that weather-driven delays in migration are due to short, extreme weather events, which our weather trend variables would not identify. During autumn, migration is likely to be influenced in part by the speed at which chicks fledge, with generally better conditions in summer likely to play an important role. Furthermore, birds in autumn may wait for bad weather to pass and therefore the timing would correlate more strongly with our trend variables (Mcnamara *et al.* 1998, Conklin *et al.* 2013). Alternatively, it is possible that the correlations between the weather trend variables and the timing of migration were because of trends in both through time. If both weather and the timing of migration has changed over time, then models will identify correlations between them irrespective of whether a true relationship exists (Post 2013). In order to address this, we included year and interactions between year and weather variables in the models, but further work using detrended weather variables could provide more conclusive results. Detrending the weather variables would reduce the chance of the correlations in our models resulting from simultaneous changes in the timing of migration and weather trends through time (Iler *et al.* 2017).

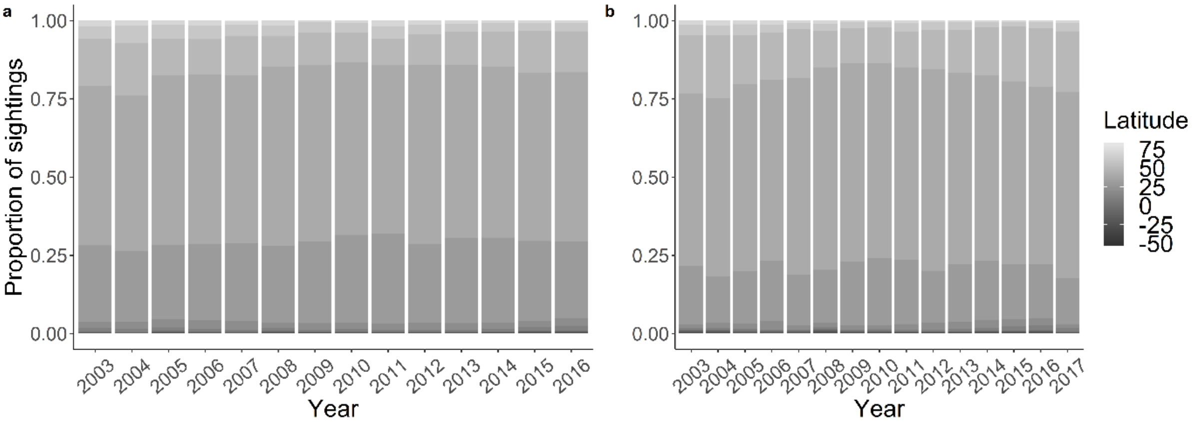
Conclusions

Documenting changes in migratory phenology at large spatial scales is important if we are to fully understand the potential impacts of climate change. Studies of individual populations provide models with which to understand mechanistic causes of change but may miss large-scale patterns. This is particularly true considering that the global effects of climate change are not uniform and that studies of individual populations may not address this variation. Furthermore, the ecological value of migratory species is dependent on their large numbers (Wilcove & Wikelski 2008), and investigating changes in these is paramount if we are to understand the potential for knock-on ecological effects. For logistical reasons it is almost impossible to investigate changes in all individuals across an entire flyway. More work incorporating citizen science and weather surveillance radar data, and on individual populations spread across entire geographic ranges, is needed. It is also important to simultaneously understand patterns of colonisation and extinction at species’ range margins, and how this might impact changes to the timing of migration.

Supplementary material



Supplementary Figure 1 Data with changes in (a) mean, (b) variance and (c) mean and variance combined. Each dataset has two changepoints, splitting the data into three segments.



Supplementary Figure 2 The proportions of sightings reported at different latitudes over the study period in (a) spring and (b) autumn.

Supplementary Material Table 1 List of the species used in the eBird changepoint analyses/

Species	Scientific name	Family	Flyway	Autumn years of data	Spring years of data
American Avocet	*Recurvirostra americana*	Recurvirostridae	Nearctic	13	13
American Oystercatcher	*Haematopus palliatus*	Haematopodidae	Nearctic	/	14
American Woodcock	*Scolopax minor*	Scolopacidae	Nearctic	/	13
Black-bellied Plover	*Pluvialis squatarola*	Charadriidae	Nearctic	11	14
Black-winged Stilt	*Himantopus himantopus*	Recurvirostridae	Afro-Palearctic	/	12
Black Turnstone	*Arenaria melanocephala*	Scolopacidae	Nearctic	10	11
Common Greenshank	*Tringa nebularia*	Scolopacidae	Afro-Palearctic	12	12
Common Redshank	*Tringa totanus*	Scolopacidae	Afro-Palearctic	13	12
Common Ringed Plover	*Charadrius hiaticula*	Charadriidae	Afro-Palearctic	/	10
Common Sandpiper	*Actitis hypoleucos*	Scolopacidae	Afro-Palearctic	13	14
Common Snipe	*Gallinago gallinago*	Scolopacidae	Afro-Palearctic	11	13
Dunlin	*Calidris alpina*	Scolopacidae	Afro-Palearctic	12	12
Eurasian Curlew	*Numenius arquata*	Scolopacidae	Afro-Palearctic	/	10
Greater Yellowlegs	*Tringa melanoleuca*	Scolopacidae	Nearctic	14	14
Killdeer	*Charadrius vociferus*	Charadriidae	Nearctic	13	12
Least Sandpiper	*Calidris minutilla*	Scolopacidae	Nearctic	/	14
Lesser Yellowlegs	*Tringa flavipes*	Scolopacidae	Nearctic	13	14
Little Ringed Plover	*Charadrius dubius*	Charadriidae	Afro-Palearctic	10	11
Long-billed Curlew	*Numenius americanus*	Scolopacidae	Nearctic	14	11
Marbled Godwit	*Limosa fedoa*	Scolopacidae	Nearctic	11	14
Northern Lapwing	*Vanellus vanellus*	Charadriidae	Afro-Palearctic	/	12
Red Knot	*Calidris canutus*	Scolopacidae	Nearctic	11	12
Ruddy Turnstone	*Arenaria interpres*	Scolopacidae	Nearctic	13	14
Sanderling	*Calidris alba*	Scolopacidae	Nearctic	10	11
Semipalmated Plover	*Charadrius semipalmatus*	Charadriidae	Nearctic	14	14
Short-billed Dowitcher	*Limnodromus griseus*	Scolopacidae	Nearctic	13	14
Solitary Sandpiper	*Tringa solitaria*	Scolopacidae	Nearctic	12	12
Spotted Sandpiper	*Actitis macularius*	Scolopacidae	Nearctic	13	14
Stilt Sandpiper	*Calidris himantopus*	Scolopacidae	Nearctic	10	/
Whimbrel	*Numenius phaeopus*	Scolopacidae	Nearctic	13	12
Willet	*Tringa semipalmata*	Scolopacidae	Nearctic	11	14

Chapter 7 General discussion

Reasons for population declines in the common sandpiper

The populations of many migratory species, like those of the common sandpiper, are declining across Europe, yet the drivers are complex and often poorly understood (Vickery *et al.* 2014, Harris *et al.* 2020b). Determining the factors that limit migratory bird populations at each lifecycle stage is important for understanding the reasons for their decline (Hewson *et al.* 2016). However, most work has been carried out on during the breeding season; we know relatively little about the wintering ecology of many species (Vickery *et al.* 2014). Furthermore, there is a lack of evidence regarding the reasons for declines in migratory waterbirds, with more work focussed on other avian groups (Vickery *et al.* 2014). In this thesis we investigated the reasons for recent declines in the British common sandpiper population (Harris *et al.* 2020b) by investigating the factors that affect reproductive success (Chapter 2), their wintering ecology (Chapter 3) and their migration (Chapter 5). In this final chapter, I address the potential influences of each lifecycle stage on population trends in this species, including the potential for carry-over effects, and investigate possible reasons for the apparently different trends in England and Scotland (Figure 7.1; Harris *et al.* 2020b).

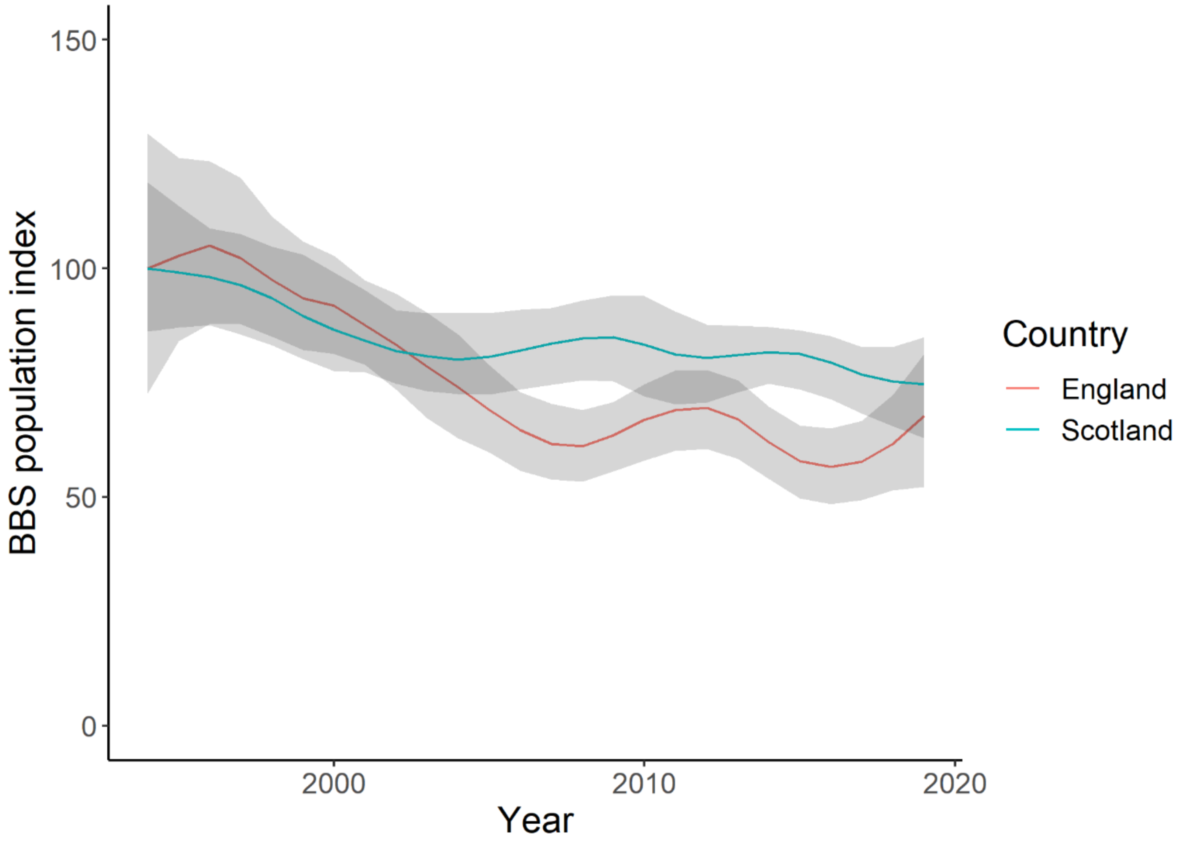


Figure 7.1 Breeding Bird Survey (BBS) smoothed population index for common sandpipers breeding in England and Scotland between 1994 and 2019.

Breeding season habitat change, disturbance and predation

Conditions during the breeding season are important determinants of the population trends of many species (Piersma 2002, Carey 2009, Pearce-Higgins *et al.* 2010, Morrison *et al.* 2016). In common sandpipers, previous studies have shown that habitat change due to human encroachment can reduce population size, but that these populations can be restored by increasing natural habitat heterogeneity (Yalden 1986, Arlettaz *et al.* 2011). Arlettaz *et al.* (2011) suggested that this was because the landscape-wide increases in habitat mosaics provided better nesting and foraging sites through increased vegetation cover and invertebrate abundance (Yalden 1986, Paillex *et al.* 2009, Dougall *et al.* 2010, Arlettaz *et al.* 2011, Elas & Meissner 2019). Indeed, natural vegetation cover is also likely to be important for nest site selection in common sandpipers in the UK (Mee 2001; Chapter 2). Furthermore, natural habitat mosaics are likely to increase the amount of both shingle and vegetation in which chicks can hide from predators (Dougall *et al.* 2010).

While we did not directly investigate the influence of habitat or habitat change on population trends, our results suggest that these could be important factors for common sandpipers in our study site through their effects on predation (Chapter 2). For example, we found that hatching success may have been influenced by the amount of surrounding farmland habitat, potentially due to their higher predator densities (Andrén & Anglestam 1988). Indeed, it is difficult to assess the influence of habitat change on our population given that we have do not have detailed long-term information regarding changes in habitat or population size. However, a survey carried out by Cuthbertson *et al.* (1951) included our study site; they estimated the population size of common sandpipers within its boundaries to be *ca.* 32 pairs, which is greater than we found in any of our years, the maximum being 25 pairs. This represents a decline of 22%, which is broadly in line with declines nationwide (Harris *et al.* 2020b). Furthermore, the habitat surrounding the rivers in our study site has changed markedly since then, due to the dramatic increase and intensification of farming since the 1950s in the UK (Robinson & Sutherland 2002, *Pers. Obs.*). It could be particularly interesting to investigate changes in population size relative to changes in habitat surrounding rivers in England and Scotland, as there is considerably more natural habitat in the latter (Rowland *et al.* 2017). This should be carried out in tandem with experiments investigating the relative influence of predators in different habitat types, as predation of both nests and chicks is likely to be an important driver of productivity and population trends (Evans 2004, Krüger *et al.* 2018). These could identify the causes of nest and chick failure using camera traps, thermal data loggers and radio transmitters (Mason *et al.* 2019).

Our work in Chapter 2 also highlighted the potential for disturbance to negatively affect common sandpiper reproductive success, as has previously been suggested (Yalden 1992). Disturbance is important because it can reduce nest attentiveness and increase predation; this has been shown to reduce productivity and population size for many species (Chapter 2; Langston *et al.* 2007, Price 2008). Human disturbance in isolation was unlikely to have a direct impact on reproductive success in our study site but possibly operated through its influence on nest predation. Understanding the mechanism through which disturbance can affect nest and chick predation will require further field-based studies. Unfortunately, we were unable to investigate the influence of disturbance on chick fledging. Given that many of the territories in our study site contained at least one footpath, there is considerable potential for an effect. Future work could focus on counting the number of intrusions by humans that common sandpipers incur during the fledgling period, similar to the study carried out by Yalden (1992), and use radio telemetry to track chicks to determine how these intrusions influence predation (Stien & Ims 2016, Mason *et al.* 2019). Disturbance could be an important factor driving the contrasting population trends in England and Scotland, given the higher population density in the former. Further work should therefore investigate correlations between proxies of human disturbance (e.g. population or footpath density) and changes in common sandpiper populations nation-wide.

Heavy rainfall is known to affect chicks because it increases the energy required for thermoregulation and can reduce intake rates (Beintema & Visser 1989, Gach *et al.* 2018). Our findings suggest that this is also true for common sandpipers, as we found that heavy rainfall in the week after hatching reduced fledging success (Chapter 2). This could potentially influence long-term population trends through reduced productivity, as the frequency of climate extremes has increased dramatically in recent decades (Cohen *et al.* 2014). In order to understand its influence on common sandpiper chicks, future work could focus on whether disturbance reduces survival during heavy rainfall. This is because adults will brood young chicks and disturbance could prevent them from doing so (Cramp *et al.* 1983). Furthermore, disturbance could influence hatching success, as clutches could be become cold if left during periods of heavy rainfall, or rainfall might increase the probability of predation (Jovani & Tella 2004, Webb *et al.* 2012, Tobolka *et al.* 2015).

Wintering ground weather and habitat change

Ours is the first study to formally investigate the wintering ecology of common sandpipers (Chapter 3), which is important considering its potential role in determining population trends (Vickery *et al.* 2014). Pearce-Higgins *et al.* (2009) suggested that wintering habitats were likely to be important because the NAO index, which is correlated with cooler drier conditions in North Africa and Europe, was negatively correlated with adult survival. Because of this, Summers *et al.* (2019) investigated long-term patterns in the NAO index but found no trends suggesting that it was the cause of their long-term population decline. We now know that common sandpipers from across Britain predominantly winter south of the River Senegal and that there is considerable large-scale overlap between populations from England and Scotland (Chapter 5). It could be that climatic changes specific to the extreme west coast of Africa are important for their decline. Indeed, droughts between the 1960s and 1990s have been linked to population crashes in many migratory species breeding in northern Europe (Zwarts & Van Horssen 2009, Thaxter *et al.* 2010, Ockendon *et al.* 2012, Morrison *et al.* 2013). However, the total rainfall in several West African countries in the rainy season (June - October) has increased since the 1980s (Figure 7.2; Giannini *et al.* 2008), while common sandpiper populations have continued declining (Figure 7.1). Large-scale increases in rainfall might mean that other factors, such as habitat change, are important drivers of population trends. It could be, for example, that the droughts caused irreversible changes to vast areas of wetland and common sandpiper populations are settling to a new 'carrying-capacity' (Nicholson 2000, Hulme 2001, Zwarts & Van Horssen 2009; but see Blackburn & Cresswell 2015a). For this species, further work investigating fine-scale habitat choice during winter might be important for understanding differences between English and Scottish population trends, as they could be linked to population-specific habitat use (Hewson *et al.* 2016, Duijns *et al.* 2017). This could be done remotely using satellite-linked GPS tags to accurately compare settlement decisions between individuals from England and Scotland.

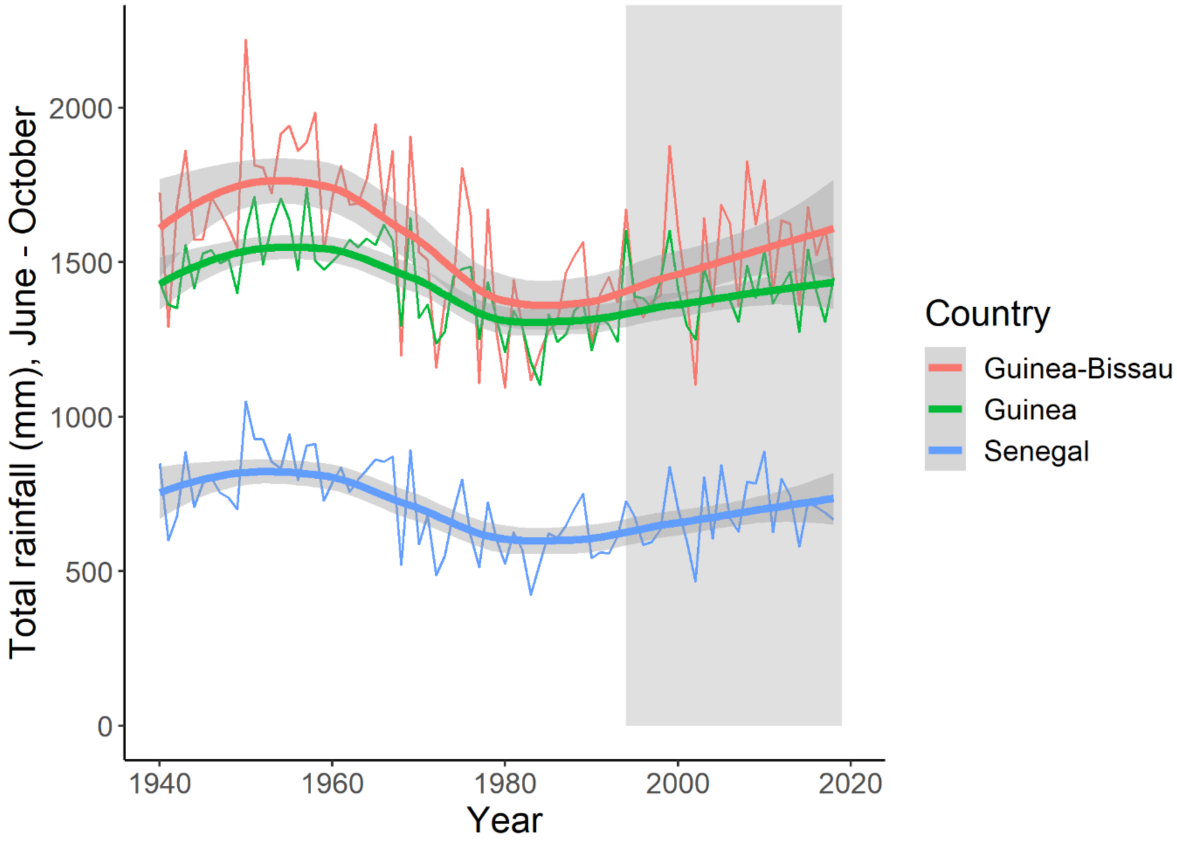


Figure 7.2 Total rainfall in July, August and September in Guinea Bissau, Guinea and Senegal. Thin lines show the raw data obtained from the University of East Anglia CRU v4.04cy dataset (Harris *et al.* 2020a); bold lines are loess smoothers and their 95% confidence intervals. The grey rectangle corresponds to the time period covered by the common sandpiper BTO BBS trend (Figure 7.1).

Recently, there has been considerable habitat change in Africa that could have influenced waterbird numbers (Vickery *et al.* 2014, Dixon *et al.* 2016). For example, natural wetlands have declined by 27% throughout Africa since the 1970s, with inland wetlands declining more (31%) than coastal wetlands (19%, Dixon *et al.* 2016). Our work in Chapter 3 provides evidence that the distribution and behaviour of common sandpipers might be influenced by changes in water chemistry; therefore, declines in natural wetland area are likely to have a significant impact on their populations. Furthermore, we showed that foraging success declined marginally in areas with high salinity, meaning that there may be important differences between coastal and terrestrial habitats (Chapter 3). Indeed, there are significant numbers that use coastal regions and the population dynamics of these individuals might differ from those inland (Cramp *et al.* 1983, Zwarts 1988, Summers *et al.* 2019). Investigating the factors that influence settlement decisions and foraging rates throughout their wintering range could be important for determining population level constraints (Piersma 2002). For common sandpipers this is likely to require colour-marked populations and focussed studies because their inconspicuous and solitary behaviour might make it difficult to count them reliably during surveys (Cramp *et al.* 1983, Wetlands International 2020). Indeed, colour-marked populations or GPS tags might also confirm whether there is non-breeding season segregation between the sexes, which could have significant implications for their conservation (Catry *et al.* 2006).

The impact that habitat change has on populations might be dependent on key behavioural traits, such as site fidelity (Blackburn & Cresswell 2016b). Individuals that are not faithful to specific sites during winter might be buffered to habitat change because they may be able to move location if local conditions become unsuitable (Brown & Long 2007). We found that common sandpipers in Djoudj National Bird Sanctuary were territorial and had very high return rates, suggesting that they are highly faithful to their wintering grounds (Chapter 3). Therefore, they may be susceptible to wintering habitat change if they are unwilling to disperse when conditions worsen. Investigating this would require continuous monitoring of marked populations through periods of habitat change, in order to determine how readily individuals move during winter and their survival (Blackburn & Cresswell 2016b, Blackburn & Cresswell 2016c). Interestingly, it is possible that, for many species, wintering ground return rates are higher than for breeding regions because there are fewer pressures causing them to disperse. For example, birds whose breeding attempts failed might move to a new breeding territory the following year to seek better quality sites (Greenwood & Harvey 1982). During winter, the primary aim is to survive; if individuals survive their first wintering season, and their habitat remains unchanged, then there may be little incentive for them to move in the following year (Cresswell 2014). Therefore, understanding juvenile settlement decisions after their first migration might be extremely valuable for investigating wintering ecology, recruitment probability and population trends (Cresswell 2014). Unfortunately, we could not investigate these effects because we did not track juveniles or have enough recruits to determine any age-specific differences in body condition or fitness.

Conditions at stopover sites and migratory behaviour

Summers *et al.* (2019) suggested that wind conditions during spring migration could be an important determinant of common sandpiper population trends. We also found that wind might be problematic (Chapter 5), which according to other studies could reduce survival and limit population sizes (Lok *et al.* 2015, Loonstra *et al.* 2019, Robinson *et al.* 2020). The importance of wind during spring migration could also increase in the future given the predicted changes in wind conditions and extreme weather events (Shamoun-Baranes *et al.* 2010b, Cohen *et al.* 2014, Shamoun-Baranes *et al.* 2017, La Sorte *et al.* 2019). Interestingly, however, our results suggest that wind patterns would not explain the contrasting population trends in England and Scotland, as there was little difference between those encountered by each population (Chapter 5).

Although Summers *et al.* (2019) showed that large-scale weather patterns have not deteriorated across Europe and North Africa, it could be that changes in habitat and weather conditions at specific stopover sites might be important. For example, climate change might have reduced the amount of suitable habitat at stopover sites, particularly in spring when constraints may be highest (McNamara *et al.* 1998, Piersma 2002, Summers *et al.* 2019; Chapter 5). Indeed, Dixon *et al.* (2016) showed that coastal wetlands throughout Europe have declined by approximately 50% in forty years, meaning that habitat change could be a major factor influencing common sandpiper population trends. Furthermore, temperatures in Morocco, Spain and France during spring migration have increased since the 1900s, whereas rainfall in this period has either stayed the same or declined (Figure 7.3). Higher temperatures could reduce the amount of wetland area suitable for common sandpipers, although might also have benefits through their effects on invertebrate abundance (Bale *et al.* 2002, Ogilvie *et al.* 2017). Understanding this would require investigating weather and habitat changes at specific stopover sites throughout western France and the Iberian Peninsula (Chapter 5), including gathering more information regarding fine-scale habitat use during migration.

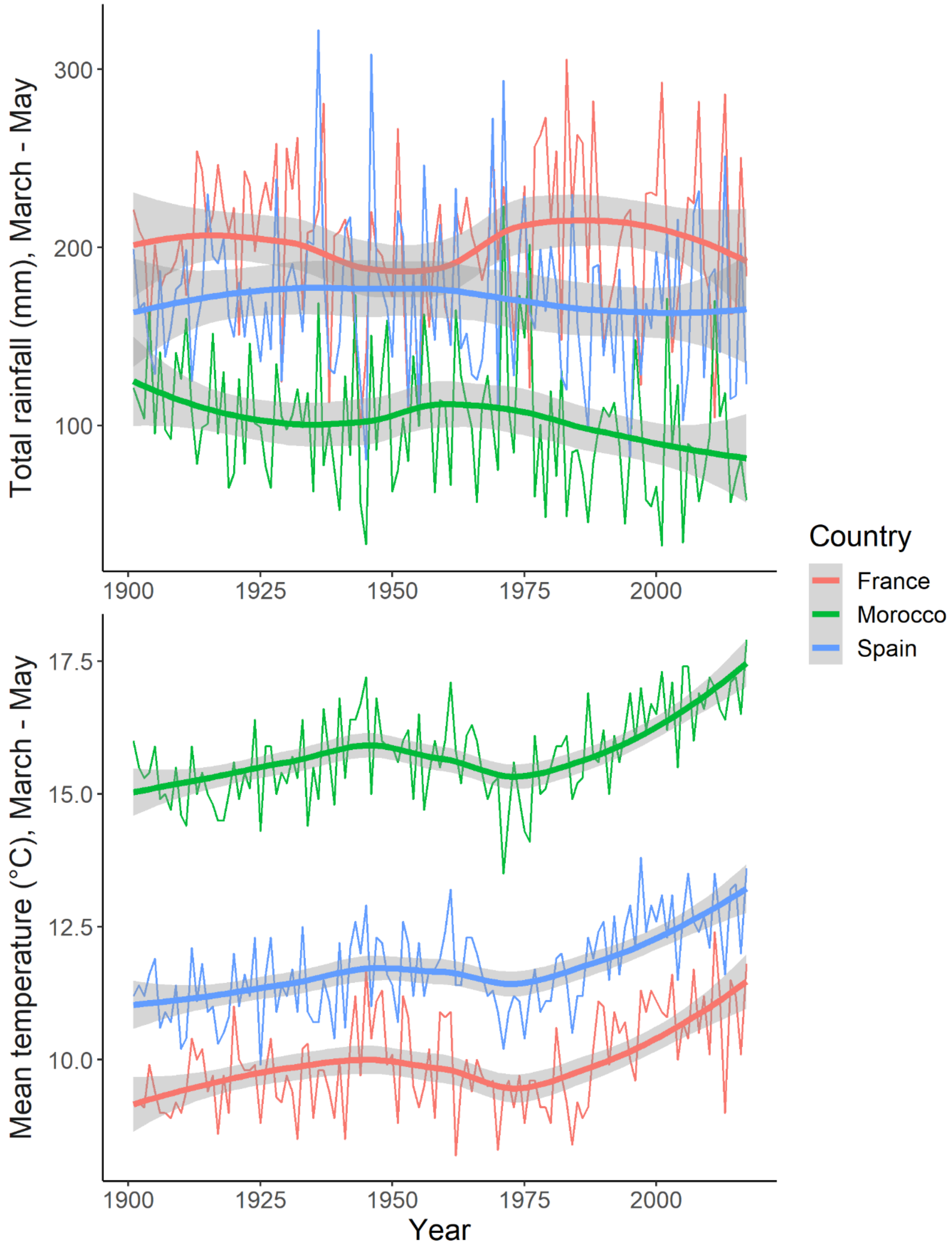


Figure 7.3 Total rainfall and mean temperature in March, April and May in France, Morocco and Spain between 1901 and 2018. These months correspond to the spring migration of common sandpipers. Thin lines show raw data obtained from the University of East Anglia CRU v4.04cy dataset (Harris *et al.* 2020a); bold lines are loess smoothers and their 95% confidence intervals.

Migratory behaviours could contribute to the population declines of common sandpipers. For example, bottlenecks in non-breeding distributions could mean that individuals from multiple breeding sites encounter poor conditions, which might cause large-scale population declines (Finch *et al.* 2017, Bayly *et al.* 2018, Kramer *et al.* 2018). This could even lead to population-specific trends if individuals from different populations are funnelled into separate geographic regions (e.g. Hewson *et al.* 2016). In order to investigate this in common sandpipers, we used the data from Chapter 5 to determine the distance between individuals at each latitude during autumn and spring migration. First, we measured the distances between individuals across all populations to determine the presence of any range-wide bottlenecks. Second, we measured the distances between individuals within each population separately, in order to determine whether migration bottlenecks could cause the contrasting population trends in England and Scotland. Even though these results are susceptible to the inaccuracies of geolocator data (Lisovski *et al.* 2012b, Rakhimberdiev *et al.* 2016) and small sample sizes, and should therefore be regarded with caution, they could provide valuable insight into a potential influence on population trends.

The distances between individuals across all populations do not suggest any bottlenecks during migration in either autumn or spring (Figure 7.4a, b), except for a slight narrowing in West Africa where almost all individuals wintered (Chapter 5). In autumn, birds from all populations appear to migrate close to the Mauritanian coastline thereby avoiding the Sahara Desert, with the median distance between individuals less than 250km. Interestingly, in spring, it appears that many birds make direct crossings from their respective wintering sites rather than flying close to the coast (Figure 7.4b). This avoidance of the Sahara Desert means that individuals migrate closer together in autumn than spring (Figure 7.4c, $\text{median}_{\text{autumn}}$ = 194km, $\text{median}_{\text{spring}}$ = 273km). This pattern is perhaps because of the pressures associated with spring migration, with individuals taking the most direct route from their wintering grounds (Mcnamara *et al.* 1998, Newton 2010).

Bottlenecks specific to common sandpiper populations breeding in England and Scotland could drive differences in population trends, even if there is considerable overlap in their non-breeding distributions (Chapter 5; Finch *et al.* 2017, Kramer *et al.* 2018) . The only apparent constriction outside of the wintering grounds is immediately north of the Strait of Gibraltar during spring migration (38˚N in Figure 7.4a and Figure 7.5). This area is a key stopover site for many migratory species as they recover after crossing the Sahara and the

Strait itself (Cramp *et al.* 1983). As already discussed, investigating weather and habitat changes at key stopover sites such as this could reveal important influences on population trends (Chapter 5). Other than this, however, there appear to be no significant constrictions for any of the populations (Figure 7.5), suggesting that migration bottlenecks do not play an important role in the different population trends in England and Scotland. Further work should investigate the population trends and migration routes of breeding populations in Eastern Europe, as these could winter further east (Briedis *et al.* 2020), and it is unclear how their populations are changing. The only European-wide population trends published to date are aggregated across the entire European continent (Vickery *et al.* 2014). Comparing the trends of common sandpiper populations that share breeding but not wintering sites, and vice versa, could reveal the relative influence of each lifecycle stage.

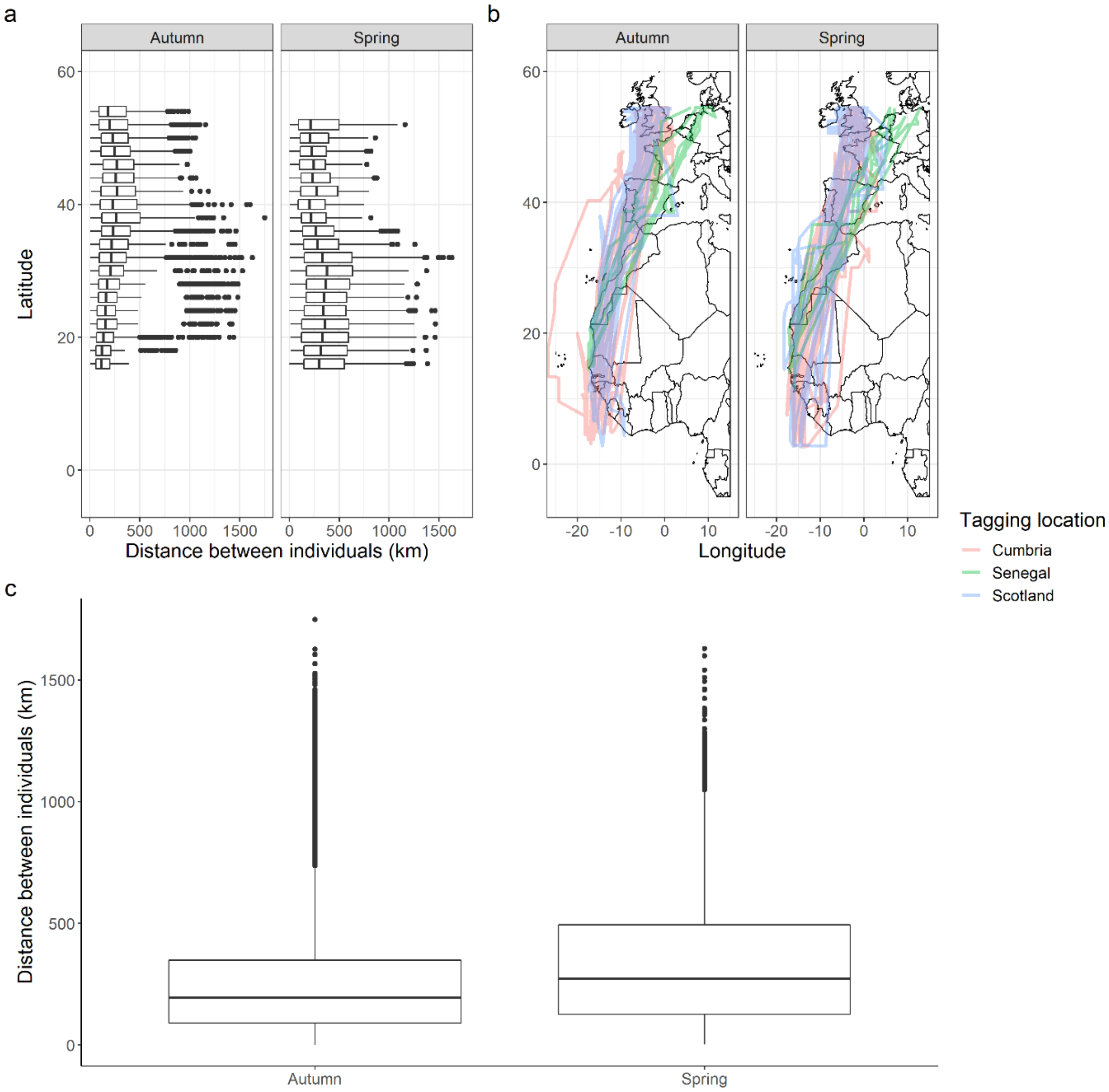


Figure 7.4 Distances between individuals from different tagging locations in autumn and spring migration. Boxplots in (a) show the distances between individuals within two-degree latitudinal bands. Boxplots are only shown for latitudinal bands in which at least 20 individuals were present (max. n_{autumn} = 25, max. n_{spring} = 22). Maps in (b) show the smoothed migration routes as determined by geolocators from different tagging locations (Chapter 5). Boxplots in (c) show distances between individuals in autumn and spring. In (a) and (c) the solid lines correspond to the 50th percentile, the boxes to the 25th and 75th percentiles, the whiskers to 1.5 times the interquartile range and the solid circles show any points beyond these.

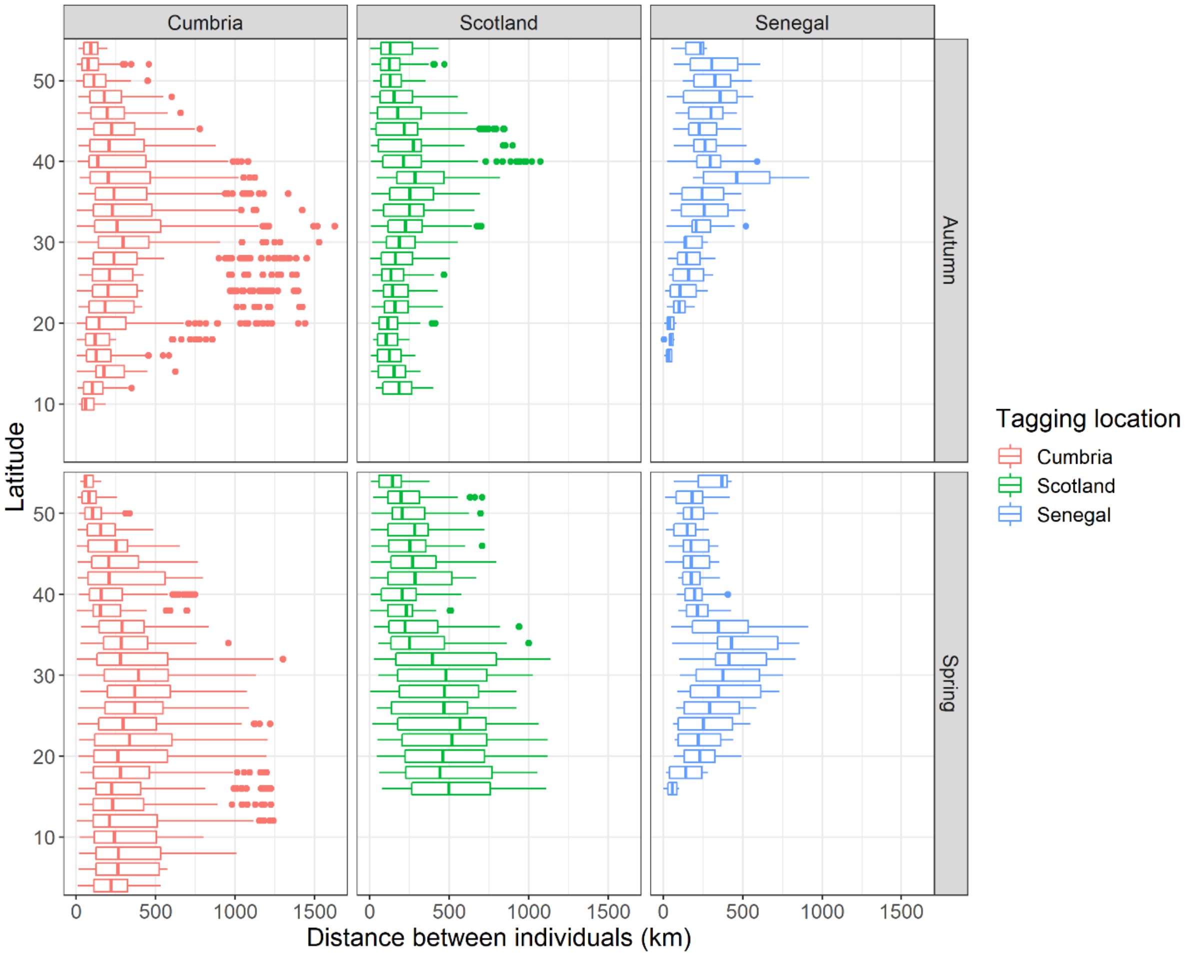


Figure 7.5 Distances between individuals from the separate tagging locations within two-degree latitudinal bands in autumn and spring. For Cumbria and Scotland, latitudes are only shown when there were more than five individuals present at a given latitude (max. $n_{Cumbria}$ = 11, max. $n_{Scotland}$ = 10); for Senegal, latitudes are only shown when there were more than two individuals present at a given latitude (max. n = 4). The solid lines correspond to the 50th percentile, the boxes to the 25th and 75th percentiles, the whiskers to 1.5 times the interquartile range and the solid circles show any points beyond these.

The role of carry-over effects

Summers *et al.* (2019) speculated that the non-breeding season might have little influence on common sandpiper population trends. However, it is possible that poor conditions could accumulate to affect individuals through carry-over or reversible state effects (Senner *et al.* 2015). As described above, there have been significant habitat changes in West Africa (Vickery *et al.* 2014, Dixon *et al.* 2016), which could have important impacts on individuals considering our findings that there might be fine-scale variation in habitat use during winter (Chapter 3). Indeed, even minor changes in wintering conditions could have drastic effects on populations if a high proportion of the population are implicated (Finch *et al.* 2017, Kramer *et al.* 2018). Poor wintering conditions could then be enhanced or buffered by breeding conditions; if breeding conditions are poor, then the influence of wintering ground conditions might be more important than in areas where breeding conditions are favourable (Senner *et al.* 2015). This could therefore drive differences in common sandpiper population trends if breeding ground conditions are generally more favourable in Scotland than England (Morrison *et al.* 2013).

No study on common sandpipers has followed the same individuals year-round, which is needed to understand the relative influence of each lifecycle stage on individual fitness. Indeed, the majority of their lifecycle is spent on the wintering grounds, meaning that body condition during that time might have long-term implications. Studies on other species have used stable isotope ratios of feathers to show that wintering ground conditions can influence arrival dates to breeding sites and reproductive success (Bearhop *et al.* 2004, Lopez Calderon *et al.* 2019). The isotopic composition of feathers reflects those of the food that individuals were eating during moult, providing an index of the habitat in which they were foraging (Bearhop *et al.* 2004). For common sandpipers, this means that the isotopic signatures of feathers are correlated with wintering ground habitat. We found that wintering habitat could have important implications for common sandpipers, which is likely to influence body condition (Chapter 3). This is corroborated by the stable isotope data from the feathers of birds caught in Senegal; $\delta^{13}C$ and $\delta^{15}N$ isotope ratios were positively correlated with body condition (Figure 7.6a). Less negative carbon values are associated with marine habitats which could be better quality for common sandpipers (Chapter 3; Arcas 2004, Tavares *et al.* 2009). Furthermore, nitrogen values are positively correlated with the level of the food chain and higher-level invertebrates are likely to be more calorific than lower-level ones. However, the isotope ratios of feathers do not appear correlated with the body condition of individuals caught in Cumbria (Figure 7.6a, b). This is possibly because individuals were caught throughout the breeding season and their body condition may therefore have already been affected by breeding ground conditions. This means that wintering conditions might be important for the body condition of individuals, but its effects are reversible through conditions at other lifecycle stages (Senner *et al.* 2015).

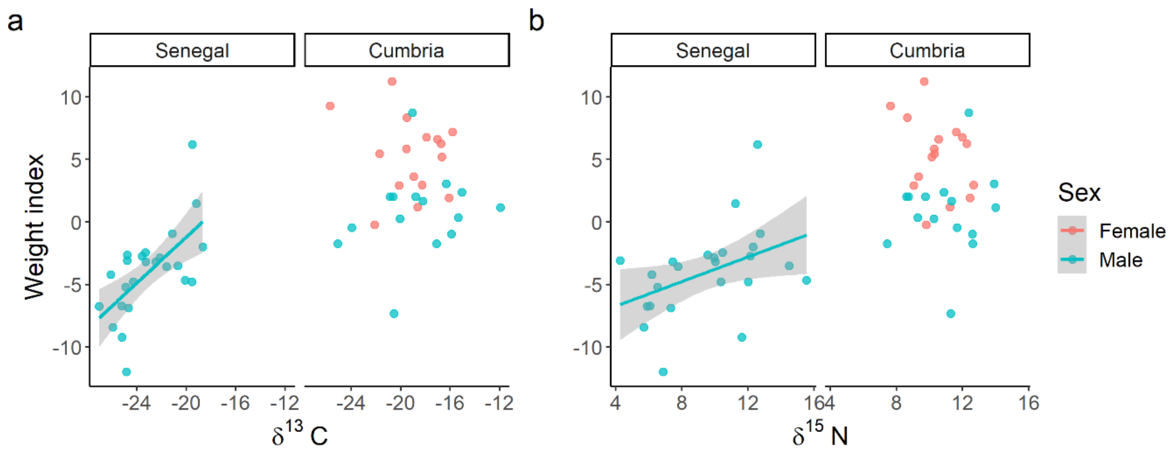


Figure 7.6 The relationship between the weight index of birds and (a) carbon and (b) nitrogen isotope ratios of feathers of birds caught in Senegal and Cumbria. We calculated the weight index as the residuals of a model regressing weight on tarsus length (as described in Chapter 4). The solid lines are predictions from a linear model and the shaded regions their 95% confidence interval; only significant relationships are plotted (Senegal$_{\text{Carbon}}$: adjusted $R^2 = 0.38$, $P < 0.001$; Senegal$_{\text{Nitrogen}}$: adjusted $R^2 = 0.14$, $P < 0.05$).

The wintering ground conditions could have important influences on individuals during the breeding season by impacting arrival date or reproductive success (Morrison *et al.* 2019). We found no correlations between arrival date and the isotopic ratios of feathers (Figure 7.7a, b), suggesting no such relationship. However, we showed that there was a quadratic relationship between first egg date and hatching success (Chapter 2), meaning that earlier breeding may not be beneficial for common sandpipers unlike for many other species (Morrison *et al.* 2019). Wintering conditions could still impact other factors known to be important for fitness, such as clutch volume or the timing of breeding, but more work is needed to investigate any possible relationships.

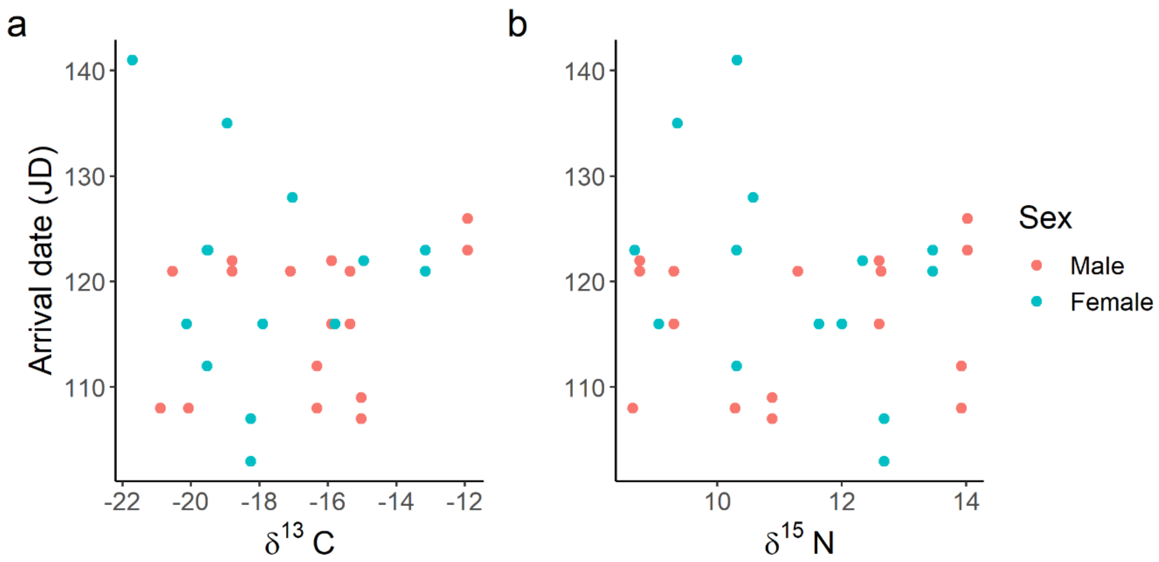


Figure 7.7 The relationships between the arrival dates of birds to the Cumbria study site and (a) feather carbon isotope ratio and (b) feather nitrogen isotope ratio. The arrival dates of two female birds have been removed as both were spotted after they had already started incubation (both JD > 160). Arrival dates are the dates the individuals were first spotted in the study site which were validated by comparing these to the arrival dates determined by geolocators (adjusted $R^2 = 0.93$, $F_{1, 8} = 118$. $P < 0.001$, $n = 10$). None of the relationships between arrival date and isotope ratio were significant (all $P > 0.2$).

Ultimately, understanding the influence of the non-breeding season on the population trends of common sandpipers is reliant on following the same individuals year-round, from their very first migration. In this way, it could be possible to determine the relative influence of different lifecycle stages and whether conditions experienced in each interact to influence survival, reproductive success and larger-scale population trends (Harrison *et al.* 2011, Fayet *et al.* 2016, Briedis *et al.* 2019, Lopez Calderon *et al.* 2019). Additionally, documenting the migrations and settlement decisions of juveniles could help to distinguish between the influence of permanent carry-over effects and reversible-state effects, which are likely to have different but fundamental implications throughout the lifecycle (Gill *et al.* 2014, Senner *et al.* 2015, Gill *et al.* 2019). For example, recent work has shown that population level phenological change reflects generational shifts in timing and not individual plasticity, meaning that understanding the influence of early-life conditions on the rest of an individual’s life is key (Gill *et al.* 2014, Gill *et al.* 2019). For many species, however, following individuals year-round will require lighter, remote download tracking devices that are currently unavailable (Wikelski *et al.* 2007, Kays *et al.* 2015). These tags would also help identify the influence of migration periods on survival, which is not possible using archival loggers (Hewson *et al.* 2016, Loonstra *et al.* 2019). Until these devices become available, more work is needed at sites across all lifecycle stages and particularly during winter (Vickery *et al.* 2014). Further work using repeat captures of individuals could also reveal the relative influences of different lifecycle stages on seasonal survival and population trends (Robinson *et al.* 2020). Investigating these mechanistic processes will be important for understanding the patterns we see at large spatial scales, both within and across species. However, large-scale patterns are also important to investigate given the ecological service that migratory individuals provide (Wilcove & Wikelski 2008, Viana *et al.* 2016a, Horton *et al.* 2019b, Kleyheeg *et al.* 2019).

The importance of scale in the study of migration

Most studies about trends in the timing of migration focus on individuals (Mckinnon *et al.* 2013, Kays *et al.* 2015). This provides valuable insight regarding the behaviours of individuals and can reveal fascinating large-scale patterns across geographic locations and species (Wikelski *et al.* 2007, Mckinnon *et al.* 2013, Kays *et al.* 2015, Van Bemmelen *et al.* 2019). Furthermore, these can be used to investigate the mechanisms driving change at an individual level, by documenting settlement decisions and responses to weather conditions (Vansteelant *et al.* 2015, Åkesson *et al.* 2016, Senner *et al.* 2018, Brust *et al.* 2019, Gill *et al.* 2019). However, as described in Chapter 6, these individual-level patterns may be unlikely to capture migratory variation at a global scale because no study will ever be able to track all individuals migrating or be immune to the biases associated with tracking devices. This means that the patterns observed at the individual-level may not reflect those occurring at large scales (Kelly & Horton 2016). Investigating large-scale patterns has become feasible relatively recently, by using citizen science and weather radar data (Sullivan *et al.* 2014, Bauer *et al.* 2019). In this way, it is possible to investigate changes in all migrating individuals, in order to understand how communities and groups of species are changing (Kelly & Horton 2016, Horton *et al.* 2019b). While these types of data will not provide detailed information about individuals, and have many biases of their own (Johnston *et al.*

2019), they do provide a method with which to investigate changes at large spatial scales that are not possible using individual-based methods.

The timing of migration has many important implications for individuals, primarily through its effects on reproductive success (Aebischer *et al.* 1996, Saino *et al.* 2004, Velmala *et al.* 2015). For most species, migration has evolved to coincide with periods of maximum food availability for their chicks. However, in recent decades, warming temperatures have advanced spring phenology at a faster rate than bird migration, causing the two to become 'mismatched' (Mayor *et al.* 2017). The predictions of changes in the timing of autumn migration are less clear, with no clear pattern emerging across species. While individual-based studies are important for the conservation of single species, the ecosystem services that migratory species provide rely on the magnitude or total numbers of birds migrating (Wilcove & Wikelski 2008). Therefore, investigating patterns at large spatial scales is paramount for understanding the full effects of environmental change. Contrary to many studies, our analysis of eBird data in Chapter 6 showed that the timing of wading bird migration across the Nearctic and Afro-Palearctic flyways has become later over the last decade, in both autumn and spring. While these patterns might appear counterintuitive according to other studies, both individual- and flyway-level studies published so far may not have accounted for the total movement of individuals (Sparks *et al.* 2007, Horton *et al.* 2019a), which could fail to determine shifts in timing due to range shifts (Chapter 6; Howard *et al.* 2018). Our research highlights the need for further work into the potential influence of range shifts on large-scale phenological patterns (Howard *et al.* 2018) and potential differences across avian orders and families. Additionally, more work is needed regarding changes in the synchrony of migration, as the earliest and latest birds might not respond in the same way to climatic change (Dorian *et al.* 2020).

Our work showed that large-scale weather trends play an important role in the timing of autumn, but not spring, migration (Chapter 6), which is consistent with our work on common sandpipers, in which we found that individuals may use winds in autumn but not spring (Chapter 5). This has also been found by many studies of other species (e.g. McNamara *et al.* 1998, Nilsson *et al.* 2013, Gutierrez Illan *et al.* 2017). We also showed in Chapter 6 that the timing of wader migration in autumn was negatively correlated with temperature trends, possibly because of the influence of warm spring temperatures on chick fledging rates (Mcgowan *et al.* 2002, Townsend *et al.* 2013). Other individual- and flyway-level studies have shown that weather conditions play an important role in migratory timing and route, and that advances in arrival to breeding sites are correlated with warmer springtime temperatures (Vansteelant *et al.* 2015, Shamoun-Baranes *et al.* 2017, Horton *et al.* 2019a). Continuous monitoring of individuals through repeated migrations may help us to understand the mechanisms that drive large-scale patterns in relation to weather conditions. For example, recent tracking studies have found remarkable individual consistency in the timing of migration events (Conklin *et al.* 2013, Gill *et al.* 2014, Carneiro *et al.* 2019). Once the level of consistency has been established, it might then be possible to investigate the role of both short and long-term weather patterns for determining individual- and population-level migratory schedules (Newton 2007, Gill *et al.* 2019).

Conclusion

Combining individual-based data with information about large-scale patterns is critical for our continued understanding of the effects of climate change on migration (Bauer & Hoye 2014, Kelly & Horton 2016, Bauer *et al.* 2019, Briedis *et al.* 2020). This is because our understanding of the patterns that we see at large scales is dependent on us investigating the mechanisms driving change in individuals, populations, species and flyways. For example, to understand how range shifts can influence the large-scale timing of migration we also need to investigate the causes of range shifts themselves (Gill *et al.* 2019, Soroye *et al.* 2020). Therefore, more work is needed across all spatial scales in order to understand the overall influence of climate change on migratory species. An understanding of the mechanism and large-scale patterns that we observe will help us implement the conservation actions needed to reverse the current declines in migratory birds (Vickery *et al.* 2014).

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