Consequences of migratory strategies in the context of anthropogenic threats

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Abstract

Migratory species – particularly long-distance migrants – are facing global population declines. Ongoing anthropogenic transformation of the environment may be disrupting the balance of fitness outcomes thought to drive the evolution and maintenance of migratory behaviours. In this thesis, we use partially migratory systems as natural experiments by which to explore the effects of migration on fitness parameters, and take a spatially explicit approach to quantifying the threats faced by Afro-Palaearctic migratory birds. In a meta-analysis of fitness consequences of migratory strategies, we find a persistent benefit to residency in birds, and across taxa, that fitness benefits of residency are more likely to come from survival than from breeding success. In a case study using long-distance partially migratory lesser kestrels (*Falco naumanni*), we find weak evidence for carryover effects of migration, with fitness instead better predicted by breeding site. Using risk-vulnerability composite threat-mapping algorithms, we combine remote-sensed maps of anthropogenic risk with distribution ranges of 103 Afro-Palaearctic migratory bird species to relate range-level exposure to population trends. We find evidence that threats relating to direct mortality – particularly in non-breeding ranges – may contribute to the population declines seen in these species. Finally, we use GPS tracking of common cuckoos (*Cuculus canorus*) as a case study by which to quantify spatiotemporal risk exposure using relevant risk surfaces. Despite greater anthropogenic transformation in Western Europe leading to higher mean hourly risk levels in the breeding season, accounting for temporal exposure reveals that total accumulated risk exposure is greatest in the non-breeding seasons in this species. Overall, this thesis provides evidence to support that the hypothesised fitness benefits conferred to individuals by migrating may be decreasing with spatiotemporal exposure to anthropogenic risks – in some cases possibly mediated by breeding season conditions – and provides a framework for quantifying spatiotemporal threat exposure.

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General Introduction

1.1 Migration and migratory variability

Migration is the reversible seasonal movements of individuals, usually as an adaptation to spatiotemporal variability in optimal conditions or resource availability (Dingle & Drake, 2007; Watts et al., 2018). Migration is a widespread behaviour, found across all major taxonomic groups (Dingle & Drake, 2007) – including in nearly one-fifth of bird species (Kirby et al., 2008) – and accounting for significant redistribution of biomass and associated intricate trophic interactions and ecosystem services (Wilcove & Wikelski, 2008).

Migratory behaviours are ubiquitous and diverse, expressed in widely varying ways between migratory species. Between-species migration distances can vary from the non-stop transhemispheric migrations of bar-tailed godwits (*Limosa lapponica baueri*) (Gill et al., 2009), to c. 12-km altitudinal migrations of bighorn sheep (*Ovis canadensis*) (Festa-Bianchet, 1988), and <500-m vertical diel migrations of zooplankton (Brierley, 2014). The reversible element of migration (differentiating it from dispersal movements (Brönmark et al., 2014)) may also vary in temporal scale, with outward and return journeys occurring within a day (in the case of vertical migrations (Brierley, 2014)), within a year (as seasonal migration is typically understood), within a generation (largely seen in diadromous semelparous ray-finned fishes (Miller et al., 2019; Quinn & Myers, 2004)), or across generations – most commonly seen in invertebrates (e.g. Chapman et al., 2012; Stefanescu et al., 2013). This thesis concentrates on yearly seasonal migratory movements, primarily of birds, although other taxa are considered in part.

Intraspecific migratory diversity is also common; individuals from a single population may vary in timing, distance, route and stopover strategy (Chapman et al., 2011b; Vardanis et al., 2011). Stark within-species differences in routes – known as migratory divides – have been observed in, for instance, common cuckoos (*Cuculus canorus*) (Hewson et al., 2016) and red-necked phalaropes (*Phalaropus lobatus*) (van Bemmelen et al., 2019). Similarly, stopover strategies of black-and-white warblers (*Mniotilta varia*) vary with individual migratory phenology (Paxton & Moore, 2017), while in Eurasian spoonbills (*Platalea leucorodia leucorodia*) certain individuals migrate over four times the distance of others using the same breeding site (Lok et al., 2015).

1.2 Anthropogenic threats to migratory birds

Population declines in migratory birds are well documented in Europe, North America and East Asia (Laaksonen & Lehikoinen, 2013; Robbins et al., 1989; Sanderson et al., 2006; Yong et al., 2015). Among those breeding in Europe, declines are steepest among habitat specialists – particularly farmland and woodland specialists (Hewson & Noble, 2009; Laaksonen & Lehikoinen, 2013) – and long-distance migrants (Vickery et al., 2014). Effects of environmental change are likely to manifest differently across taxonomic groups, trophic levels, latitudes, ecological systems (Parmesan, 2006; Walther et al., 2002), and importantly may also vary across migratory strategies. The susceptibility of migratory species to negative impacts of anthropogenic change is not easily discernible (Chapman et al., 2011b), and is unlikely to be uniform across species. In general, however, their dependence on a wider range of temporally and spatially distributed habitats and resources is thought to expose migrants – especially long-distance migrants – to increased potential risks (Both et al., 2010; Gilroy et al., 2016; Robinson et al., 2009; Wilcove & Wikelski, 2008). Furthermore, migratory species are more common at higher latitudes (possibly relating to the increased seasonality – and hence variability in favourable conditions – in the northern hemisphere (Robinson et al., 2009; Somveille et al., 2013)), where climate warming has also so far been most evident (IPCC, 2013).

Consequences of environmental change for migrants

Migratory species' inherently itinerant life-histories may lead to greater cumulative exposure to a wider variety of anthropogenic risks (Gilroy et al., 2016; Wilcove & Wikelski, 2008) – particularly threats posed by human settlement and infrastructure (Loss et al., 2012). Migratory great bustards (*Otis tarda*), for instance, face mortality rates up to 3.5 times higher than those of non-migratory conspecifics, with collisions with powerlines the single largest contributor to mortality (Palacín et al., 2017). Collision risks posed by windfarms has similarly been linked to populations declines (Loss et al., 2013, 2015; Zimmerling et al., 2013), while avoidance behaviours can result in potentially costly deviations to migratory journeys – as measured in common eider (*Somateria mollissima*) (Masden et al., 2009). The illumination of offshore windfarms may also attract migrating birds, heightening collision risk and disrupting migratory routes (Hüppop et al., 2006). Artificial light at night may similarly exacerbate the considerable collision risks posed by buildings (Lao et al., 2020; Loss et al., 2014; Van Doren et al., 2017) – to which migratory species may be particularly susceptible when travelling through novel environments, particularly nocturnal migrants (Cabrera-Cruz et al., 2018; Loss et al., 2014). Fluxes of migrating birds are, in certain parts of the world, at particular risk of hunting by humans (Bairlein, 2016; Brochet et al., 2016), which has contributed to drastic population declines in certain species (Hung et al., 2014; Jiguet et al., 2019; Kamp et al., 2015).

Loss of natural habitats to anthropogenic land-use is also considered to be a major contributor towards population declines in migratory birds (Cresswell et al., 2007; Vickery et al., 2014). Large-scale modelling of European breeding migrants has yielded evidence that land cover change in the non-breeding ranges may be particularly relevant to population trends (Howard et al., 2020), while changing land-use practices in the Sahel – particularly those resulting in the loss of wetland and woodland habitats – is linked to ongoing population declines in Afro-Palaearctic arid-zone migrants (Adams et al., 2014; Walther, 2016). Similarly, negative population trends in shorebirds using the East Asian–Australasian flyway have been linked to reliance for refuelling on the Yellow Sea tidal mudflats, which have seen drastic degradation in recent years (Studds et al., 2017); reliance on this region also predicts sensitivity to Arctic climatic conditions in the subsequent breeding season (Dhanjal-Adams et al., 2019). Non-breeding ecology in migratory species is generally less well studied than that of the breeding season (Marra et al., 2015); predicting population impacts of land-use change will improve with greater understanding of non-breeding season habitat requirements, which may be complex or idiosyncratic (e.g. Buchanan et al., 2020).

There is growing evidence that these threats posed by habitat degradation can interact with those posed by changing climatic conditions (Howard et al., 2020; Robinson et al., 2009; Vickery et al., 2014). Warming in the northern hemisphere may directly affect survival by influencing food availability (van Gils et al., 2016), and associated advancing spring temperatures have been linked to shorter and earlier migrations (Jonzén et al., 2006; Usui et al., 2017; Visser et al., 2009), range shifts (Barbet-Massin et al., 2009; La Sorte & Thompson, 2007), and earlier breeding (Both et al., 2004; Tomotani et al., 2017). Such changes are neither necessarily beneficial (e.g. Jovani & Tella, 2004; Van Der Jeugd et al., 2009), nor sufficiently adaptive (Visser & Both, 2005). Furthermore, not all migrants display the spatiotemporal plasticity to respond to climate change (Fraser et al., 2013; Robinson et al., 2009), with negative demographic consequences for those less able to adapt (Both et al., 2006, 2010; Møller et al., 2008). Anthropogenic climate change is also bringing about greater frequency of extreme climatic events (Coumou & Rahmstorf, 2012; Ummenhofer & Meehl, 2017), with corresponding effects for migratory birds. Links between the particularly severe droughts in

West Africa in the second half of the twentieth century and population declines in migratory birds to these regions have been well established (Møller, 1989; Peach et al., 1991; Szép, 1995). Similarly, extreme climatic events may also bring about delayed breeding (Gordo et al., 2005; Rockwell et al., 2012; Tøttrup et al., 2012), or even influence migratory behaviour (Acker et al., 2021).

Importance of seasonal conditions

The more pronounced population declines generally seen in longer-distance migratory birds (Sanderson et al., 2006; Vickery et al., 2014) point to the importance of conditions outside of the breeding season (passage and wintering periods), and/or a reduced capacity to respond to changes occurring at the breeding grounds (Møller et al., 2008). Despite growing within- and between-species investigation into the relative importance of seasonal conditions, the evidence is equivocal. Variability in migratory route is associated with different demographic outcomes in, for instance, common cuckoos (Hewson et al., 2016), and congeneric shorebirds (Lisovski et al., 2020), while population trends of Afro-Palaearctic migratory birds have been linked to precipitation levels in the wintering grounds (Ockendon et al., 2014; Peach et al., 1991; Szép, 1995), and elsewhere to breeding site conditions (Morrison et al., 2013; Ockendon et al., 2013). The relative importance of certain conditions for population trends may also vary between seasons (Howard et al., 2020; Vickery et al., 2014), carryover from one season to the next (Dhanjal-Adams et al., 2019; Finch et al., 2014), or operate at different spatial scales (Morrison et al., 2010). Understanding when and where population limiting mechanisms are acting will shed necessary light on underlying demographic processes (Morrison et al., 2013), and ultimately allow targeted conservation actions. The complex evidence concerning the relative demographic relevance of seasonal and inter-seasonal conditions points to the importance of full-season and spatiotemporally explicit approaches for understanding drivers of population declines in migratory species (Marra et al., 2015; Runge et al., 2014).

1.3 Partial migration as a model system

A particularly discrete categorisation of within-population migratory variability is partial migration, defined as when a population comprises migratory and non-migratory (resident) individuals (Chapman et al., 2011a; Lundberg, 1988). An increasing proportion of migratory species are recognised as having partially migratory populations (Chapman et al., 2011b), with such populations occurring across taxonomic groups and biomes. Partial migration has been observed, for instance, in impala (*Aepyceros melampus*) in Zimbabwe (Gaidet & Lecomte, 2013), delta smelt (*Hypomesus transpacificus*) endemic to San Francisco (Hammock et al., 2017) and greater flamingo (*Pheonicopterus roseus*) in France (Sanz-Aguilar et al., 2012). This coexistence of migrants and residents within a population for certain seasons makes partially migratory systems valuable models through which to explore migratory trade-offs and seasonal effects (e.g. Acker et al., 2021; Grist et al., 2017).

Types of partial migration

Partially migratory systems can be classified according to the season in which resident and migrants are allopatric: non-breeding partial migration is where migrants and residents are allopatric during the winter and sympatric during the breeding season – seen, for instance, in European robins (*Erithacus rubecula*) (Adriaensen & Dhondt, 1990) – and is the most well-documented form (Chapman et al., 2011b; Shaw & Levin, 2011). Breeding partial migration, conversely, is characterised by sympatric wintering and allopatric breeding – such as occurs in elk (*Cervus canadensis*) (Chapman et al., 2011b; Robinson & Merrill, 2013). A third type – skipped breeding partial migration – has also recently been defined, in which partial migration results from individuals forgoing migration and reproduction (Shaw & Levin, 2011). This is likely to relate to condition-dependent trade-offs between current and future reproductive success – as seen in Atlantic herring (*Clupea harengus*) (Engelhard & Heino, 2005). Breeding partial migration by definition results in the reproductive isolation of migrants and residents, and therefore has fairly straightforward potential consequences for speciation (Chapman et al., 2011b). Non-breeding partial migration, however, may also result in limited gene flow between migrants and residents: migratory strategy may result in differential breeding phenology or breeding site location – potentially resulting in assortative mating (Chapman et al., 2011b), e.g. (Anderson et al., 2016; Bearhop, 2005). Despite being considered a possible evolutionary stepping-stone between full residency and full migration (or vice versa) (Sekercioglu, 2010), the evolutionary implications of partial migration have not been well-studied (Chapman et al., 2011b).

Evolutionary background to migration and partial migration

As migration – particularly long-distance migration – can represent a potentially hazardous (Lindström, 1989; Ydenberg et al., 2004) and costly (Alerstam et al., 2003; Wikelski et al., 2003) undertaking (though see Shamoun-Baranes et al. (2017)), there must be strong selective pressure for migratory behaviour to evolve, such that the risks of migration are outweighed by benefits to breeding success or survival (Griswold et al., 2010; Zúñiga et al., 2017) – via, for instance, more suitable climatic conditions and resources (Alerstam et al., 2003), predation escape (McKinnon et al., 2010) and parasitism escape (Shaw et al., 2019).

The coexistence of migrants and residents in partially migratory systems represents a behavioural polymorphism, the maintenance of which over evolutionary time points to approximately balanced fitness outcomes for both strategies (Chapman et al., 2011b; Lundberg, 1987). This may occur if each strategy yields benefits to different demographic parameters; in non-breeding partial migration, for instance, migration may yield survival benefits through escape of inclement conditions, while residency confers reproductive success benefits through early access to breeding resources (Lundberg, 1988; Zúñiga et al., 2017). Strategies may also be condition-dependent, such that fitness benefits are context-specific but balanced over the population (Lundberg, 1987; Vélez-Espino et al., 2013). Such contexts may be extrinsic environmental or population conditions (Griswold et al., 2010; Taylor & Norris, 2007), intrinsic individual traits, or both (Chapman et al., 2011b). Facilitated by increasing feasibility of individual monitoring throughout the year, there is a growing literature concerning partially migratory systems (Chapman et al., 2011a; Meller et al., 2016), particularly describing the potential drivers and fitness consequences of the two strategies. The extent to which historically stable fitness balances between residents and migrants are now being perturbed by anthropogenic change remains poorly understood, and poses an interesting and important question for the conservation of migratory populations.

Conditional strategy hypotheses

Individual traits have been identified as (sometimes interacting) predictors of migratory strategy – such as age, sex and morphology – underpinning hypotheses for context-specific strategy benefits. For instance, observations of migrants being significantly larger than residents, (e.g. Hegemann, Marra, & Tieleman, 2015; Warkentin, James & Oliphant, 1990) have given rise to hypotheses that, using body size as a measure of fitness or quality, these individuals may be able to forgo the energetic expenses of migration (Ketterson & Nolan, 1976). This may be due to improved ability to withstand winter temperatures ('thermal tolerance hypothesis') and lower food availability ('fasting endurance hypothesis') (Chapman et al., 2011b; Ketterson & Nolan, 1976), or due to greater ability to outcompete conspecifics during periods of low resource availability ('dominance hypothesis') (Chapman et al., 2011b; Gauthreaux, 1982). Hypotheses are not necessarily mutually exclusive – between or within ecological systems. The 'arrival time' hypothesis (Chapman et al., 2011b), for instance, builds on evidence that early-returning migrants benefit from higher reproductive fitness (e.g.

Gienapp & Bregnballe, 2012), owing to early access to optimal breeding opportunities and conditions (Ketterson & Nolan, 1976). This, it is suggested, should logically promote residency, especially in the sex which establishes breeding territories (Chapman et al., 2011b; Ketterson & Nolan, 1976), as seen in European blackbirds (*Turdus merula*) (Fudickar et al., 2013). It does not, however, preclude the concept that it is the larger or higher-quality individuals best able to survive – and therefore reap the predicted benefits of – residency; support for both arrival time and body size hypotheses has been simultaneously documented, for instance, in red-spotted newts (*Notophthalmus viridescens*) (Grayson et al., 2011)

Strategy consequences in partial migrants

The evidence concerning the relative fitness consequences of the two strategies in partially migratory systems is also broad and varied, with little indication of any overarching trends. Migratory strategy has been found in some instances to confer no discernible benefit to individual survival, such as in spruce grouse (*Falcipennis canadensis*) (Herzog & Keppie, 1980) and moose (*Alces alces*) (White et al., 2014), while elsewhere, survival is higher among residents – as in great bustard (*Otis tarda*) (Palacín et al., 2017) and red deer (*Cervus elaphus*) (Hebblewhite & Merrill, 2011), in these cases owing to migrants facing greater risk of anthropogenic and predation mortality respectively. Conversely, migratory American dippers (*Cinclus mexicanus*) have higher survival than residents (Gillis et al., 2008; Whitehorne, 2009), possibly as a result of the energetic costs of defending a territory the full year round, while migratory impala have been found to be in better body condition than residents, linked to higher-quality diet available in the migratory range (Gaidet & Lecomte, 2013). Similarly, breeding success in Svalbard reindeer (*Rangifer tarandus platyrhynchus*), is greater in migrants than in residents, possibly due to links between female fecundity and the higher-quality forage found in the migrant range (Hansen et al., 2010).

Experiences in one season may have immediate within-season effects, but may also have longer-term sub-lethal effects, which are manifest in the subsequent season(s) – known as carryover effects (Harrison et al., 2011). The consequences of migratory strategies may manifest in such a fashion, with effects of migration or residency felt in the following non-migratory season. In Lanyu scops owls (*Otus elegans botelensis*), residents have greater reproductive fitness than individuals that migrated in the preceding season, possibly owing to limited breeding sites: foregoing migration afforded resident males greater competitive ability in establishing higher-quality territories earlier, while resident females were better able to assess nest-site quality (Bai et al., 2012).

The majority of studies exploring fitness differences in partially migratory populations do not examine systems in which there are explicitly known major differences in the magnitude of migration (though see (Hegemann et al., 2015)). In the well-studied partially migratory populations of American dipper, for instance, migrants travel only c. 6 km upstream of their resident counterparts (Gillis et al., 2008; Green et al., 2015; Morrissey, 2004; Whitehorne, 2009). Studies of partial migration in mammals similarly often contrast residents with migrants relocating to nearby areas at higher elevation, with migratory individuals defined as such through non-overlapping seasonal home-ranges (Eggeman et al., 2016; Qviller et al., 2013). Certain studies also exist that explore fitness differences between residents and apparent long-distance migrants, in which the latter are defined as such through absence of evidence on the breeding grounds in winter, with their long-distance migration therefore assumed (e.g. Massemin-Challet et al., 2006). Although the cumulative effects of absolute migratory distance will not be uniform across species – varying with differences in movement efficiency related to body size, locomotion and fluid dynamics (Alerstam et al., 2003; Alexander, 2002) – it remains the case that few studies of partial migration consider systems with extreme differences in strategy (e.g. intercontinental migrations).

1.4 Migratory flexibility as a population response to environmental change

As migrants may be particularly susceptible to the negative effects of environmental change, partial migration may to some extent mitigate population-scale consequences, by having a section of the population not subject to the threats posed by migration (Chapman et al., 2011b), or if variation in migratory strategy is indicative of greater capacity to adapt migratory behaviour to changing conditions (Gilroy et al., 2016). It has been predicted that ongoing environmental change will bring about a set of conditions – particularly in the Northern Hemisphere – under which the fitness benefits of migration are diminished, and will consequently drive an increase in residency (Berthold, 2001; Pulido & Berthold, 2010), or in migratory plasticity (Reid et al., 2018). Resident individuals are better placed to react to any breeding site environmental cues (Cobben & van Noordwijk, 2017; Visser et al., 2004), and are less susceptible to trophic asynchrony arising as a result of advancing spring temperatures (Møller et al., 2008; Pulido & Berthold, 2010). Decreasing seasonality may also alter the selective pressures favouring migration, if milder winters are easier for resident individuals to survive (Nilsson et al., 2006). Temperature increases have, for instance, been linked to higher fitness in resident masu salmon (*Oncorhynchus masou*) (Morita et al., 2014), and in resident red deer (Middleton et al., 2013).

Increasing incidence of residency has been reported in certain species (Hebblewhite & Merrill, 2011; Meller et al., 2016; Van Vliet et al., 2009), while it has also been suggested that the reduction in migration distances travelled by certain migratory species (e.g. Visser et al., 2009) may represent a transition to full residency (Berthold, 2001; Meller et al., 2016). Assessing the presence and direction of population-scale responses to environmental change will shed light on the evolutionary dynamics of migratory behaviours, and aid in predicting how migratory species will respond to increasing anthropogenic threats.

1.5 Thesis structure

This thesis explores fitness and risk exposure consequences of migration and migratory strategies in the context of ongoing anthropogenic transformation of the natural environment. The research presented here has been undertaken at varying scales (from single-species studies to multi-taxa macroecology), using a range of study systems and technological approaches. In Chapters 2 and 3 we use partially migratory systems as natural experiments by which to explore whether migrants experience fitness outcomes inferior to those experienced by residents, building on the hypothesis that formerly balanced fitness consequences for migrants and residents increasingly favour residency, as a result of migrants' greater exposure to human-induced risk (Berthold, 2001; Pulido & Berthold, 2010). In Chapters 4 and 5 we then explore when and where in the annual cycle migratory birds face the greatest exposure to anthropogenic threats, and the extent to which such exposure may drive population trends. In presenting evidence from complementary approaches, this thesis aims to provide an holistic approach to furthering understanding of drivers of population declines in avian migrants.

Growing availability of individual-level movement data from tracking devices has brought about an increase in studies measuring fitness consequences of migratory strategies (Chapman et al., 2011b), representing a unique opportunity for quantitative synthesis. In Chapter 2, we present the results of a multi-taxon (mammals, herpetofauna, fishes and birds) meta-analysis conducted using these studies, to explore if there is a pervasive signal in the published partial migration literature for one strategy yielding enhanced fitness outcomes than the other – and over which demographic parameters (breeding success or survival) such a benefit may occur. This chapter is published in the *Journal of Animal Ecology*.

As an individual case study of fitness consequences of migratory strategies, in **Chapter 3** we explore breeding season fitness in partially migratory lesser kestrels (*Falco naumanni*) breeding in southern Spain – a relatively uncommon example of true partial migration in a long-distance migrant to sub-Saharan Africa. We use light-level geolocators, ring resighting data and stable isotope analysis to determine migratory strategy, and relate strategy to subsequent condition and reproductive success to examine for carryover effects of long-distance migration. This chapter is published in *Scientific Reports*.

Addressing population declines in migratory birds will require nuanced understanding of if, when and where migrants face exposure to population limiting anthropogenic threats. In **Chapter 4** we take a macro-ecological approach to explore the relative strength and spatial distribution of relevant human-induced threats. We use remote-sensed spatial data and a survey of expert opinion to map sixteen anthropogenic threats across the Afro-Palaearctic region, (encompassing human infrastructure, relative hunting pressure, land-use change and climate change) and develop composite risk-mapping algorithms to combine (cor)related threats with species-specific traits-based threat vulnerability weightings. We use these to calculate seasonal range-scale threat exposure scores for 103 Afro-Palaearctic migratory birds, and relate these to their long-term population trends. This chapter is currently in review at *Global Ecology and Biogeography*.

Over the last decade, the British Trust for Ornithology has conducted a satellite telemetry project on UK-breeding common cuckoos, yielding novel insights into variable migratory routes to wintering grounds in central Africa, and flyway-specific mortality rates (Hewson et al., 2016). In **Chapter 5**, we combine this tracking data with the risk surfaces and composite risk-mapping algorithms defined in the previous chapter to explore individual-level risk exposure. By accounting for time spent exposed to risks, we present a spatiotemporally explicit approach to quantifying exposure to anthropogenic risk, allowing for between-season and between-flyway comparisons of accumulated threat exposure. This chapter will be submitted to *Ecography*.

In **Chapter 6**, the general conclusions, I summarise the results presented in this each chapter of this thesis, and attempt to discuss broader implications of this research and potential future directions.

I have presented each chapter in the style of a standalone publication, with references and supplementary information presented at the end of each chapter.

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Fitness consequences of different migratory strategies in partially migratory populations: a multi-taxa meta-analysis

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CB, JG and AF designed the study. CB collected the data, conducted the statistical analyses and wrote the manuscript. AF and JG provided statistical advice. AF, IC and JG critically revised the manuscript. All authors contributed to interpreting results and gave final approval for publication.

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ABSTRACT

Partial migration – wherein migratory and non-migratory individuals exist within the same population – represents a behavioural dimorphism; for it to persist over time, both strategies should yield equal individual fitness. This balance may be maintained through trade-offs where migrants gain survival benefits by avoiding unfavourable conditions, while residents gain breeding benefits from early access to resources. There has been little overarching quantitative analysis of the evidence for this fitness balance. As migrants – especially long-distance migrants – may be particularly vulnerable to environmental change, it is possible that recent anthropogenic impacts could drive shifts in fitness balances within these populations. We tested these predictions using a multi-taxa meta-analysis. Of 2939 reviewed studies, 23 contained suitable information for meta-analysis, yielding 129 effect sizes. Of these, 73% (n=94) reported higher resident fitness, 22% (n=28) reported higher migrant fitness, and 5% (n=7) reported equal fitness. Once weighted for precision, we found balanced fitness benefits across the entire dataset, but a consistently higher fitness of residents over migrants in birds and herpetofauna (the best-sampled groups). Residency benefits were generally associated with survival, not breeding success, and increased with the number of years of data over which effect sizes were calculated, suggesting deviations from fitness parity are not due to sampling artefacts. A pervasive survival benefit to residency documented in recent literature could indicate that increased exposure to threats associated with anthropogenic change faced by migrating individuals may be shifting the relative fitness balance between strategies.

2.1 INTRODUCTION

Migratory species are found across all major taxonomic groups (Dingle & Drake, 2007), an increasing number of which are recognised as partial migrants (Chapman et al., 2011b; Meller et al., 2016; Reid et al., 2018), wherein migratory and non-migratory individuals exist within the same population of a species (Chapman et al., 2011a; Lundberg, 1988). Previously underrepresented in migration literature (Chapman et al., 2011a; Sekercioglu, 2010), partial migration has seen an increase in published studies only in recent years (Meller et al., 2016) – at least in part owing the greater empirical research enabled by advances in tracking technologies (Chapman et al., 2011b, 2011a; Reid et al., 2018). The emergence of rigorous study on this topic represents an opportunity to address unanswered questions surrounding the evolution and maintenance of partial migration (and behavioural polymorphisms in general), the ecological consequences of different migratory patterns and the evolution of migration itself (Chapman et al., 2011b; Sekercioglu, 2010).

Migratory behaviours typically arise where temporary spatial displacement is an advantageous response to environmental variation (Alerstam et al., 2003; Dingle, 1980). The potential costs of migration are high: migratory individuals may encounter unfamiliar environments with novel threats, as well as the energetic costs of movement (Wikelski et al., 2003), predation risks (Lindström, 1989; Ydenberg et al., 2004), and temporal investment to the detriment of time otherwise invested in breeding fitness (Alerstam et al., 2003). The biological processes underlying the evolution of migration are little known (Griswold et al., 2010; Townsend et al., 2018; Vélez-Espino et al., 2013), but in order to have evolved, migration must – in sufficient instances – offer a benefit relative to not migrating ('residency' hereafter) to either breeding success or survival (Griswold et al., 2010; Lundberg, 1988; McKinnon et al., 2010; Zúñiga et al., 2017).

Partial migration represents a behavioural dimorphism; in order for it to be maintained, either the two strategies yield equivalent fitness returns – an evolutionary stable state – or they confer overall balanced relative benefits which differ according to circumstance, known as a conditional strategy (Chapman et al., 2011b; Kokko, 2011; Lundberg, 1988). It follows, therefore, that in partially migratory populations residency may offer complementary fitness benefits to those offered by migration (Lundberg, 1988; Zúñiga et al., 2017). In the case of conditional strategies, these may refer to individual states such as sex or body condition (Hegemann et al., 2015; Warkentin et al., 1990), or external conditions, such as population density (Grayson & Wilbur, 2009) or environmental conditions (Chapman et al., 2011b; Lack, 1968; Lundberg, 1987; Meller et al., 2016). Additionally, the prevalence of each strategy within a population may itself influence the relative fitness benefits conferred by either (Kokko, 2011; Lundberg, 1987).

Two of the main demographic parameters controlling population size are breeding success and survival (Griswold et al., 2011; Lundberg, 1987), though the extent of the influence of each parameter on population size may differ between populations (Morrison et al., 2013). Theories surrounding the maintenance of partial migration have hypothesised that the balance of benefits between migration and residency hinges on differential advantages to survival versus breeding success between the strategies (Griswold et al., 2010; Lundberg, 1988; Zúñiga et al., 2017). These generally predict that migration confers survival benefit as it allows individuals to escape unfavourable climatic conditions and low resource abundance, while residency promotes breeding success through early access to better resources – such as territories or breeding locations (Chapman et al., 2011b; Kokko, 2011; Lundberg, 1987). Although relative fitness benefits have been quantified in many partially migratory populations (Bai et al., 2012; Hansen et al., 2010; Hebblewhite & Merrill, 2011; Palacín et al., 2017), the generality of this prediction across taxa has not been tested previously. Assessing the prevalence of fitness parity between migrants and residents – and any patterns evident in the deviation from this parity – has the potential to add to our understanding of the ontogeny of migratory behaviours, as well as shed light on how migratory species will respond to increasing anthropogenic threats.

Migratory individuals depend on a wide range of temporally and spatially distributed habitats and resources across the annual cycle, which is thought to expose migrants – especially long-distance migrants – to increased potential risks (Both et al., 2010; Gilroy et al., 2016; Robinson et al., 2009; Wilcove & Wikelski, 2008). Rising temperatures have been linked to poleward range shifts in migratory species (Breed et al., 2013; La Sorte & Thompson, 2007), shorter migration distances (Heath et al., 2012; Visser et al., 2009), earlier arrival times (Jonzén et al., 2006; Usui et al., 2017), and earlier breeding times (Both et al., 2004; Tomotani et al., 2017). Furthermore, the capacity of migratory species to adapt to climate change is not universal (Fraser et al., 2013; Robinson et al., 2009), and inability to do so has been linked to population declines (Møller et al., 2008). Partial migration may confer some resilience to environmental change, since some individuals are not exposed to the threats posed by migration (Chapman et al., 2011b); indeed, partial migration has been shown to be a positive predictor of population trends in European birds (Gilroy et al., 2016). Climate change has been predicted to make residency increasingly beneficial, and accordingly bring about a decrease in migratory tendency among partial migrants (Berthold, 2001; Pulido & Berthold, 2010). This may be particularly relevant in populations where selection pressures favouring migration are weaker, such as at lower latitudes, where the reduced seasonality – and associated lower variability in resources – (Robinson et al., 2009; Somveille et al., 2013) means fitness benefits may be more closely balanced between resident and migrant strategies. Again, however, the generality of these patterns has not been tested across taxa.

The growing bank of research surrounding partial migration represents an unexplored opportunity for quantitative synthesis, rendered particularly timely by the growing impacts of global environmental change on migratory species (Robinson et al., 2009). Here, we employ a meta-analytic approach to assess whether the individual fitness benefits of migration and residency are indeed balanced in partially migratory populations. We also evaluate the generality of patterns relating to the type of benefit – breeding success or survival – for either strategy. Additionally, we consider the potential influence of latitude and migratory distance on these relative benefits, further predicting that, were environmental change driving a change in balance, it would result in more benefits to residency in long-distance migrants or low-latitude systems.

2.2 METHODS

Data collection

We carried out a systematic search of studies published until December 2017 using the search terms outlined in Table 2.1 via ISI Web of Science and Google Scholar, without constraining our results to any specific taxonomic group(s). For each search phrase, we extracted all results that fell into any of the Web of Science-defined categories deemed potentially relevant to partial migration (Behavioural Sciences, Biodiversity Conservation, Biology, Ecology, Entomology, Environmental Sciences, Environmental Studies, Evolutionary Biology, Fisheries, Marine Freshwater Biology, Ornithology, Zoology). For the results of the Google Scholar search, we extracted the first 120 results for each search phrase using a browser-based web-scraping tool (Data Miner, 2017). The search syntax differs slightly to that used for Web of Science; Google Scholar automatically inserts the Boolean operator 'AND' between all search terms unless another is specified. Furthermore, truncation is not recognised by Google, which instead uses automatic word stemming as part of a suite of 'query expansion' measures (Google, 2018).

Table 2.1 – Search terms used to create unfiltered reference library.

Database/search engine	Search terms				
ISI Web of Science	benefits	AND	migration		
	benefits	AND	migration	AND	strategy
	benefits	AND	migratory	AND	strategy
	benefits	AND	partial	AND	migration
	benefits	AND	resident	AND	migrant
	consequences	AND	partial	AND	migration
	consequences	AND	partial	AND	strategy
	reproduct*	AND	benefits	AND	migration
	reproduct*	AND	partial	AND	migration
	fitness	AND	partial	AND	migration
	survival	AND	benefits	AND	migration
	survival	AND	partial	AND	migration
Google Scholar	benefits migration				
	benefits migration strategy				
	benefits migratory strategy				
	benefits partial migration				
	benefits resident migrant				
	consequences partial migration				
	consequences partial strategy				
	reproduction benefits migration				
	reproductive benefits migration				
	reproduction partial migration				
	reproductive partial migration				
	fitness partial migration				
	survival benefits migration				
	survival partial migration				

Following Stewart and colleagues (Stewart et al., 2007) (and cited elsewhere as good practice (Côté et al., 2013, p. 47)), we also conducted supplementary literature searches in order to add to – and validate the accuracy of – the results of the keyword search. These consisted of searching the reference lists of papers already in our accepted reference library and of the narrative review of partial migration by (Chapman et al., 2011b). We also carried out additional searches with altered keywords to ensure our results encompassed taxonomic groups whose literature employs different migration terminology (e.g. diadromy in fish).

We filtered the resulting papers according to their potential relevance to our research question. Filtering was done initially by abstract, then again by full-text, retaining any studies for which it appeared possible they could fulfil the following criteria:

> Does the study compare either a resident and migrant population of the same species or a short-distance migrant and long-distance migrant population of the same species?
>
> Does the study measure outcomes deemed by its authors to be a potential consequence of migratory strategy?
>
> Does the study measure outcomes deemed by its authors to be ecologically beneficial/detrimental to the survival or reproductive success of individuals?
>
> Can these outcomes be considered direct indicators of fitness?
>
> Does the study report extractable data necessary for calculation of effect measures?
>
> Are the data reported either raw observations or predicted by models fitted to raw data? (I.e. experimental data and theoretical models excluded.)

We included studies comparing short-distance migrants to long-distance migrants (in addition to those comparing residents to migrants) in an attempt to encompass more of the spectrum of migratory differences, and acknowledging that distinctions between residents and migrants may in any case not necessarily be strictly dichotomous (Reid et al., 2018). We only considered effect sizes relating to traits we deemed directly indicative of survival or breeding success; this resulted in a smaller sample size by excluding measures of, for instance, oxidative stress, predation risk, and body size (see Table S2.1), but ensured that metrics could be reliably interpreted as direct measures of fitness. See Data sources section for a list of all data sources used in the analysis.

Data extraction

We extracted means and standard deviations for all reported results that fulfilled the inclusion criteria. For each effect size, we also extracted sample size, year(s) over which the data were gathered, species, location of study, migratory distance, and type of fitness metric (breeding success or survival). Means and standard deviations were derived from raw data where these were given, and were otherwise were model-predicted (from models fitted to raw data – see

Inclusion criteria). In instances where standard deviations were missing, we calculated these from standard errors or confidence intervals; bounded data were logit-transformed prior to these calculations. Where data were presented only in graphical format, we used digitising software (WebPlotDigitizer v. 4.1 (Rohatgi, 2018)) to extract these. Means, standard errors and sample sizes were then used to calculate Hedges' *d* standardised mean difference as a measure of effect size (Appendix S2.1) (Hedges, 1981; Hillebrand & Gurevitch, 2016) using the 'metafor' package in R (Viechtbauer, 2010). We arbitrarily assigned effect sizes positive (>0) when resident individuals showed a fitness benefit, and negative (<0) when migrants showed a benefit. Benefits were considered as such according to the interpretations of the individual paper authors.

Various measures of biological fitness exist, with different metrics more relevant for certain taxonomic groups/ecological systems than others. Indices of fitness were classed as pertaining either to breeding success (e.g. clutch size, offspring survival) or to survival (absolute survival, growth rate) (see Table S2.1).

Meta-analysis

We obtained overall predicted mean effect sizes (d) and their associated within-study variance (ψ) using meta-analytic random effects models via maximum likelihood estimation, weighting effect sizes by their inverse variance (1/ψ), a metric of precision/statistical power. We considered the resulting mean effect sizes as significant if the 95% confidence intervals did not include zero. As individual papers frequently yielded multiple effect sizes, we included 'study' as a random effect to account for within-study non-independence (Mengersen et al., 2013). Even within studies, the methods and systems associated with each effect size were not identical, so the individual identity (ID) of each effect size was also included as a random effect (Viechtbauer, 2010). We assessed the presence of heterogeneity using Cochran's Q test, a significant result of which indicates that variation between effect sizes is greater than the expected result of chance sampling variability (Viechtbauer, 2007). We created models for each taxonomic group individually (bird, fish, herpetofauna and mammal), as well as across all species.

Meta-regression

To explore causes of heterogeneity and assess the influence of ecological predictors on the relative benefits of residency, we then added moderators (equivalent to fixed effects) to a meta-analytic random effects model, with taxonomic group as an additional random effect.

The response variable in these models was again the standardized effect size (d), representing study-observed fitness benefit of residency over migration. We tested the influence of three moderators: latitude, migratory distance and type of fitness metric. Latitude was the approximate latitude of area shared by migrants and residents – i.e. the breeding ground if non-breeding partial migrants and the wintering ground if breeding partial migrants. The distance moderator was the natural log (to achieve a normal distribution) of the one-way distance residents 'saved' by not migrating. In cases where residents were truly resident (n = 109), this was simply equal to the distance travelled by migrants. In cases where 'residents' were in fact short-distance migrants being contrasted with long-distance migrants (n = 20), the 'distance saved' was the difference in distance travelled. Type of fitness metric was a two-level categorical predictor based on whether the fitness measure related to survival or to breeding success (Table S2.1). Continuous moderators (latitude and distance) were scaled and centred prior to analysis.

We followed an information theoretic approach to assess the influence of moderators, in which we fitted random effects models with all possible combinations of the main effects. We also considered the potential influence of two-way interactions, but found these to be unimportant and excluded these from further analysis. This resulted in a candidate set of eight models. We used Akaike's Information Criterion adjusted for small sample size (AICc) to compare model fit, and used the 'glmulti' package (Calcagno & de Mazancourt, 2010) to average over models in each candidate set within two AICc units of the best-ranked model to obtain AICc-weighted average coefficients and predictions (Burnham & Anderson, 2002). We examined the 95% confidence intervals of model-averaged coefficients in order to assess the importance of moderators.

Study duration

We assessed the impact of study duration (number of years' data contributing to effect size estimates) on the detection of fitness differences, to evaluate whether deviations from the expected parity of fitness between residents and migrants were more likely to arise in shorter studies (and hence potentially reflect sampling artefacts). We fitted a meta-analytic random effects model to measures for all species, with study duration as a continuous moderator on standardised effect size, and inferred moderator significance from coefficient confidence intervals. Multi-level meta-analytical models carried out in 'metafor' automatically conduct an omnibus test for the significance of the influence of parameters on effect size (Viechtbauer, 2010); we also considered the results of this when interpreting the results of the model.

Publication bias and sensitivity analysis

We evaluated the dataset for publication bias – which can result in unreliable conclusions (Jennions et al., 2013) – using a modification of Egger's regression test (Sterne & Egger, 2005). We fitted a multilevel random effects model to the data with effect size standard deviation ($\sqrt{\psi}$) as a moderator; if the intercept of this model differs significantly from zero ($P<0.1$), then the data is considered biased (Habeck & Schultz, 2015; Jennions et al., 2013). As meta-analyses can be susceptible to the effects of outlying datapoints (Viechtbauer & Cheung, 2010), we assessed the sensitivity of our results. Following (Habeck & Schultz, 2015), we classified any effect size with a hat value (a measure of leverage: the influence of observed values on fitted values) of more than double the mean hat value of the dataset *and* standardised residuals greater than ± 3 as an influential outlier (Stevens, 1984). Where such outliers existed, we re-ran the analyses without them to assess their influence on our results. Although a common approach in meta-analyses, weighting by inverse variance has recently been argued to result in biased results in some instances (Hamman et al., 2018). We therefore also ran all analyses weighting by sample size, but found no difference in our results. We therefore report results from the inverse variance weighted models in the remainder of the paper.

Unless stated otherwise, results given are model-predicted standardised mean effect sizes (d) and associated 95% confidence intervals. All statistical analyses were carried out in R version 3.4.2 (R Core Development Team, 2018).

2.3 RESULTS

Of 2939 studies found in the systematic literature search, 23 fulfilled all inclusion criteria and contained suitable information for meta-analysis. We extracted 129 fitness measures from these 23 studies, representing data from 18 species spread over twelve orders. Data relating to species from the order Passeriformes (perching birds) accounted for 44% (n=57) of all effect sizes extracted. The dataset encompassed studies from twelve different countries, of which all but one (the Republic of Seychelles, contributing five datapoints) were in the northern hemisphere. Years of data collection spanned 38 years (1976 to 2013), but there was a strong skew towards more recent studies, with 84% of effect sizes collected between 2000 and 2013 (Figures S2.1–S2.3). Of these effect sizes, 73% (n=94) reported higher fitness in residents, 22% (n=28) reported higher fitness in migrants and 5% (n=7) as being equal.

Meta-regression

For meta-regression models fitted to all measures (n=129), model selection revealed metric-type to be an important predictor of whether either migratory strategy was advantageous, with residency yielding benefits for survival but not breeding success metrics (model-averaged coefficient estimate: 0.81, CIs: 0.17, 1.44) (Figure 2.1, Tables 2.2 and 2.3). Neither latitude nor migratory distance emerged as important predictors of strategy benefits (model-averaged coefficient estimates – latitude: -0.05, CIs: -0.24, 0.15, distance: 0.03, CIs: -0.12, 0.17) (Table S2.2).

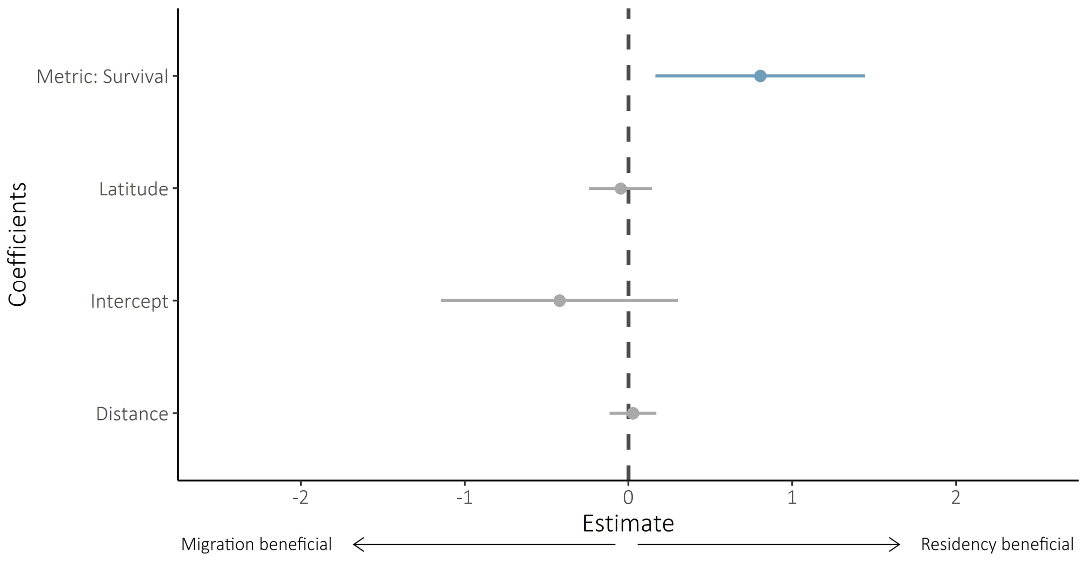

Figure 2.1 – Model-averaged coefficient estimates for fitness measures (n=129). Positive estimates indicate a benefit to residency, negative values indicate a benefit to migration. Error bars represent 95% confidence intervals. Confidence intervals of blue points exclude zero, those of grey points include zero

Table 2.2 – Model-averaged coefficients from models fitted to dataset of effect sizes (n=129) within two AICc units of the top model (n=3) showing influence of moderator variables on standardised effect size.

Moderator	Estimate	Unconditional variance	n models	Importance	L95%	U95%
Distance	0.03	0.01	1	0.21	-0.12	0.17
Latitude	-0.05	0.01	1	0.26	-0.24	0.15
Intercept	-0.42	0.14	3	1	-1.15	0.30
Metric: survival	**0.81**	**0.11**	**3**	**1**	**0.17**	**1.44**

Table 2.3 – Candidate models fitted to dataset of effect sizes (n=129) ranked by AICc.

Model	AICc	Δ AICc	Weights
d ~ 1 + Metric type	401.80	0	0.38
d ~ 1 + Metric type + Latitude	403.24	1.44	0.19
d ~ 1 + Metric type + Distance	403.69	1.89	0.15
d ~ 1 + Metric type + Latitude + Distance	404.11	2.31	0.12
d ~ 1	405.48	3.67	0.06
d ~ 1 + Latitude + Distance	406.56	4.76	0.04
d ~ 1 + Distance	406.59	4.79	0.03
d ~ 1 + Latitude	407.02	5.21	0.03

Individual taxonomic group models

Across all fitness measures for all species (n=129), we found no significant difference in fitness for migrants or residents (d = 0.20, CIs: -0.27, 0.66) (Figure 2.2). However, there were differences within taxonomic groups: residency conferred fitness benefits for birds (d = 0.55, CIs: 0.06, 1.03) and herpetofauna (d = 0.35, CIs: 0.04, 0.67), while migration was beneficial to mammals (d = -0.30, CIs: -0.60, -0.01), and neither strategy conferred a fitness benefit to fish (d = -1.31, CIs: -3.68, 1.05). For all taxonomic groups barring mammals, Cochran’s Q test was significant, indicating substantial unexplained heterogeneity among effect sizes (Table S2.3).

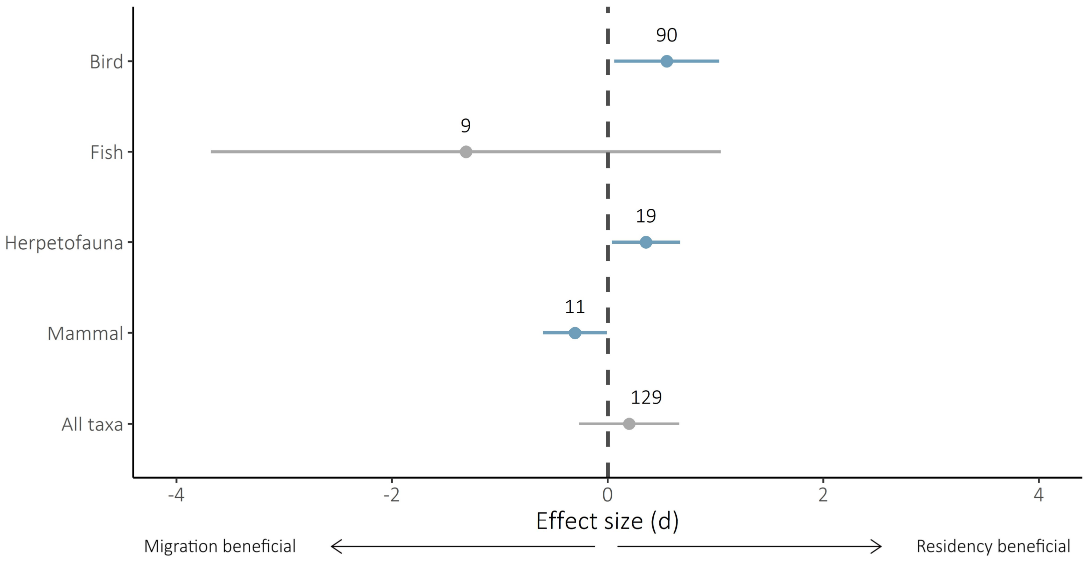

Figure 2.2 – Effect sizes (d) predicted by individual meta-analytic random effects models fitted to taxonomic subsets of all fitness measures (n=129). Effect sizes greater than zero (dashed no-effect line) indicate a benefit to residency, effect size values below zero indicate a benefit to migration. Error bars represent 95% confidence intervals. Confidence intervals of blue points exclude zero, those of grey points include zero.

Study duration and publication bias

Mean benefits of residency over migration increased with the number of years over which effect sizes were calculated (coefficient estimate: 0.09, CIs: 0.02, 0.28, QM *P*-value: 0.0049) (Figure 2.3). Among models that found a significant effect of migratory strategy on fitness, only the herpetofauna subset showed any evidence of publication bias (intercept *P*-value: 0.0113) (Table S2.4). This was, however, the group with the fewest studies contributing data, and Egger’s test is potentially unreliable in cases with few studies (Cochrane Collaboration 2011). Sensitivity analysis did not reveal any influential outliers in the dataset (Figure S2.4).

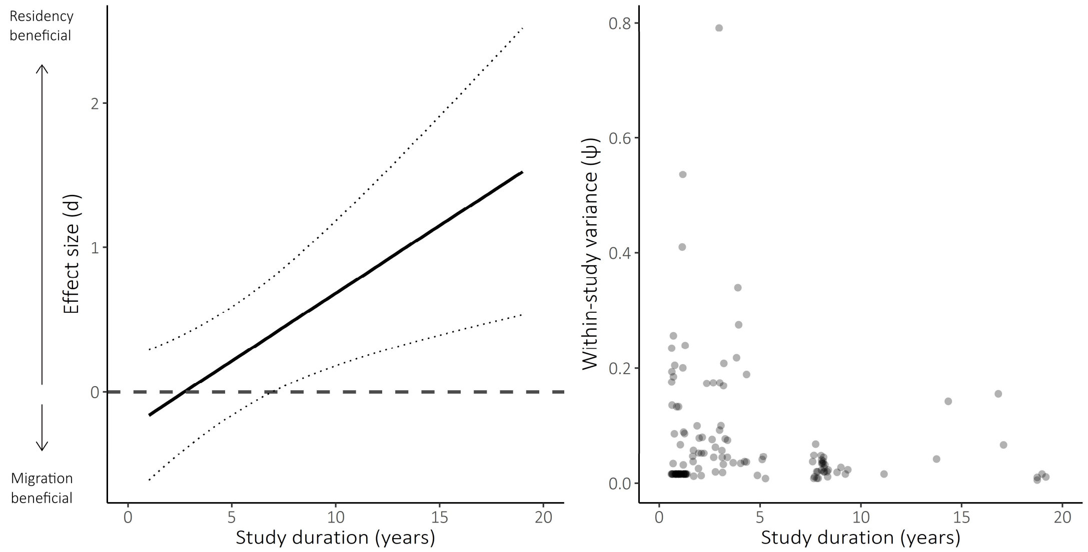

Figure 2.3 – LEFT: Predicted effect of study duration on effect size (d) for fitness measures of all species (n=129). Positive effect size values indicate a benefit to residency, negative values indicate a benefit to migration. Dotted lines indicate 95% confidence intervals. RIGHT: Raw values of effect size variance varying with study duration.

2.4 DISCUSSION

Little is known about the fitness balances of migratory strategies necessary for the evolutionary maintenance of partial migration, or the extent to which global environmental change may be altering this balance through differential impacts on migratory individuals. We provide evidence that many partially migratory populations studied in recent decades show greater fitness in resident individuals, with these benefits generally relating to survival rather than breeding success. These results are contrary to predictions surrounding the ontogeny of migratory behaviours (Chapman et al., 2011b; Lundberg, 1987), but are in line with predictions relating to the impacts of recent anthropogenic change on the survival of migratory individuals (Berthold, 2001). The presence of residual heterogeneity in all models indicates that additional unexplored environmental factors may also be influencing effect sizes.

Survival benefits of residency

Seasonal variability is considered one of the main drivers of migration, where migration may have evolved as a means of enhancing survival by allowing individuals to escape unfavourable conditions (Lundberg, 1987). This meta-analysis provides evidence that residency, rather than migration, confers a survival benefit – a result obtained from a synthesis of data gathered over the last four decades, a time marked by the cumulative impacts of increasing anthropogenic environmental change (IPCC, 2013). Changes in seasonality – particularly warmer winters in the Northern Hemisphere (IPCC, 2013) – could plausibly alter the fitness costs associated with enduring a (formerly) harsh winter or undertaking migration (Berthold, 2001, 2003). Milder winters (Nilsson et al., 2006) and year-round availability of artificial food sources (see Satterfield *et al*., 2018) may render it unnecessary to undergo the costs of migration to escape unfavourable conditions, while advancing spring temperatures also favour residents, as they are less likely than migrants to suffer phenological mismatches (Pulido & Berthold, 2010). By forgoing migration, residents are better able to exploit earlier optimal conditions, on which migrants may miss out if unable to advance sufficiently their spring arrival (Møller et al., 2008). Residents are also in a better position than migrants to react to environmental cues on the breeding grounds (Cobben & van Noordwijk, 2017; Visser et al., 2004). Simultaneously, anthropogenic activity may be making migratory journeys increasingly hazardous. Migratory individuals' exposure to and reliance on a greater range of resources and geographic regions puts them at greater risk to the dangers of an increasingly unpredictable world (Gilroy et al., 2016; Vickery et al., 2014). The predicted increase in extreme weather events brought about by climate warming – notably droughts at low latitudes – may be particularly detrimental to migratory species (IPCC, 2013; Robinson et al., 2009). Increasing infrastructure and land-use change may also add to mortality risks associated with migration. The construction of power lines, for instance, is associated with greater mortality in migrating birds (Palacín et al., 2017), while agricultural intensification, damming and hunting are all thought to have negative consequences for migratory birds (Adams et al., 2014; Vickery et al., 2014).

Various other mechanisms could also explain the observed survival benefit of residency over migration. For instance, higher rates of emigration among migrants compared to residents could artificially increase 'apparent survival' in residents, such that our observed results reflect sampling error. However, as migrants tend to show high philopatry (Newton, 2008), it seems unlikely that this would be the sole driver of our results. Alternatively, as discussed above, the observed survival benefits of residency could reflect other individual traits such as sex, body size, and age, if these traits are themselves linked to migratory strategy (Chapman et al., 2011b). However, for this to explain a pervasive survival benefit of residency across studies, the underlying trait linkages would have to be common across species, which seems unlikely. A further possibility is that parity of fitness is not in fact required for partial migration to persist over evolutionary time. It is possible for some behavioural polymorphisms to be maintained despite differences in mean fitness, if there is a high variability associated with the more beneficial strategy (Calsbeek et al., 2002). If, within a population, residency offers on average a greater survival benefit, but is a high-risk strategy associated with a large variance in survival, a migratory strategy could also persist within the population despite lower mean fitness. Nevertheless, a number of studies have reported that residency is increasing in certain species (Hebblewhite & Merrill, 2011; Meller et al., 2016; Van Vliet et al., 2009), and migration distances declining (Visser et al., 2009) (Berthold, 2001; Meller et al., 2016) – findings which lend credence to an association between differential strategy fitness and recent anthropogenic change. Given the widespread incidence of partial migration across ecosystems, it is likely that responses to climate changes will be far from uniform across species (Chapman et al., 2011b; Griswold et al., 2011), and not necessarily straightforward (Nilsson et al., 2006).

We did not find a benefit to breeding success of residency, contrary to expectations based on their presumed greater capacity to respond to phenological mismatches and achieve early access to breeding resources (Pulido & Berthold, 2010). Theoretical models indicate that, at least for populations that share a breeding range, improved wintering conditions in the breeding range can result in better productivity for both migrants and residents, in addition to improved survival for residents (Griswold et al., 2011). If this were the case, we would not expect to detect breeding measures having an influence on the relative benefits of migratory strategies, as these would be balanced. Rather, this would simply contribute to a survival benefit of residency.

Latitude and migratory distance

Although the direction of the model-averaged coefficient estimates for latitude and migratory distance were in line with our predictions (that residency should be increasingly beneficial in long-distance and low-latitude systems), both were close to zero and neither were statistically important (Figure 2.1, Table 2.1), indicating a high degree of uncertainty in these trends. The lack of a strong signal for the influence of migratory distance on the fitness returns of residency may be related to our controlling for taxonomic group. General between-taxa differences in locomotive efficiency, body size and fluid dynamics (Alerstam et al., 2003; Alexander, 2002) mean different migratory distances are differentially adaptive between – and accordingly correlated with – different taxonomic groups. For the fitness measures included in our meta-regression, mean (±SD) migratory distance for birds was 978.11 km (±1915.53), while for fish, herpetofauna and mammals was 17.77 km (±19.1), 0.69 km (±0.81) and 38.22 km (±4.38) respectively. The lack of distance effect may also indicate that the apparent survival benefit to residency is driven by increasingly mild wintering conditions experienced by residents, rather than by greater mortality risks associated with migration.

We predicted that the lesser seasonality associated with low latitudes would lead to lower selection pressures on migration, and therefore a more delicate balance between strategies, more likely to shift in response to environmental change. However, higher latitudes are currently seeing a greater impact of climate change (IPCC, 2013), leading to the opposing pressures of traditionally higher seasonality alongside a greater decrease in seasonality brought about by climate change – the individual effects of which it is not possible to tease apart here.

Taxonomic differences

Our results suggest the within-taxonomic group variability in our data is less marked than the between-group differences; in addition to the stark differences in migratory distance between taxonomic groups, between-taxa variances in body size, general physiology and life histories may also be driving differences in relative fitness benefits and susceptibility to the effects of climate change. Altitudinal migrants, such as in the ungulate populations which comprised our mammal data, may benefit from climate change-induced longer vegetation growth periods, resulting in comparatively more forage of higher nutritional value in the higher-altitude migrant ranges (Rolandsen et al., 2017). Differences between taxa may also not necessarily be down to direct taxonomic differences; we did not, for instance, distinguish between different models of partial migration, which differ according to which season (breeding or non-breeding) residents and migrants are allopatric (Chapman et al., 2011b). These different models may result in different benefits to either strategy. A reduction in resource-variability at a shared non-breeding range is predicted to improve resident breeding success, while the same for a shared breeding range should bring about higher survival in residents (Griswold et al., 2011). Non-breeding partial migration was much more common in our data for birds, fish and herpetofauna, while all mammal fitness measures were from breeding partial migrants. Additionally, differences between the highly variable migratory systems found in fish – freshwater/marine/estuarine, catadromous/anadromous – may go some way towards explaining variance within that group. Indeed, there is an argument to move away from traditional dichotomous models of partial migration in general, which – while useful – may ultimately be more simplistic than realistic (Reid et al., 2018).

Study duration

That we found residency to be increasingly beneficial as individual study duration suggests that deviations from parity in fitness benefits detected in our meta-analyses were unlikely to be due to sampling artefacts. Furthermore, if individual fitness benefits were balanced between strategies through facultative migratory tendency – with individuals switching strategy between years – we would expect longer-running studies to be more likely to find parity between strategies, but we find the opposite result. This also implies that short-term studies may be inadequate as a means of uncovering differences in demographic parameters between migratory strategies. Similar results have been found by Pearce-Higgins and colleagues (Pearce-Higgins et al., 2015), whose recommendations concerning the importance of long-term studies as a means of determining impacts of climate change we echo.

Future recommendations

This study represents a step towards a more comprehensive understanding of migratory strategies within partial migrants. The results of this meta-analysis are in part a reflection of the nature of the available literature the concerning partial migration. Taxonomic biases, particularly the ornithocentrism in animal migration literature found elsewhere (Bauer et al., 2009), are partly a result of migratory behaviour being more common in certain groups, and partly a reflection of feasibility: species more readily tracked and monitored are more likely to be the subject of studies relevant to this topic. Similarly, while the prevalence in this study of data from the northern hemisphere is in part a product of a more general bias found across ecological literature (Amano & Sutherland, 2013; Martin et al., 2012), there is also greater prevalence of terrestrial migratory species in the northern hemisphere due to a combination of high seasonal variability and greater land mass (Somveille et al., 2015).

That we had a strong temporal skew towards more recent years (Figure S2.3) is unsurprising; as well as the increase in ecological research over time (Hillebrand & Gurevitch, 2016), partial migration as a topic has become more prominent in recent years, and rendered more feasible as tracking methodologies become more advanced. The study is subject to certain practicalities of meta-analyses – such as the necessary exclusion of studies not reporting the required statistics for calculation of our chosen standardised effect size. Statistical rigour and quality of reporting has improved with time (Hillebrand & Gurevitch, 2016) – making recent papers more suitable for inclusion in meta-analyses. The continuation of these trends may better enable future temporal analyses of relative fitness benefits, which may shed more light on responses to increasing anthropogenic influence.

2.5 CONCLUSIONS

We provide evidence that residency results in higher fitness than migration in certain partially migratory populations, and that residency confers a greater benefit to survival than to breeding success. While not conclusive, this accords with the prediction that global environmental change may be altering the fitness balance in favour of residency (Berthold, 2001), through milder climatic conditions lessening pressures to migrate, and increased mortality risks associated with migration. If accurate, this indicates that anthropogenic change may alter selection pressures to increasingly promote residency – or, indeed, promote plasticity in migratory strategy in response to environmental unpredictability (Reid et al., 2018). Despite the growing literature devoted to partial migration, only twenty-three studies were ultimately suitable for inclusion in this meta-analysis. Continued research, especially examining direct fitness measures, coupled with improved/more standardised reporting (sample sizes, measures of variance), will facilitate deeper investigation into the topic, while our results concerning study duration point to the value of long-term studies. Climate warming is predicted to continue at an unprecedented rate, with significant implications for global biodiversity (IPCC, 2013; Parmesan, 2006). Understanding whether migratory species may be able to mediate its negative consequences – and the demographic processes through which this may occur – is critical for effective conservation measures (Newson et al., 2009), while also providing an opportunity to shed light on the evolution of migratory behaviours.

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Chapter 2 Supplementary Materials

Table S2.1 Classification of fitness measures relating to survival or breeding success

Appendix S2.1 Hedges' *d*

Figure S2.1 Effect sizes by taxonomic group

Figure S2.2 Effect sizes by country

Figure S2.3 Effect sizes by year

Table S2.2 Model summaries: meta-regression

Table S2.3 Model summaries: individual meta-analytic models

Table S2.4 Egger's regression test

Figure S2.4 Sensitivity analysis

Table S2.1 – *Breakdown of direct fitness measures encountered classified according to survival or breeding success. We classified metrics as directly or indirectly indicative of fitness, calculating effect sizes only for measures considered direct. Survival metrics excluded for being too indirect: body condition, body fat, body height, body mass, body size, food availability, growth efficiency, gut fullness, haematocrit, immune system function, and oxidative stress. Breeding metrics excluded for being too indirect: egg size, offspring size, breeding phenology*

Fitness measure	Metric-type	n effect sizes calculated
Absolute survival	Survival	66
Breeding lifespan	Survival	1
Individual growth rate	Survival	8
Breeding attempts	Breeding	5
Breeding frequency	Breeding	1
Clutch frequency	Breeding	3
Clutch size	Breeding	9
Surviving offspring	Breeding	23
Success	Breeding	13

Appendix S2.1 Hedges' *d*

Hedges' *d* is calculated using the formula:

$$d = \frac{(\overline{x}_T - \overline{x}_C)}{S} \times J$$

Where $\overline{x}_T$ is the mean treatment response and $\overline{x}_C$ is the mean control response. S and J represent pooled standard deviation and a bias correction factor respectively, and are given by the formulae:

$$S = \sqrt{\frac{(n_T - 1){SD_T}^2 + (n_C - 1){SD_C}^2}{n_T + n_C - 2}}$$

$$J = \frac{\Gamma \frac{n_T + n_C - 2}{2}}{\Gamma \sqrt{\frac{n_T + n_C - 2}{2}} \; \frac{n_T + n_C - 3}{2}}$$

where n_T is the treatment sample size, n_C the control sample size, SD_T is the standard deviation about the treatment mean and SD_C is the standard deviation about the control mean.

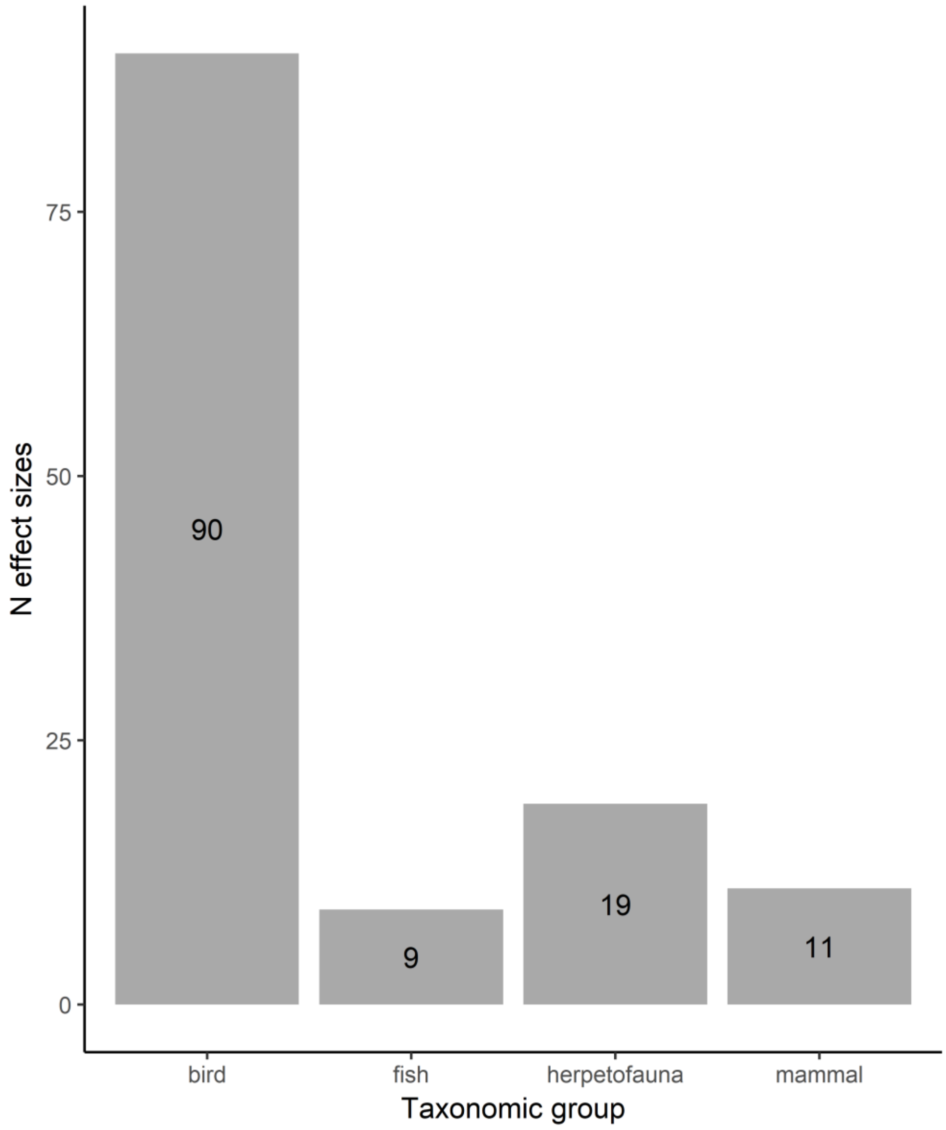

Figure S2.1 – Breakdown of effect sizes by taxonomic group.

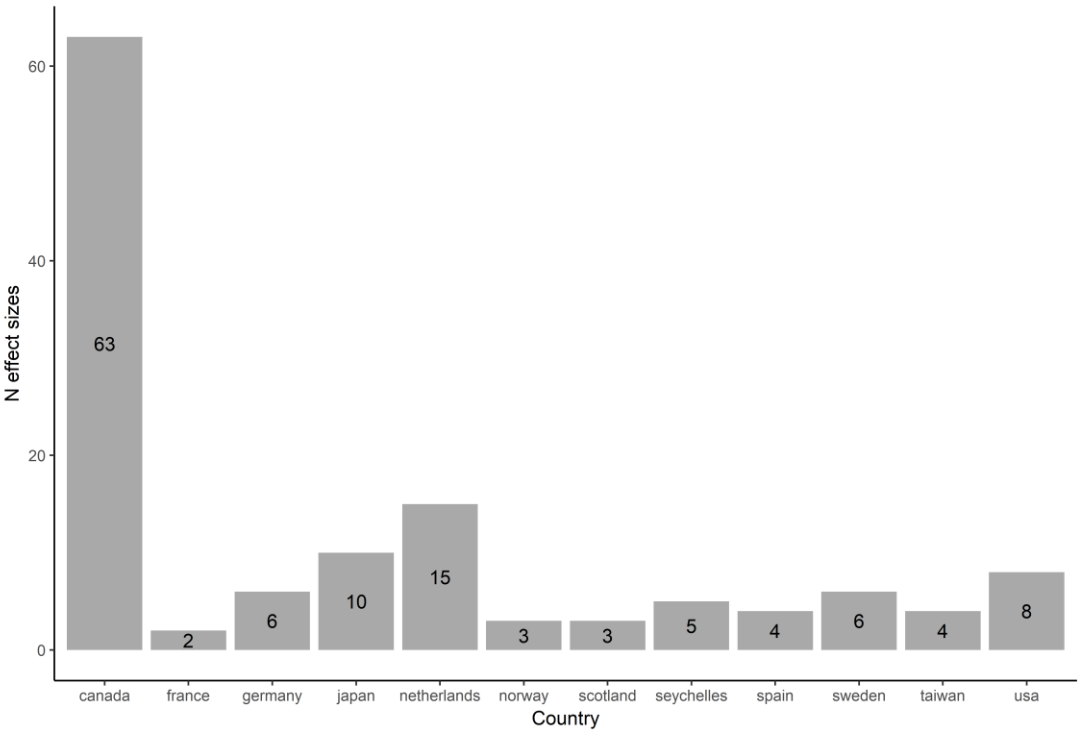

Figure S2.2 – Breakdown of effect sizes by country in which the study took place.

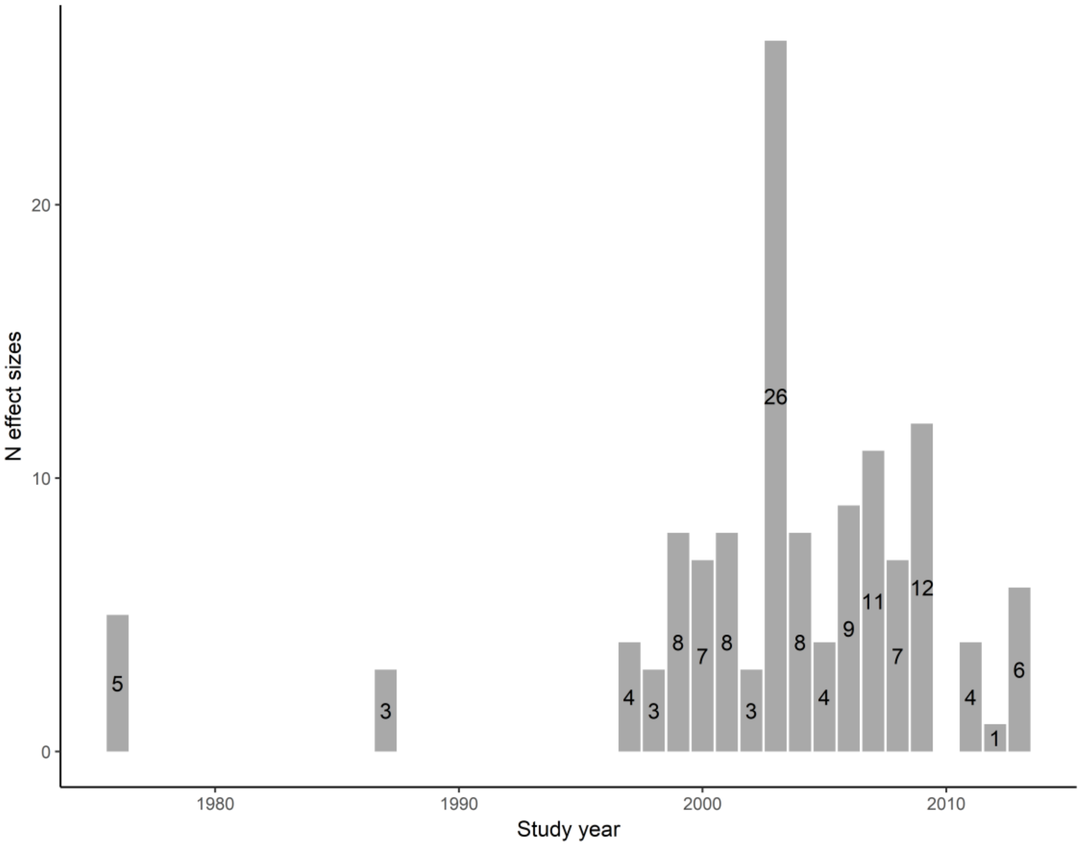

Figure S2.3 – Breakdown of effect sizes by year in which data were collected. Median year of data collection is used for effect sizes calculated over multiple years.

Table S2.2 – Coefficient estimates [95% confidence intervals] and model statistics for meta-regression models over which averaged coefficients were obtained. All models included effect size identity nested within study identity and taxonomic group as random effects.

	Model structure			Model statistics			
Model rank	Metric: survival	Latitude	Distance	Heterogeneity	Omnibus moderator test	AICc	Weight
1	0.81 [0.17, 1.45]	-	-	QE = 5207.00 *P* < 0.001	QM = 6.12 *P* = 0.013	401.80	0.38
2	0.81 [0.18, 1.45]	-0.18 [-0.59, 0.22]	-	QE = 5206.74 *P* < 0.001	QM = 7.05 *P* = 0.030	403.24	0.19
3	0.78 [0.13, 1.42]	-	0.13 [-0.30, 0.57]	QE = 4315.52 *P* < 0.001	QM = 6.45 *P* = 0.040	403.69	0.15

Table S2.3 – Results of individual meta-analytic models estimating mean effect size. Negative mean effect sizes indicate a possible benefit of migration; positive mean effect sizes indicate a possible benefit of residency. Models with significant mean effect sizes are highlighted in bold. All models included effect size identity nested within study identity as random effects.

Dataset	n effect sizes	Estimated mean effect size [95% CI]	*P*-value	Heterogeneity statistics
All	129	0.12 [-0.27, 0.66]	0.400	Q = 5405.09 *P* < 0.001
Birds	**90**	**0.55** **[0.06, 1.03]**	**0.028**	Q = 3799.12 *P* < 0.001
Fish	9	-1.31 [-3.68, 1.05]	0.276	Q = 835.18 *P* < 0.001
Herpetofauna	**19**	**0.35** **[0.04, 0.67]**	**0.028**	Q = 125.96 *P* < 0.001
Mammals	**11**	**-0.30** **[-0.60, -0.01]**	**0.043**	Q = 59.38 *P* < 0.001

*Table S2.4 – Model results for Egger's regression test for publication bias on the main dataset and taxonomic subsets thereof. Significant effects (*P *< 0.10) are highlighted in bold.*

Dataset	n effect sizes	Intercept	Lower 95% CI	Upper 95% CI	*P*-value
All	**129**	**0.68**	**0.03**	**1.33**	**0.040**
Birds	90	0.20	-0.45	0.84	0.551
Fish	**9**	**4.66**	**-0.42**	**9.74**	**0.072**
Herpetofauna	**19**	**0.93**	**0.21**	**1.65**	**0.011**
Mammals	11	-0.18	-1.29	0.93	0.752

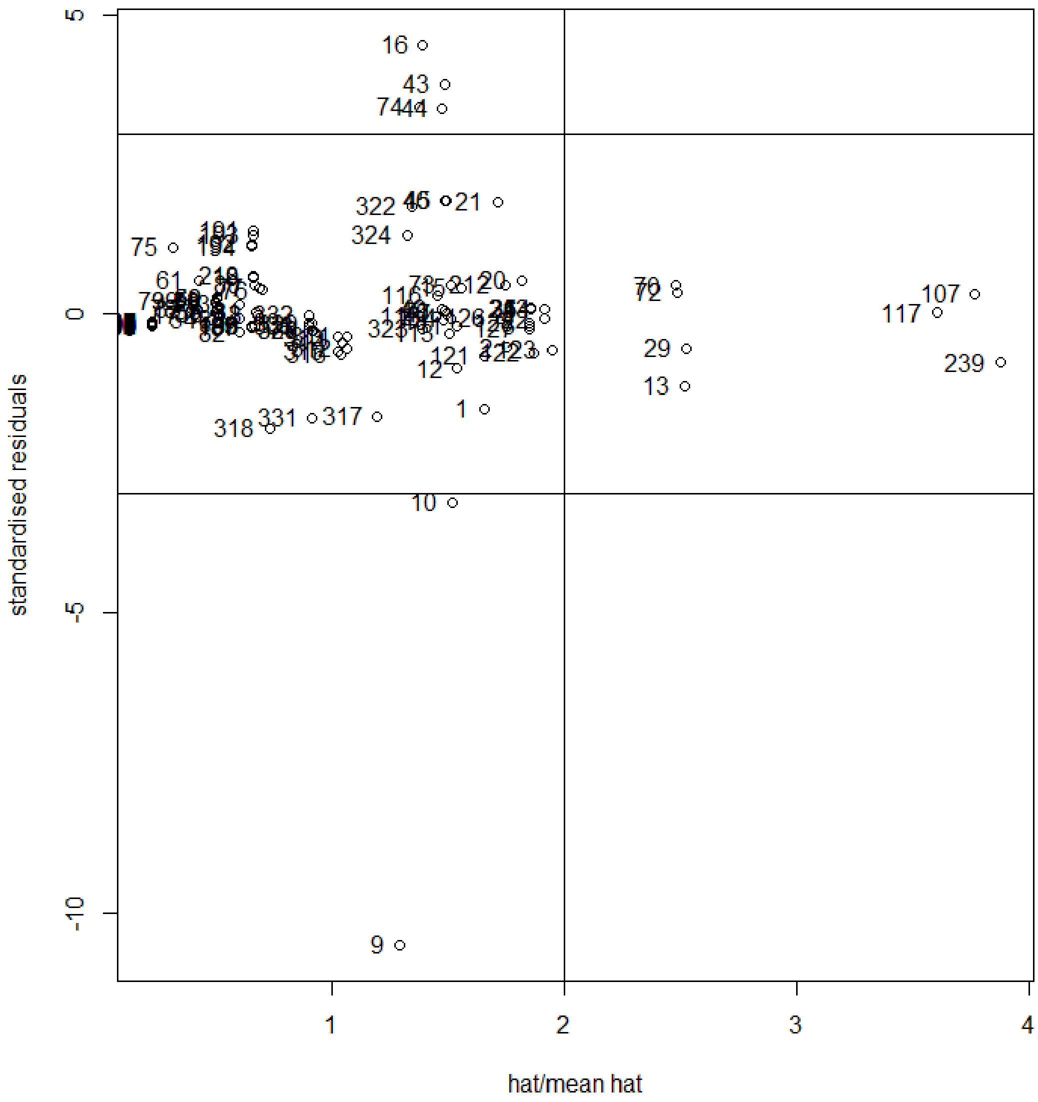

Figure S2.4 – Sensitivity analysis plot for all effect sizes (n=129). No points were considered influential outliers – these would fall in the top or bottom right hand sections of the plot, indicating an effect size with both a hat value of more than twice the mean hat value (vertical line) and a standardised residual of more than ±3 (horizontal lines).

Carryover effects of long-distance avian migration are weaker than effects of breeding environment in a partially migratory bird

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AUTHOR CONTRIBUTIONS

All authors were involved in designing the study. CB, JG and JMG collected the data, supported by IC and JB. CB conducted the statistical analyses and wrote the manuscript. AF and JG provided statistical advice. AM conducted the isotope-ratio mass spectrometry. All authors critically revised the manuscript, contributed to interpreting results and gave final approval for publication.

PUBLICATION

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ABSTRACT

Migration may expose individuals to a wide range of increasing anthropogenic threats. In addition to direct mortality effects, this exposure may influence post-migratory reproductive fitness. Partial migration – where a population comprises migrants and residents – represents a powerful opportunity to explore carryover effects of migration. Studies of partial migration in birds typically examine short-distance systems; here we studied an unusual system where residents breed in mixed colonies alongside long-distance trans-Saharan migrants (lesser kestrels (*Falco naumanni*) in Spain). Combining geolocator data, stable isotope analysis and resighting data, we examined the effects of this stark difference in migratory strategy on body condition, breeding phenology and breeding success. We monitored four colonies in two regions of southern Spain for five consecutive years (2014–2018), yielding 1962 captures, determining migratory strategy for 141 adult bird-years. Despite a 3000-kilometre difference in distance travelled, we find no effect of strategy on breeding parameters. We find weak evidence for a short-term negative carryover effect of migration on body condition, but this was only apparent in the breeding region with lower primary productivity. Our results indicate that carryover effects of even highly divergent migratory strategies may be minimal relative to effects of conditions experienced on breeding grounds.

3.1 INTRODUCTION

Migration represents a significant seasonal undertaking with potential for strong carryover effects (Norris, 2005; Ockendon et al., 2013). Environmental conditions during spring migration can influence arrival time and body condition at the breeding grounds, with consequences for subsequent breeding success. Poor body condition following migration can lead to reduced resource investment in reproduction (Lehikoinen et al., 2006), or later arrival on breeding grounds due to less time-efficient migration (Bearhop et al., 2004). Breeding success is generally lower for later breeding attempts (Rowe et al., 1994), via (likely interacting) mechanisms relating to seasonal deterioration in conditions, correlates of individual quality, and lost opportunity for additional breeding attempts (Morrison et al., 2019). Climatic conditions experienced in the winter (Gill et al., 2001) and while on migration (Finch et al., 2014) can influence breeding phenology, while stresses experienced on spring staging grounds has been linked to subsequent lower breeding success (Legagneux et al., 2012).

Given the potential for migratory carryover effects to be cumulative, between-individual differences in the magnitude of carryover effects might be expected in populations where individuals differ markedly in migratory behaviour. Migratory routes, distances and timings can vary significantly within populations (Newton, 2008), sometimes leading to significant variation in survival (Lok et al., 2015). Such differences may also apply to non-lethal carryover effects; larger migratory distances have been linked to later arrival on breeding grounds (Bregnballe et al., 2006) and lower breeding success (Hötker, 2002). Large differences in the magnitude of migratory movement within a population may therefore be expected to precipitate significant differences in subsequent fitness.

Partial migration, where migrant and non-migrant individuals exist within the same population (Chapman et al., 2011a; Lundberg, 1988), provides a powerful natural experiment to explore these carryover effects, by comparing fitness parameters of migrants and residents (Buchan et al., 2020). Although parity in fitness under both strategies is necessary for the evolutionary maintenance of partial migration (Lundberg, 1988) (especially if migratory strategy is heritable (Mueller et al., 2011)), it is hypothesised that this balance is maintained through trade-offs where migratory costs that reduce fitness in one parameter (survival or breeding success) are compensated by higher fitness in another (Griswold et al., 2010; Lundberg, 1988). For instance, residents may suffer higher energetic costs of enduring colder climates and lower food availability, but enjoy higher reproductive success due to early access to breeding resources (Chapman et al., 2011b; Kokko, 2011). We may therefore expect to see differences in carryover effects between migrants and residents across different fitness components.

Anthropogenic change may also be influencing fitness differences within long-distance partially migratory populations. Migratory individuals can face greater exposure to threats (e.g. land-use change, extreme climatic events, novel infrastructure) than residents, which may interact and accumulate along migratory routes (Newton, 2004; Robinson et al., 2009). Simultaneously, climate warming and accompanying decreases in seasonality – at least in the northern hemisphere (IPCC, 2013) – may favour residency (Berthold, 2003). Increasingly clement wintering conditions may also create phenological mismatches that disproportionately affect longer-distance migrants (Møller et al., 2008). If anthropogenic change leads to a breakdown in the parity of fitness between migrants and residents it could lead to rapid changes in migratory behaviour, potentially ultimately leading to the disappearancae of migration (de Zoeten & Pulido, 2020). In light of the potential for cumulative carryover effects to manifest in the subsequent breeding season, we might expect long-distance migrants in partially migratory populations to be in worse condition than residents, breeding later and with lower reproductive fitness.

Most studies of within-population partial migration in birds are in short-distance systems (Buchan et al., 2020). Here we examine carryover effects in an unusual example of long-distance partial migration (lesser kestrels, *Falco naumanni*), where non-migratory individuals are fully resident in the Spanish breeding grounds throughout the year, while migrants undertake a c. 3000-km trans-Saharan migration, such that individuals may be exposed to very different costs between the two strategies. We combine geolocator tracking, ring-resighting and stable isotope analysis to determine migratory strategies of individuals, and examine effects on body condition and breeding parameters. We hypothesise that stark differences in migratory strategy will lead to measurable differences in each of these parameters, reflecting the contrasting winter conditions experienced. We additionally compare the strengths of these differences relative to colony-specific differences in breeding environment.

3.2 METHODS

All bird handling and fieldwork protocols were conducted according to the relevant national and institutional regulations on animal welfare, and were approved by the Junta de Andalucía: Dirección General de Gestión del Medio Natural y Espacios Protegidos (Ntra. Ref: 2016107300003028/IRM/MDGC/mes) and the University of East Anglia Animal Welfare and Ethical Review Board.

Study system

The lesser kestrel is a small, colonial raptor (Negro, 1997), breeding largely in abandoned agricultural structures or in towns (Bustamante, 1997), with a largely insectivorous diet (Lepley et al., 2000). We studied four colonies in two regions of Andalucía, southern Spain: three in the province of Seville, breeding in abandoned agricultural buildings on the border between Doñana National Park and surrounding arable farmland in the Guadalquivir basin (37°05'N 6°19'W), and a fourth in the province of Cádiz, breeding in a church tower in Los Barrios town (36°11'N 5°30'W).

Monitoring breeding phenology and success

We monitored breeding parameters in 2014–2018 (Seville colonies) and 2014–2017 (Cádiz colony), visiting colonies weekly to monitor all accessible cavities and collect data on nesting phenology, clutch size and fledging success (number of chicks aged >20 days per nest); chicks were also ringed and measured prior to fledging. First egg dates were either observed directly or back-calculated as 32 days prior to the first hatch date (Donázar et al., 1992). Our data indicate that wing growth of lesser kestrels is linear between the ages of 14 and 30 days, with non-linear growth likely to occur after day 30 (Figure S3.1, see also Braziotis et al., 2017; Donázar et al., 1991). If neither first egg date nor first hatch date were directly observed (n = 17 clutches), we therefore estimated these using a linear mixed-effects model of wing chord measurements against known-ages of chicks measured in 2018 (n = 96, marginal R^2 = 0.89) (see Figure S3.1). We deemed a nest successful if at least one bird reached an age greater than 20 days.

Determining migratory strategies

We used a combination of wintering observations, geolocator data, and feather isotope analysis to determine individual strategies (migrant or resident). At each colony, we captured adults via opportunistic captures during nest visits, mist-netting close to roost sites, spring-traps baited with insect or small mammal prey, and nocturnal visits to colonies. All individuals were colour-ringed, aged and sexed according to plumage features. We measured mass, wing chord and eighth descendant primary (P8) length at each capture, and collected a c. 1 cm^2 section of vane from the trailing edge of the winter-grown ninth or tenth primary (P9/P10) feather of each adult bird once per calendar year for isotope analysis. We classified migratory strategies of each individual in each year (henceforth ‘bird-years’), and related these strategies to metrics of body condition and breeding success in the following season.

Direct observations

Colonies were visited weekly during the winter (Nov–Jan) from 2013 to 2018 to identify residents through resightings. Any individual detected in Seville or Cádiz between 01 November and 15 January was considered a resident bird-year for the breeding season immediately following (date thresholds represent a two-week buffer around our earliest observations of known migratory individuals). Additionally, one bird was a confirmed migrant from an opportunistic resighting in Senegal in 2017.

Geolocators

We deployed 36 geolocators (British Antarctic Survey model Mk14, 1.5g, attached on Teflon harnesses as back mounts) during the 2014 and 2015 breeding seasons, of which 16 were subsequently recovered and 13 provided adequate data. Geolocators were pre- and post-calibrated for seven days, and analysed using the ‘FLightR’ package following (Lisovski et al., 2020; Rakhimberdiev et al., 2016). Individual twilights were excluded if light-dark transitions were erratic two hours either side of the twilight. Individuals were assumed to be resident if they showed no fixes south of 36°N between 01 November and 15 January, and migratory if they showed at least two fixes south of 23°N within that period.

Feather isotopes

We used δ^{13}C values (ratios of the stable isotopes ^{13}C to ^{12}C) of winter-grown flight feathers P9/10 (Forsman, 2006) to identify migrant individuals (see Appendix S3.1). As some individuals moult P9/P10 prior to migration (Bounas, 2019; Gilbert, 2015), birds with an Iberian isotopic signature (lower δ^{13}C values) for winter-grown feathers cannot be assumed to be resident, as they could have moulted the feather on the breeding grounds prior to migrating. We therefore only used isotope values to identify migrants, not residents.

We analysed δ^{13}C values from the feathers of 276 bird-years, to which we added isotope data from an additional 128 bird-years collected from other colonies in the same region (37°21'N 5°13'W). We classified any feather with a δ^{13}C value higher than -20 ‰ to come from a migrant individual, deeming a $\delta 1^{3}$C value of -20 ‰ a conservative buffer around the clustering of lower δ^{13}C values representing feathers grown on the breeding grounds, and excluding all known residents (Figure S3.2). This cut-off also aligns with the δ^{13}C feather isoscape for Africa created by Hobson and colleagues (Hobson et al., 2012). We expect at least 70% individuals in the study populations to be migratory (Negro et al., 1991; Tella & Forero, 2000), and this conservative cut-off likely excludes a number of migrants from our analysis, but as we were not assessing prevalence of strategies, we analysed only those individuals we could confidently classify as long-distance migrants. We also undertook a sensitivity analysis of the -20 ‰ cut-off value, running all analyses on two additional datasets, with isotope-defined migratory status created according to either a more conservative or less conservative $\delta^{13}C$ cut-off (± 0.5 ‰). Altering this value did not change our results for any analyses, indicating the results reported are robust to variations in this threshold – see Appendix S3.2.

Condition metrics

To estimate adult condition at capture, we divided mass by P8 length to distinguish dynamic body condition from structural size (Piersma & Davidson, 1991). We then developed an index of bird condition relative to the population average, controlling for sex and stage of the annual cycle, using generalised additive mixed-effect models (GAMMs) with penalised regression splines, adding bird identity as a random effect to account for recaptures (n = 566 captures across all years of data – Figure 3.1). We took the residuals from these models as our index of body condition relative to the population-wide mean condition for individuals of that sex at that date. We created GAMMs using the package ‘gamm4’ (Wood & Scheipl, 2017), with default selection of smoothing parameters. For chick condition, we again divided mass by P8 length to account for chicks having been measured at different ages, and averaged this condition across siblings to create a single mean chick condition for each brood.

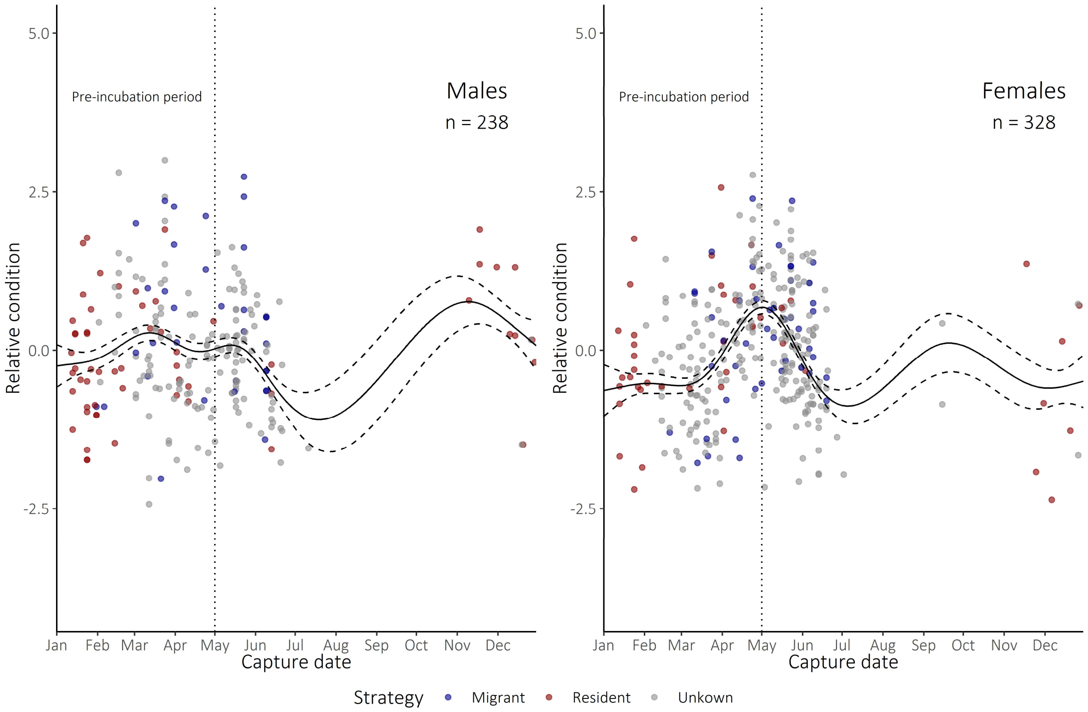

Figure 3.1 – Relative body condition (scaled mass/P8 length) of adult lesser kestrels caught throughout the year. Black lines indicate model-predicted mean condition, dashed line indicates associated standard error. Colours indicate migratory strategy during the winter preceding the breeding season in the calendar year of capture. Captures occurring prior to the date indicated by the dotted line (May 01) were used in the pre-incubation condition analysis.

Statistical analysis

For all final analyses, we excluded data from 2018, as there was an imbalance in sampling effort between the two study regions (Figure S3.3).

We modelled the relationship between relative adult body condition and migratory strategy using GLMMs with a Gaussian distribution, including bird identity as a random effect, using the package 'lme4' (Bates et al., 2015). We also included capture date, study area and sex as fixed effects, and allowed for an interaction between strategy and study area (Cádiz vs. Seville) to examine whether carryover effects differed between areas. Because short-term carryover effects of migratory strategy might be strongest immediately after pre-breeding migration, we repeated the analysis using only condition measures taken prior to the peak in mean female condition (02 May, Figure 3.1), corresponding with the onset of incubation – henceforth referred to as the 'pre-incubation period' – considering this to represent the point after which body condition becomes more strongly affected by breeding effort than by the preceding winter. We conducted a post-hoc multiple comparison test on the resulting final model, using the package 'multcomp' (Hothorn et al., 2008).

We analysed the influence of migratory strategy on breeding phenology (first egg date), clutch size, number of fledglings, nest outcome (success or failure), fledging probability (proportion of eggs successfully fledged) and chick condition. Study area was included in all models. For all productivity analyses barring chick condition, we also considered first egg date as a fixed effect, hypothesising that phenology may affect productivity. For the chick condition analysis we had a relatively small sample size (n=41, Figure S3.3), within which first egg date was confounded with study area, and was therefore excluded.

We analysed breeding parameters for all adults of known migratory strategy for which there was clutch data. For clutches where the migratory strategy of both parents was known (n=10), one parent was excluded at random to avoid duplicating these clutches in the dataset (see Figure S3.3 for sample sizes). We used generalised linear models with a Gaussian distribution for phenology and chick condition, and Poisson distribution for number of fledglings, with a log link function. For clutch size we used a Conway-Maxwell Poisson model (Rousset & Ferdy, 2014) to account for underdispersion, using automatic estimation of the under-dispersion parameter (v) (Lynch et al., 2014; Shmueli et al., 2005). We used a binomial distribution with logit link function for nest outcome, and modelled fledging probability (weighted by clutch size) using a quasibinomial distribution – to handle overdispersion (pertinent for binomial models using proportion data) – and logit link function.

In all instances, we followed a model-theoretic approach (Burnham & Anderson, 2002), creating a subset of reduced models from each global model, then ranking these by Akaike's Information Criterion adjusted for small sample size (AICc) to determine the best-fitting models, using the package 'MuMIn' (Bartoń, 2019). We used quasi-AICc (QAICc) values for the fledging probability analysis, as AIC values cannot be calculated for models with quasi-distributions. Where we had multiple competitive models (within Δ2 (Q)AICc units of the highest-ranked model), we selected the model with the fewest parameters within the Δ2 subset as our final model (Burnham & Anderson, 2002), as model-averaging is not feasible for model sets including interaction terms (Cade, 2015).

We scaled and centred all continuous variables via Z-score transformations, and carried out all analyses in R version 3.5.0 (R Core Team, 2018).

3.3 RESULTS

Determining strategies

We were able to determine the migratory strategy (migrant or resident) of 116 individuals across 151 bird-years (90 residents, 61 migrants – see Table S3.1). Of these, 107 individuals were adults, yielding 141 bird-years (81 residents, 60 migrants), which we carried forward to subsequent analyses (Figure S3.3). Contrary to previous findings (Negro et al., 1991), we found no evidence for residents being disproportionately male, with approximately balanced sex ratios in both residents (44 males, 37 females) and migrants (27 males, 33 females). Of 25 adult individuals (59 bird-years) for which we determined migratory strategy in multiple years (17 individuals for two years, seven for three years and one for four years), 21 maintained a consistent migratory strategy, three individuals switched from migrants to residents, and one individual switched from being a resident to being a migrant.

Adult body condition

Analysis of year-round condition values showed no enduring effect of migratory strategy, but did show an effect of study area (the two colony locations), indicating that birds at Cádiz were consistently in better condition than those at Seville (Figure 3.2a).

For condition values measured during the pre-incubation period (see Figure 3.1), the most parsimonious model retained the interaction between migratory strategy and study area (Figure 3.2b), indicating higher condition in residents compared to migrants in Seville. However, a post-hoc multiple comparisons test was not significant ($p=0.09$), suggesting uncertainty around this effect (Table S3.2). Regardless of strategy, birds at Cádiz were in better condition than those in Seville during the pre-incubation period ($p<0.01$, Figure 3.2b, Table S3.2).

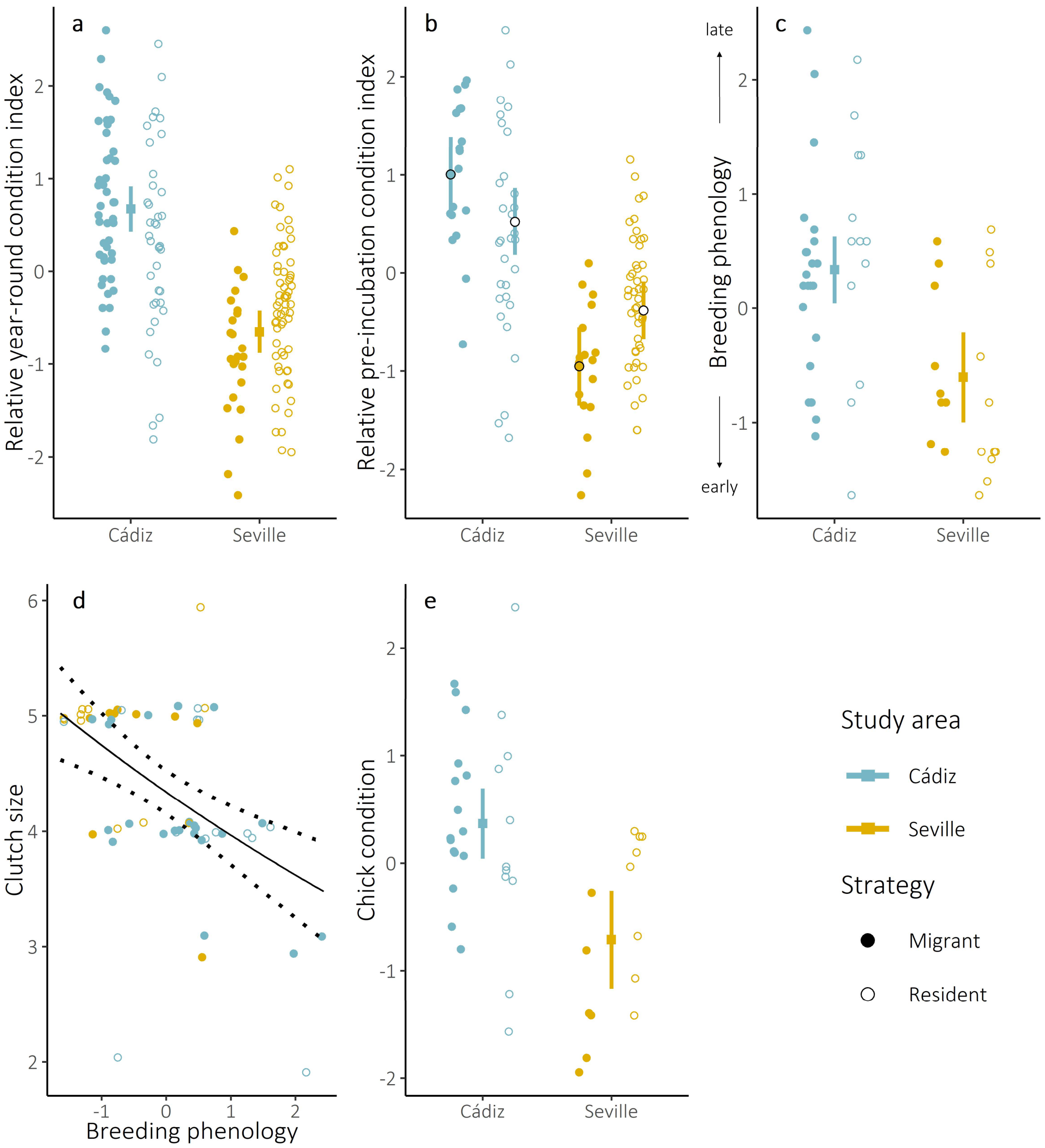

Figure 3.2 – Effects of migratory strategy, breeding site area and breeding phenology on fitness parameters, according to the final model for each analysis. (a, b): Relative year-round and pre-incubation condition of adult lesser kestrels captured in the two study areas. Migratory strategy of individual was not an important predictor of year-round condition, but was an important predictor of pre-incubation condition. (c): Breeding phenology (scaled first egg date) of lesser kestrel clutches in the two study areas. (d): Lesser kestrel clutch size did not vary with study area, but decreased over the season. (e): chick condition from lesser kestrel clutches in the two study areas. Migratory strategy of clutch parent was not an important predictor of breeding phenology, clutch size or chick condition. Points with error bars (a–c and e) or solid line with surrounding dashed lines (d) represent model-predicted means and associated 95% confidence intervals. All continuous variables were scaled and centred via z-score transformation.

Breeding success

The most parsimonious model for breeding phenology (first egg date) retained study area as the sole predictor, with lesser kestrels at Cádiz nesting later than at Seville (Figure 3.2c). First egg date in turn was the sole important predictor of clutch size, with clutch sizes decreasing over the course of the season (Figure 3.2d). Study area was the only predictor in the best model for mean clutch chick condition, with Seville birds having chicks in lower condition than those at Cádiz (Figure 3.2e). For all remaining productivity analyses (number of fledglings, nest outcome, fledging probability), the null models were the most parsimonious.

The final and global models of each analysis are summarised in Table S3.3 and S3.4 respectively.

3.4 DISCUSSION

We found no evidence for carryover effects of long-distance migration on phenology, reproductive success or year-round body condition. We identified differences in adult body condition, breeding phenology, clutch size and chick condition between study areas, and weak evidence for short-term carryover effects of migratory strategy on body condition in one study area, with residents in better condition than migrants during the pre-incubation period.

Breeding phenology was similar between migrants and residents, contrary to other studies reporting an association between earlier-breeding and shorter migratory distances (Anderson et al., 2016; Hötker, 2002; Lok et al., 2017). Migrant lesser kestrels typically return by mid-February (Catry et al., 2011), significantly earlier than the start of the breeding season (mid-April), which varies depending on the emergence dates of large invertebrate prey (Rodríguez et al., 2010). Residents therefore do not necessarily experience breeding-suitable conditions any earlier than migrants in this species, meaning both strategies may yield similar opportunities to assess the optimal time to commence breeding.

Despite the stark differences in migratory strategy, we also found no significant differences between migrants and residents in clutch size, number of fledglings, nest outcome, fledging probability or chick condition. This may in part be explained by sampling limitations, as we were able to determine the migratory strategy of both parents in only a few cases, and were therefore only able to examine the association between a clutch and the strategy of one parent (see Methods). As there is no evidence for phenological differences between migrants and residents, nor observed evidence for assortative mating (of ten known-strategy pairs, three were mixed-strategy), it is possible that carryover effects in these clutches were moderated by a counterbalancing effect of migrant-resident pairs. Carryover effects of migratory strategy on breeding parameters have elsewhere been shown to be strongest where there is a multiplicative effect of matched-strategy pairs (Grist et al., 2017). Alternatively, carryover effects of migratory strategy may only manifest later in the season; we did not, for instance, assess post-fledging condition or survival. It may also be the case that, where migratory strategy influences reproductive fitness, it does so to such an extent that individuals simply forego breeding (or do not survive to breed), and are therefore not detected or included in the breeding analysis. Finally, that we do not detect an effect of migratory strategy on productivity may simply indicate that both migrants and residents face different but approximately balanced fitness costs (Lundberg, 1988) associated with winter experience (trans-Saharan migration versus enduring harsh winters), ultimately resulting in equal allocation of resources to reproduction.

Variation in breeding phenology was, to some extent, explained by study area, with birds in Cádiz breeding later than those in Seville (raw mean ±SD first egg date: Cádiz: 28 April ±10, Seville: 17 April ±10). Local habitat conditions may play an important role in determining lesser kestrel breeding phenology (Rodríguez et al., 2010). The Normalized Difference Vegetation Index (NDVI), considered indicative of food availability for insectivores (Morganti et al., 2016), was consistently higher in Cádiz than in Seville, and peaked later there (Figure 3.3). If NDVI correlates with invertebrate abundance, the later NDVI peak at Cádiz could explain the delayed breeding at that site. This aligns with the patterns observed in nineteen Palaearctic migrant species (Ockendon et al., 2013), where conditions on breeding grounds have a greater effect on breeding phenology than wintering conditions.

Although our results suggest breeding phenology to be the main driver of variation in clutch size – with broods getting smaller over the breeding season, as is commonly found in avian populations (Rowe et al., 1994) – the relationship between breeding phenology and colony area means it is difficult to tease apart the extent to which clutch size is driven by breeding phenology or effects of local breeding conditions. Number of fledglings, nest outcome and probability of fledging were all similar between the two study areas, but chick condition was slightly higher in Cádiz than in Seville (raw mean ±SD chick condition (mass/P8): Cádiz: 2.93 ±1.10, Seville: 1.86 ±0.59). Adult individuals in Cádiz also showed better year-round body condition, regardless of migratory strategy, again highlighting the importance of local breeding-site conditions for individual fitness.

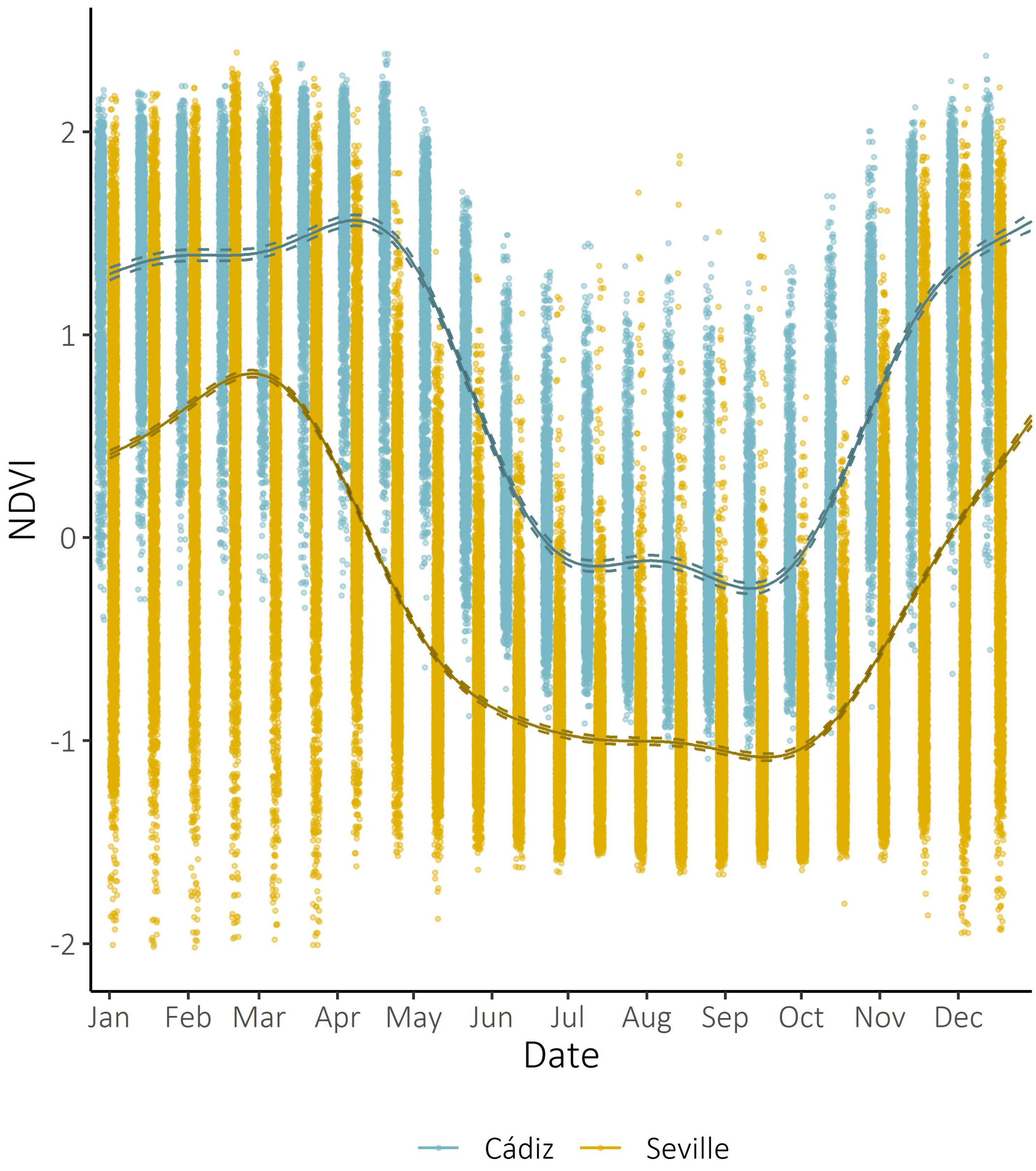

Figure 3.3 – Change in relative primary productivity (scaled NDVI) across the calendar year in the two study areas. We used data from Terra MODIS (Didan, 2015) and CORINE Land Cover 2012 (Büttner, 2014) to extract NDVI values (2014–2018) for each 250-m^2 pixel classified as suitable foraging habitat (Table S3.5) within a 3-km radius of each colony (Franco et al., 2004). We used GAMMs to model NDVI against date smoothed with penalised regression splines, interacting with colony area, with pixel ID as a random effect. The interactions between date and the two levels of study area were significant in the model ($p<0.0001$).

We found some statistical support for an effect of migratory strategy on pre-incubation body condition, with resident individuals showing better relative body condition than migrants in the Seville area (Figure 3.2b). This may suggest a short-lived carryover effect, with long-distance migration being more costly than residency during the studied period. We might expect this result if migration is a conditional strategy (Chapman et al., 2011b; Kokko, 2011) where only high-quality individuals are able to endure winter north of the Sahara (e.g. Hegemann et al., 2015). This pattern also aligns with the theory that ongoing environmental change may be disproportionately detrimental to long-distance migrants, increasing relative costs. While not affecting subsequent breeding success, this short-lived carryover effect could plausibly influence survival, with some low-condition migrants not surviving to the subsequent breeding season (Lok et al., 2015; Palacín et al., 2017).

No differences were found in year-round body condition between migrants and residents, potentially suggesting that any short-lived carryover effect is counterbalanced by the energetic pressures of reproduction, or buffered by increased food availability during the breeding season. Elsewhere, spring migratory conditions have been found to compensate for the carryover effects of winter conditions on post-winter body condition, with no subsequent effects on breeding success (Clausen et al., 2015).

It is notable that the potential effect of migratory strategy on pre-incubation adult body condition appeared relevant only in Seville, and not Cádiz, indicating that conditions at the breeding site may override migratory carryover effects. Conditions on breeding grounds have elsewhere been linked to differential manifestations of carryover effects (Legagneux et al., 2012; Wilson et al., 2011); if migration has a greater negative effect on body condition than residency, it is feasible that migrants breeding in more productive habitats recover their condition more quickly upon arrival than individuals in poorer habitats.

Regional differences in the effect of migratory strategy on pre-incubation condition could also arise if there were strong migratory connectivity at this scale, such that migrants from Seville had a distinct and more costly migratory experience than migrants from Cádiz. However, given the proximity of the two areas, strong connectivity seems unlikely. In 2007, a single roost of over 28,000 lesser kestrels was observed in Senegal, representing 30-50% of the western European population (Pilard et al., 2011), and geolocator studies from elsewhere in Iberia indicate a high degree of spatial aggregation in winter (Catry et al., 2011; Rodríguez et al., 2009). Finally, we might expect regional variation in the effects of migratory strategy if partial migration is both condition- and density-dependent (Griswold et al., 2010), with different mechanisms underpinning migration and residency in the two areas (Marra et al., 2015; Norris & Taylor, 2006).

Sample size limitations may have influenced our overall power to detect carryover effects of migratory strategy, although our main finding – that breeding site effects are of greater relevance to fitness than migratory strategy – concerns the relative magnitude of effects, rather than their absolute size. Carryover effects of strategy on breeding may be buffered in broods with mixed-strategy parents, something we were unable to analyse. That we were only able to assess the effect of migratory strategy of one clutch-parent may have undermined our capacity to detect carryover effects on breeding parameters. We did not examine survival, recruitment or population trends – strong effects of migratory behaviour on fitness could therefore be concealed if they operate largely on survival parameters rather than reproductive success. Similarly, knock-on effects of reproductive effort and body condition may only be reflected in subsequent mortality. Measuring survival in conjunction with post-fledging survival and/or recruitment would shed further light on population-level effects of migratory variability.

3.5 CONCLUSIONS

Despite marked differences in the wintering experiences of migrant and resident lesser kestrels, carryover effects of migratory strategy were limited and idiosyncratic, with conditions on the breeding grounds being of greater relevance for adult and chick body condition. We hypothesised that anthropogenic change could be having a disproportionate effect on migrants, and thereby disrupting the balance in fitness benefits of each strategy. We found little evidence to support this, suggesting that costs of migration associated with exposure to anthropogenic impacts may be counterbalanced by costs experienced by resident individuals, such as variability in winter conditions. This apparent parity of fitness between the two strategies is in accordance with theory on the evolutionary stability of partially migratory populations (Lundberg, 1988). Detailed information on adult survival and chick recruitment may facilitate more comprehensive understanding of the interactions between migratory strategies, breeding conditions and demographic effects.

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Chapter 3 Supplementary material

Appendix S3.1 Isotope analysis methods

Distinct photosynthetic processes used by different plant species result in varying ratios of the stable isotopes ^{13}C to ^{12}C (expressed as $\delta^{13}C$). The spatial distributions of these species dictate geographically varying values of $\delta^{13}C$: the photosynthetic pathway used by plant species adapted to hot, dry climates (the C_4 pathway) results in higher $\delta^{13}C$ values in regions where these plants are more prevalent than elsewhere (Hobson et al., 2010; Still & Powell, 2010). Feathers incorporate (via trophic interactions) the approximate isotopic signature of the environment in which they are grown; feather $\delta^{13}C$ values can therefore be used to infer the broad location of this environment (Hobson et al., 2010) – see Still & Powell (2010) for isoscape, subsequently adapted specifically for feathers (based on +2‰ accumulation of $\delta^{13}C$) (Hobson et al., 2012).

Lab work was carried out at the University of East Anglia (UEA); each sample was analysed for carbon and nitrogen in the year of its collection (though only carbon values were used for strategy determination). Feather samples were rinsed in a 2:1 chloroform: methanol solvent to clean surface oils and air-dried for 48 hours. From each cleaned sample, a cutting of approximately 0.2 cm^2 was encapsulated in tin foil, subsequently combusted in a Costech elemental analyser interfaced with a Thermo Scientific Delta XP continuous flow mass spectrometer. We simultaneously analysed an internal reference material (casein) and laboratory internal standard material (collagen). Stable isotope ratios are measured in parts per thousand (per mille: ‰) and expressed in δ notation, relative to an international standard, which for carbon is the Vienna-Pee Dee Belemnite carbonate (VPDB) and for nitrogen is atmospheric nitrogen (AIR N_2). The precision of carbon composition varied from 0.1–0.3 ‰, while the precision of nitrogen composition varied from 0.1–0.4 ‰.

Table S3.1 – Total bird-years (individual birds within a specific year) of all ages with known migratory strategies, as identified through three main strategy determinants: observations, geolocator data and feather isotope signatures.

Resident strategy determinant	Number identified	Total residents (bird-years)
Observed resident	89	90
Geolocator resident	4 (of which 1 additional to those observed in winter)	
Migrant strategy determinant	Number identified	Total migrants (bird-years)
Observed migrant	1	61
Geolocator migrant	9	
Isotope signature ($\delta^{13}C > -20$ ‰)	53 (of which 51 additional to geolocator migrants)	

Table S3.2 – Outputs of post-hoc test of multiple comparisons carried out on the final best-ranked GLMM assessing the effect of migratory strategy and study area on adult pre-hatching condition. See Figure 3.2b.

Pairwise comparison			Estimate	SE	z-value	*P*-value
Cádiz resident	–	Cádiz migrant	-0.48	0.26	-1.84	0.255
Seville migrant	–	Cádiz migrant	-1.96	0.28	-6.94	< 0.001
Seville resident	–	Cádiz migrant	-1.39	0.25	-5.65	< 0.001
Seville migrant	–	Cádiz migrant	-1.48	0.27	-5.51	< 0.001
Seville resident	–	Cádiz resident	-0.91	0.23	-3.95	< 0.001
Seville resident	–	Seville migrant	0.57	0.25	2.32	0.093

Table S3.3 – Effect size summary for each analysis, with coefficient estimates (± standard error) for parameters retained in the relevant final model. The reference categories for the two two-level categorical variables (Strategy and Study Area) are Migrant and Cádiz, respectively. Parameters marked with a dash were present in the global model for the relevant analysis but not retained in the most competitive model; greyed out parameters were not included in the relevant global model.

n	Figure	Response	Model structure:					
			Strategy (Resident)	Study area (Seville)	Strategy(Resident)*Study area(Seville)	First egg date	Capture date	Sex
170	3.2a	Year-round body condition	-	-1.33 (±0.17)	-	▨	-	-
112	3.2b	Pre-incubation body condition	-0.48 (±0.26)	-1.96 (±0.28)	1.05 (±0.35)	▨	-	-
56	3.2c	Breeding phenology	-	-0.94 (±0.25)	-	▨	▨	▨
56	3.2d	Clutch size	-	-	-	-0.81 (±0.20)	▨	▨
56	-	Fledglings	-	-	-	-	▨	▨
56	-	Nest outcome	-	-	-	-	▨	▨
56	-	Fledglings per egg	-	-	-	-	▨	▨
41	3.2e	Chick condition	-	-1.08 (±0.29)	-	▨	▨	▨

Table S3.4 – Global models for each analysis, with coefficient estimates (± standard error) for parameters. The reference categories for the two two-level categorical variables (Strategy and Study Area) are Migrant and Cádiz, respectively. Greyed out parameters were not included in the relevant global model.

n	Response	Model structure						
		Intercept	Strategy (Resident)	Study area (Seville)	Strategy(Resident)* Study area(Seville)	First egg date	Capture date	Sex (Male)
170	Year-round body condition	0.83 (±0.20)	-0.32 (±0.24)	-1.71 (±0.24)	0.72 (±0.33)		0.00 (±0.00)	-0.02 (±0.17)
112	Pre-incubation body condition	1.00 (±0.30)	-0.46 (±0.28)	-1.96 (±0.28)	1.07 (±0.36)		0.00 (±0.00)	-0.09 (±0.18)
56	Breeding phenology	0.24 (±0.19)	0.26 (±0.31)	-0.70 (±0.36)	-0.52 (±0.51)			
56	Clutch size	15.47 (±0.32)	-0.04 (±0.54)	0.55 (±0.60)	0.16 (±0.85)	-0.66 (±0.23)		
56	Fledglings	1.12 (±0.12)	0.08 (±0.20)	-0.16 (±0.24)	-0.07 (±0.33)	-0.13 (±0.09)		
56	Nest outcome	1.80 (±0.61)	1.15 (±1.21)	-1.37 (±1.00)	-0.44 (±1.62)	-0.62 (±0.43)		
56	Fledglings per egg	0.97 (±0.40)	0.35 (±0.70)	-0.68 (±0.70)	-0.35 (±1.02)	-0.19 (±0.29)		
41	Chick condition	0.44 (±0.21)	-0.18 (±0.33)	-1.72 (±0.40)	1.17 (±0.56)			

Table S3.5 – CORINE Land Cover (CLC) habitat categories deemed suitable for lesser kestrel foraging. Pixels classified as these habitat categories within a 3-km radius of a colony were used for the assessment of study area primary productivity (NDVI). See Kosztra et al. (2017) for detailed land cover definitions.

Land cover category	CLC Code
Roads and rail networks and associated land	122
Non-irrigated arable land	211
Permanently irrigated arable land	212
Pastures	231
Annual crops associated with permanent crops	241
Complex cultivation patterns	242
Land principally occupied by agriculture, with significant areas of natural vegetation	243
Agro-forestry areas	244
Natural grassland	321
Inland marshes	411

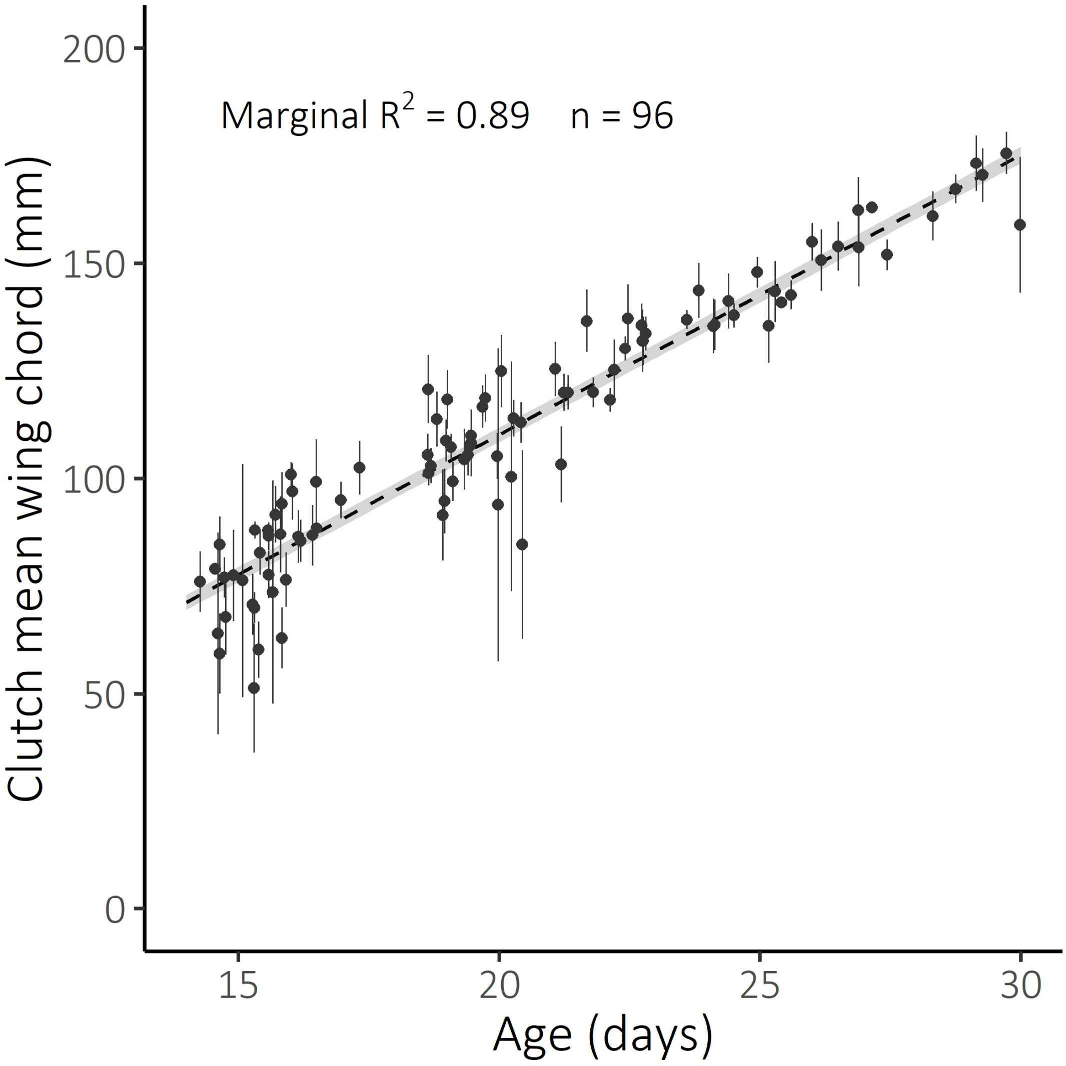

Figure S3.1 – Relationship between clutch age (days since first hatch date) and chick wing chord measurements taken in 2018 from the Seville colonies. Points represent mean clutch wing chord, with associated standard error shown by vertical lines. Black dashed line represents the effect of age on mean clutch wing chord as predicted by a linear mixed-effects model with clutch as a random effect; grey ribbon represents standard error. The formula of this linear mixed-effects model (y = -19.8 + 6.5x) was used to calculate clutch age for those clutches for which neither first egg date nor first hatch date were observed (n=17). Clutch age is therefore given by: (wing chord + 19.8)/6.5.

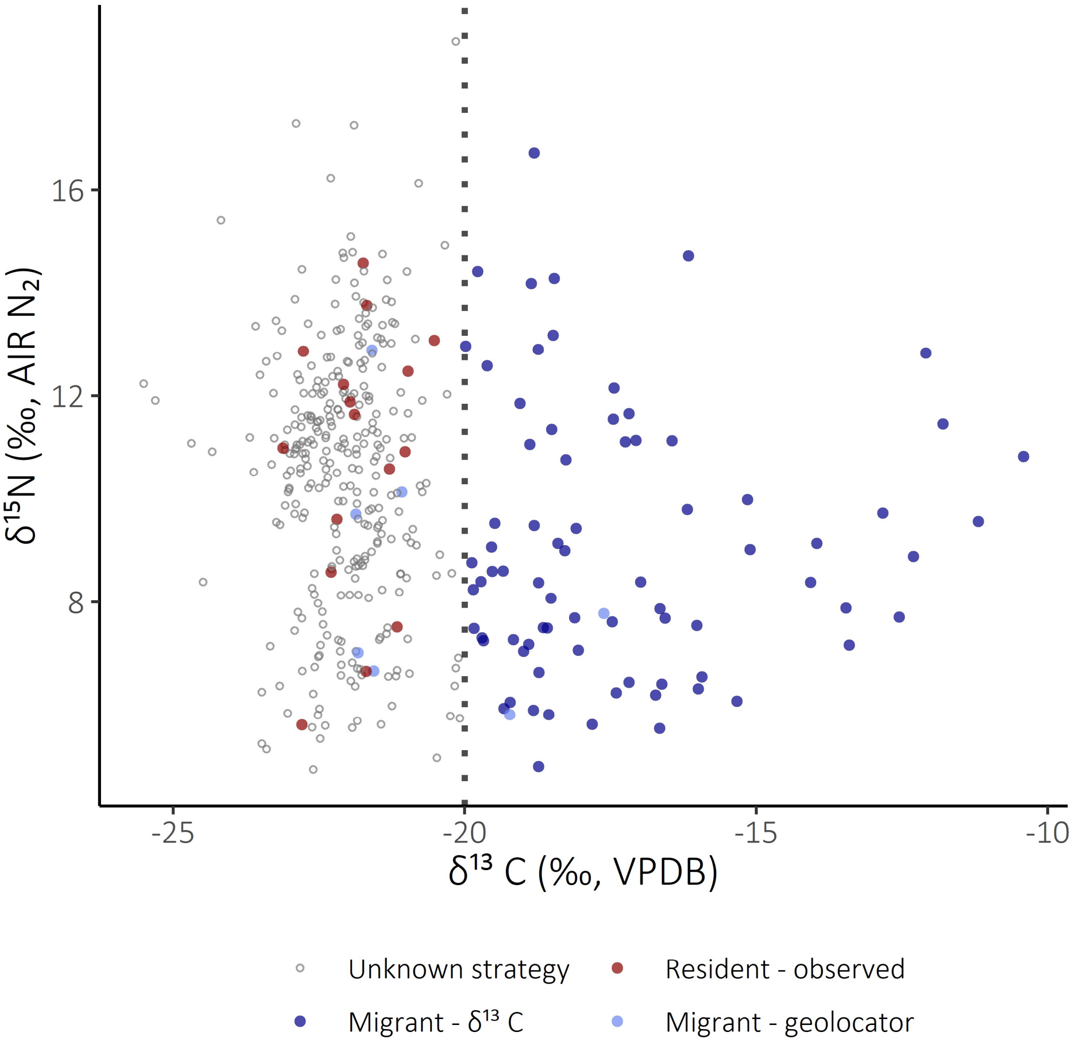

Figure S3.2 – Feather isotope values (δ^{15}N plotted against δ^{13}C) collected from individuals of known and unknown migratory strategies (n=404). Point colour indicates strategy and strategy-determinant method. Dotted line indicates the δ^{13}C migratory strategy-determinant cut-off – individuals with δ^{13}C values higher than -20 ‰ were determined to be migrants. Individuals with values lower than this cut-off could either be residents or migrants that moulted prior to migration – for this reason, individuals with values lower than -20 ‰ were classed as unknown strategy unless directly observed as a resident or geolocated as a migrant. Neither the single observed migrant nor the four geolocator residents had associated feather isotope data; these are therefore not represented on this plot.

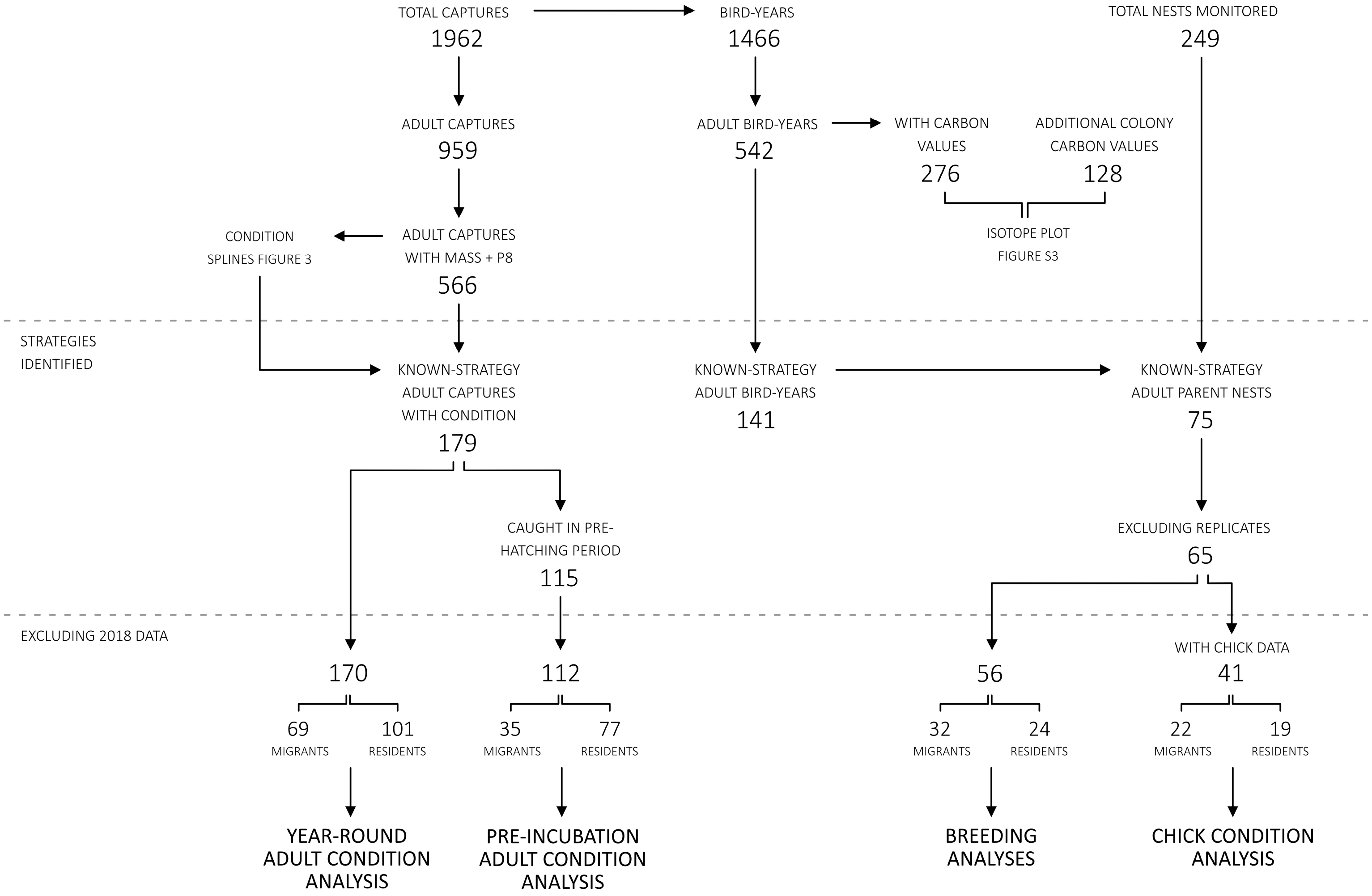

Figure S3.3 – Visualisation of data-filtering and resulting sample sizes for each analysis.

Appendix S3.2 Isotope sensitivity analyses

The results reported in the manuscript were conducted on a dataset in which isotope-defined migrants were identified according to a $\delta^{13}C$ cut-off value of -20 ‰ (Figure S3.2). To assess the sensitivity of our results to the cut-off value, we repeated all analyses on two additional datasets, one with a less conservative cut-off of -20.5 ‰ (and therefore a greater number of isotope-defined migrants), and one with a more conservative cut-off of -19.5 ‰ (fewer isotope-defined migrants – Figure S3.4). The alteration in cut-off value by ±0.5 ‰ was decided based on the highest $\delta^{13}C$ signature of a known resident bird (-20.52 ‰).

In both additional analyses, all final models retained the same parameters as the final models in the original analyses, with comparable coefficient estimates and standard errors (Tables S3.6 and S3.7) – indicating that our results are robust to variations in the cut-off value for defining migrants from $\delta^{13}C$.

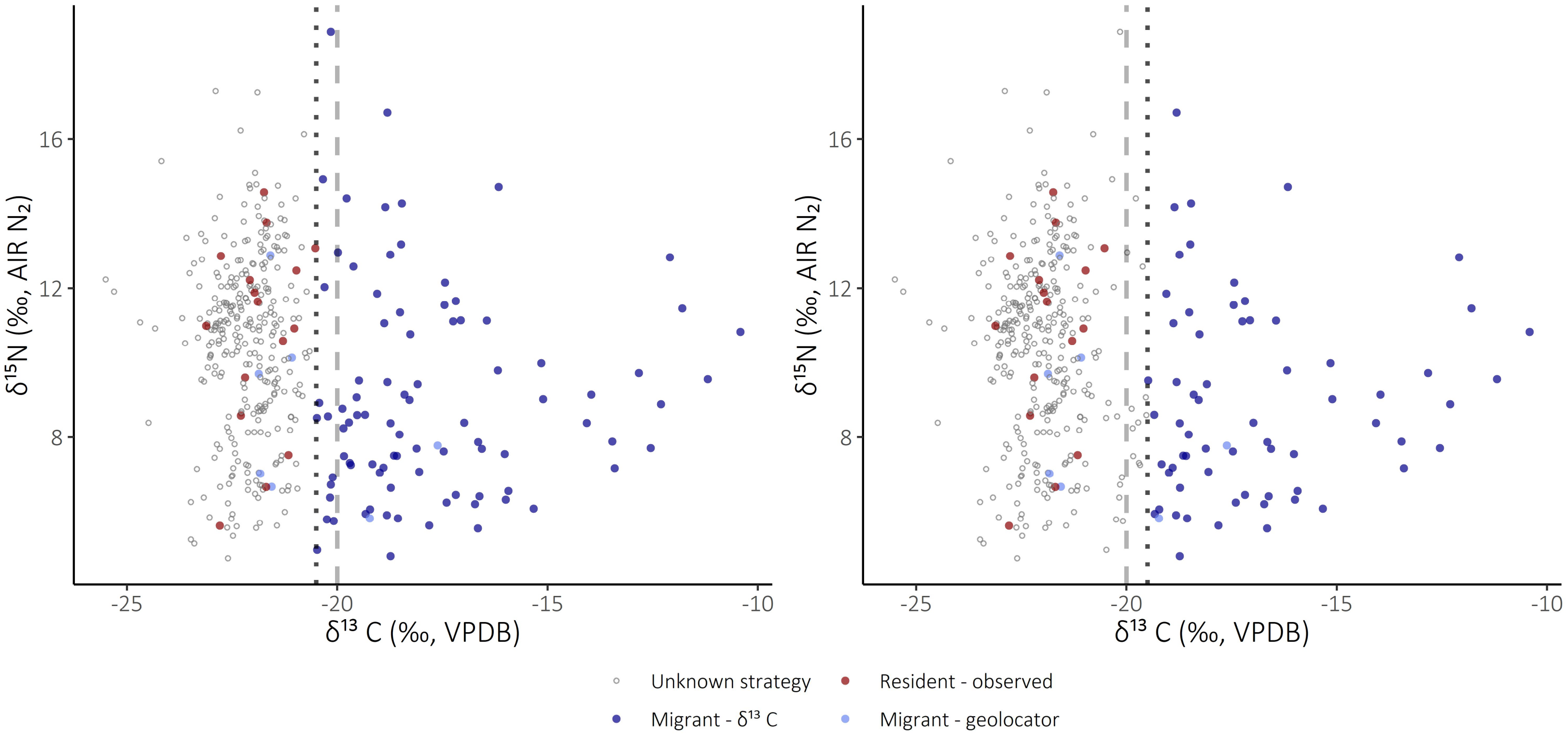

Figure S3.4 – Visualisation of the shift in the $\delta^{13}C$ migratory-determinant cut-off value from the original (Figure S3.2), showing the migrant datapoints gained (L) and lost (R) in datasets underlying the two sensitivity analyses. Feather isotope values ($\delta^{15}N$ plotted against $\delta^{13}C$) collected from individuals of known and unknown migratory strategies (n=404). Point colour indicates strategy and strategy-determinant method. Dotted line indicates the new $\delta^{13}C$ migratory strategy-determinant cut-off – individuals with $\delta^{13}C$ values higher than -20.5 ‰ (L) or -19.5 ‰ (R) were determined to be migrants. Faint dashed line indicates the original -20 ‰ migratory strategy-determinant cut-off used in the main analysis.

Table S3.6 – Effect size summary for sensitivity analyses conducted on the dataset with isotope-defined migrants identified using a (less conservative) $\delta^{13}C$ cut-off value of -20.5 ‰. Coefficient estimates (± standard error) for parameters retained in the relevant final mode can be compared to those of the main analysis given in Table S3.3. Delta n indicates the change in sample size from the original dataset. The reference categories for the two two-level categorical variables (Strategy and Study Area) are Migrant and Cádiz, respectively. Parameters marked with a dash were present in the global model for the relevant analysis but not retained in the most competitive model; greyed out parameters were not included in the relevant global model.

n	Δ n	Response	Model structure:					
			Strategy (Resident)	Study area (Seville)	Strategy(Resident)*Study area(Seville)	First egg date	Capture date	Sex
178	+8	Year-round body condition	-	-1.19 (±0.17)	-		-	-
113	+1	Pre-incubation body condition	-0.48 (±0.26)	-1.94 (±0.28)	1.03 (±0.36)		-	-
63	+7	Breeding phenology	-	-0.80 (±0.24)	-			
63	+7	Clutch size	-	-	-	-0.78 (±0.18)		
63	+7	Fledglings	-	-	-	-		
63	+7	Nest outcome	-	-	-	-		
63	+7	Fledglings per egg	-	-	-	-		
48	+7	Chick condition	-	-0. 88 (±0.28)	-			

Table S3.7 – Effect size summary for sensitivity analyses conducted on the dataset with isotope-defined migrants identified using a (more conservative) δ^{13}C cut-off value of -19.5 ‰. Coefficient estimates (± standard error) for parameters retained in the relevant final mode can be compared to those of the main analysis given in Table S3.3. Delta n indicates the change in sample size from the original dataset. The reference categories for the two two-level categorical variables (Strategy and Study Area) are Migrant and Cádiz, respectively. Parameters marked with a dash were present in the global model for the relevant analysis but not retained in the most competitive model; greyed out parameters were not included in the relevant global model.

n	Δ n	Response	Model structure:					
			Strategy (Resident)	Study area (Seville)	Strategy(Resident)*Study area(Seville)	First egg date	Capture date	Sex
159	-11	Year-round body condition	-	-1.29 (±0.18)	-		-	-
107	-5	Pre-incubation body condition	-0.30 (±0.29)	-1.86 (±0.31)	0.93 (±0.39)		-	-
51	-5	Breeding phenology	-	-0.92 (±0.26)	-			
51	-5	Clutch size	-	-	-	-0.80 (±0.21)		
51	-5	Fledglings	-	-	-	-		
51	-5	Nest outcome	-	-	-	-		
51	-5	Fledglings per egg	-	-	-	-		
37	-4	Chick condition	-	-1.05 (±0.30)	-			

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Spatially explicit risk mapping reveals direct anthropogenic impacts on migratory birds

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AUTHOR CONTRIBUTIONS

CB, JG and AF designed the study. CB collated and processed the data, undertook the statistical analyses and wrote the manuscript. AF, JG and IC provided advice on statistical approaches and interpretation. AG and AK provided data. All authors critically revised the manuscript and gave final approval for publication.

ABSTRACT

Migratory species rely on multiple ranges across the annual cycle, rendering them vulnerable to a wide range of spatially disparate anthropogenic threats. The spatial distribution of these threats will strongly influence the magnitude of their population-scale effects, but this has not been quantitatively assessed for most species. We combined remote-sensed data and expert opinion to map sixteen anthropogenic threats relevant to migratory birds across Europe, Africa and the Middle East – including the first spatially-explicit pan-continental assessment of relative hunting pressure. By combining the resulting composite threat maps with morpho-behavioural traits-based weightings (reflecting relative threat susceptibility), we created species-specific risk maps for 103 Afro-Palaearctic migratory birds breeding in Europe and evaluated how spatial threat exposure relates to long-term population trends. We found that greater exposure to direct mortality threats (including hunting pressure, infrastructure and nocturnal lights), especially in the non-breeding season, is associated with declining bird population trends. Our results emphasise the importance of spatially explicit approaches to quantifying anthropogenic drivers of population declines. Composite risk maps represent a valuable resource for spatial analyses of anthropogenic threats to migratory birds, allowing for targeted conservation actions.

4.1 INTRODUCTION

Increasingly sophisticated modelling of satellite-derived data has transformed biodiversity monitoring and conservation (Goldewijk et al., 2011; Hansen et al., 2013; Turner, 2014), allowing high-resolution mapping of anthropogenic impacts on the natural world. Studies often focus on evaluating spatial exposure of populations to individual threats (Buchanan et al., 2020; Møller et al., 2014; Tracewski et al., 2016), but effects of these can be difficult to detect when viewed in isolation, especially if different threats are interactive or their effects only manifest cumulatively (Akresh et al., 2019; Howard et al., 2020; Kennedy et al., 2019; Mahon et al., 2019; Raiter et al., 2014). Large-scale mapping of combined stressors offers a powerful approach to gain a more holistic understanding of human impacts on biodiversity, including composite threat assessment (Theobald, 2013; Venter et al., 2016), evaluating threats to marine ecosystems (Halpern et al., 2008), water security (Vörösmarty et al., 2010), and conservation prioritisation (Allan et al., 2013; Kennedy et al., 2019). Here we present the first application of this multidimensional spatial approach to threat evaluation in migratory species.

Migrants' reliance on resources found in geographically distinct areas throughout the annual cycle may render them particularly vulnerable to human-induced threats (Newton, 2004; Robinson et al., 2009; Wilcove & Wikelski, 2008), necessitating more spatially-nuanced conservation efforts than are needed for non-migratory species (Runge et al., 2014, 2015; Sanderson et al., 2016). Migratory birds breeding in Europe and North America – especially long-distance migrants – are declining at a greater rate than non-migratory species (Laaksonen & Lehikoinen, 2013; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014), potentially as a result of their cumulative exposure to spatially disparate threats.

A suite of anthropogenic threats are known to impact bird populations, ranging from human settlement and associated infrastructure, overharvesting, land-use change, and anthropogenic climate change (Bairlein, 2016; Kirby et al., 2008; Loss et al., 2015; Maxwell et al., 2016). Accounting for spatial variation in the degree of exposure to threats is essential in pinpointing areas for conservation intervention (Tulloch et al., 2015), and identifying the relative importance of conditions within migrants' spatially disparate seasonal ranges is necessary to understand and counter mechanisms driving negative population trends. Pronounced declines in long-distance migrants suggest a substantial influence of conditions during migration or on the non-breeding grounds, with population trends being sensitive to migratory routes (Hewson et al., 2016; Newton, 2006; Tøttrup et al., 2008), as well as non-breeding climatic conditions (Ockendon et al., 2012) and habitat change (Adams et al., 2014; Cresswell et al., 2007). However, influential anthropogenic threats may occur throughout the annual cycle (Sergio et al., 2019; Thaxter et al., 2010), and seasonal effects can interact with conditions experienced earlier in the annual cycle (Buchan et al., 2021; Morrison et al., 2013). This potential for between-season cumulative and/or synergistic effects highlights the need for full-cycle approaches for understanding – and ultimately, targeting – threats to migratory species (Calvert et al., 2009; Marra et al., 2015; Martin et al., 2007; Small-Lorenz et al., 2013; Zurell et al., 2018).

Here, we combine a suite of large-scale data sources to generate novel composite risk maps for anthropogenic threats across the Afro-Palearctic region, including the first spatially explicit map of hunting pressure for migratory birds. We then examine the extent to which spatially explicit indices of threat exposure correlate with breeding population trends for 103 Afro-Palaearctic migratory birds. We assess cumulative exposure to risk by grouping threats according to whether they pose direct mortality threats to birds (Loss et al., 2012; 2015) (e.g. overharvesting, collision risks), or threats mediated through diffuse impacts of environmental change (e.g. habitat degradation and climate change). We use trait-based vulnerability weightings for each species to calculate combined risk exposure across species' seasonal ranges, allowing us to partition the effects of different anthropogenic risks on population trends, and evaluate the extent to which these vary between the breeding and non-breeding ranges.

4.2 METHODS

4.2.1 Data layers

Overview of risk mapping

We assembled sixteen spatial datasets representing three broad anthropogenic threat types: direct mortality, habitat change and climate change. Each layer measured the current extent of human modification of the natural environment, relative either to a baseline period (climate variables and afforestation) or to an equivalent un-modified landscape (land-use and infrastructure) (Table 4.1). We combined the constituent layers for each threat type into composite surfaces using either linear summation for threats posing additive risks or fuzzy algebraic summation for potentially correlative threats (Kennedy et al., 2019) – see *2.4 Composite risk-mapping algorithm*. We adapted generic threat maps into species-specific risk surfaces (where risk is the combination of threat with vulnerability) by applying trait-based threat vulnerability weightings (D'Amico et al., 2019; Foden et al., 2013; Mason et al., 2019) (see *2.3 Species' threat-vulnerability weightings*) for each constituent threat layer (Figure 4.1).

Table 4.1 – Summary of risk layers and respective data sources

Threat layer	Risk type	Data source(s)	Reference
Roads	Direct mortality	GLOBIO GRIP4	Meijer et al., 2018
Nocturnal lights	Direct mortality	DMSP OLS	NOAA, 2013
Human population density	Direct mortality	GPW 4.11	CIESIN, 2018
Hunting	Direct mortality	Survey of expert opinion UNEP Protected Planet* GLOBIO GRIP4* GPW 4.11* EC JRC GHS-BUILT*	- UNEP-WCMC and IUCN, 2019 Meijer et al., 2018 CIESIN, 2018 Corbane et al., 2018
Powerlines	Direct mortality	OpenInfra World Bank	Garrett, 2018 World Bank, 2017
Windfarms	Direct mortality	Global wind 2020	Dunnett et al., 2020
Urbanisation	Direct mortality and habitat change	EC JRC GHS-BUILT	Corbane et al., 2018
Cropland	Habitat change	HYDE 3.2.1	Klein Goldewijk et al., 2017
Grazing land	Habitat change	HYDE 3.2.1	Klein Goldewijk et al., 2017
Fertilizer use	Habitat change	UN FAO HYDE 3.2.1	FAO, 2019a Klein Goldewijk et al., 2017
Pesticide use	Habitat change	UN FAO HYDE 3.2.1	FAO, 2019b Klein Goldewijk et al., 2017

Threat layer	Risk type	Data source(s)	Reference
Afforestation	Habitat change	ISAM LUCC NASA MODIS	Meiyappan & Jain, 2012 Friedl & Sulla-Menashe, 2015
Absolute temperature anomaly	Climate change	CRU TS 4.03	Harris et al., 2020
Absolute temperature variability anomaly	Climate change	CRU TS 4.03	
Absolute precipitation anomaly	Climate change	CRU TS 4.03	
Absolute precipitation variability anomaly	Climate change	CRU TS 4.03	

*for masking out protected areas, accessibility and urban concentrations. See text for full description of creation of hunting layer

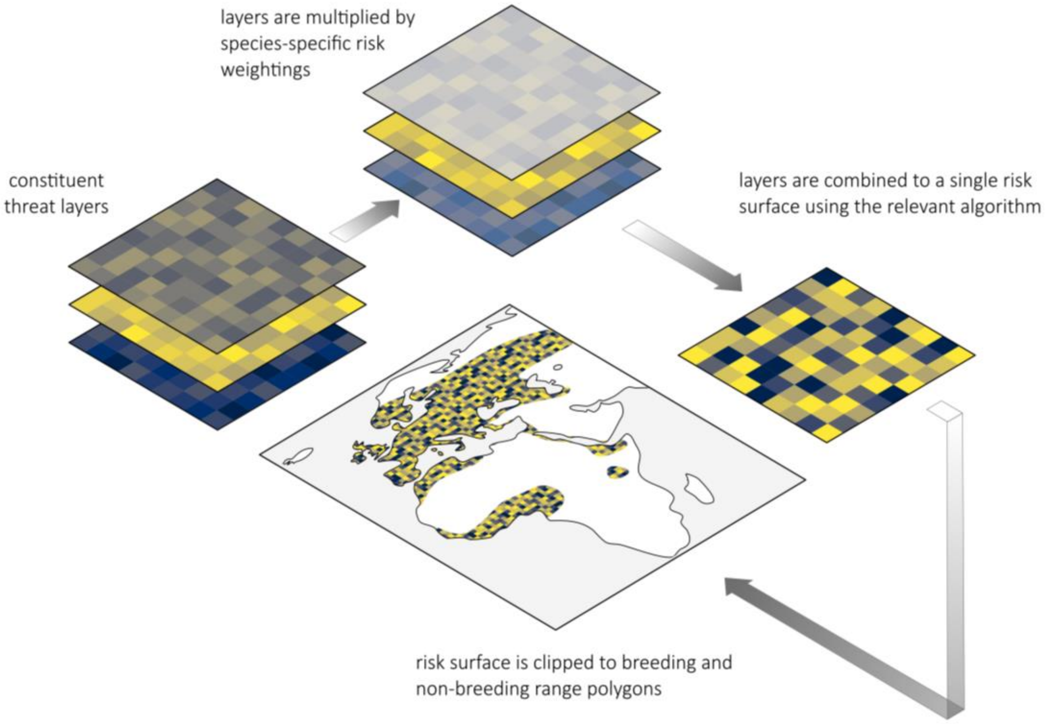

Figure 4.1 – Schematic illustrating the process of deriving composite risk surfaces from individual constituent threat layers for each of the three risk types (direct mortality, habitat change and climate change; Table 4.1) for each species' (n=103) breeding and non-breeding ranges.

Direct mortality threats

Infrastructure associated with human settlement poses significant collision mortality risks – particularly to nocturnally migrating birds – in the form of roads (Erritzoe et al., 2003; Loss, Will, & Marra, 2014; Santos et al., 2016) and buildings (Loss et al., 2015; Loss, Will, Loss, et al., 2014). To capture these threats, we used maps of built-up area density (Corbane et al., 2018) and total roads density (Meijer et al., 2018), combining all road types. For species that make nocturnal movements, bird-building collision risks are exacerbated by artificial light at night (Lao et al., 2020; Van Doren et al., 2017); we mapped this using the DMSP-OLS Nighttime Lights Time Series (NOAA, 2013). We used human population density (CIESIN, 2018) as an index to capture other direct anthropogenic mortality risks (Anadón et al., 2010; Kerr & Currie, 1995; McKee et al., 2004) including disturbance (Gill, 2007; Mallord et al., 2007) and invasive species (Newbold et al., 2015; Spear et al., 2013) – in particular the impacts of domestic and feral cats (*Felis catus*) (Aegerter et al., 2017; Loss et al., 2012, 2013b).

Bird mortality due to powerline collision or electrocution can occur at rates sufficient to have population-level effects (Bernardino et al., 2018; Loss et al., 2012; Schaub et al., 2010), and bring about changes in migratory behaviour (Palacín et al., 2017). To map overhead powerlines we combined World Bank (World Bank, 2017) and OpenStreetMap (Garrett, 2018) datasets. Windfarms also pose direct collision risks to birds (Loss et al., 2013a, 2015; Zimmerling et al., 2013), which we mapped using a OpenStreetMap-derived global windfarm dataset Dunnett et al. (2020).

Overharvesting is among the most significant direct threats to birds (Kirby et al., 2008), linked to population declines (Jiguet et al., 2019; Kamp et al., 2015) and even extinction (Hung et al., 2014). While it is well known that high levels of hunting occur in Palaearctic/Eurasian hotspots (Brochet et al., 2016; Brochet, Jbour, et al., 2019; Schneider-Jacoby & Spangenberg, 2010), and in sub-Saharan Africa (Whytock et al., 2016), relative hunting pressure has not previously been systematically mapped for migratory birds. To map hunting threats at a pan-continental scale, we surveyed expert opinion on legal and illegal hunting of migratory birds within each country in the study region; example survey is given in Appendix S4.1. To target experts for this survey, we approached the BirdLife International partner organisations and their contacts, other local ornithological institutes and conservation NGOs monitoring bird hunting, hunters and hunting federations, and academics researching bird hunting in the relevant areas. Hunting pressure varies between species as well as spatially (Brochet, Van Den Bossche, et al., 2019; Schneider-Jacoby & Spangenberg, 2010); we therefore asked respondents to rank country-level and within-country regional variation in the relative levels of hunting of small- and large-bodied birds separately (size relative to a feral pigeon), and modified the resulting spatial hunting indices according to metrics of accessibility (roads and human population density – see Appendix S4.2) (Milner-Gulland et al., 2003; Venter et al., 2016). Following Benítez-López et al. (2019), we masked areas with >90% urban cover (Corbane et al., 2018) or with the highest levels of protected area status (UNEP-WCMC and IUCN, 2019) from hunting pressure surfaces due to low likelihood of hunting taking place there (Figure 4.2). We validated the results of the hunting survey by relating country-level responses to the estimated number of birds illegally killed given in Brochet et al. (2016), Brochet, Jbour, et al. (2019), and Brochet, Van Den Bossche, et al. (2019), showing strong correlation between our estimates and published values for the subset of countries for which quantitative hunting values are available – see Appendix S4.2.

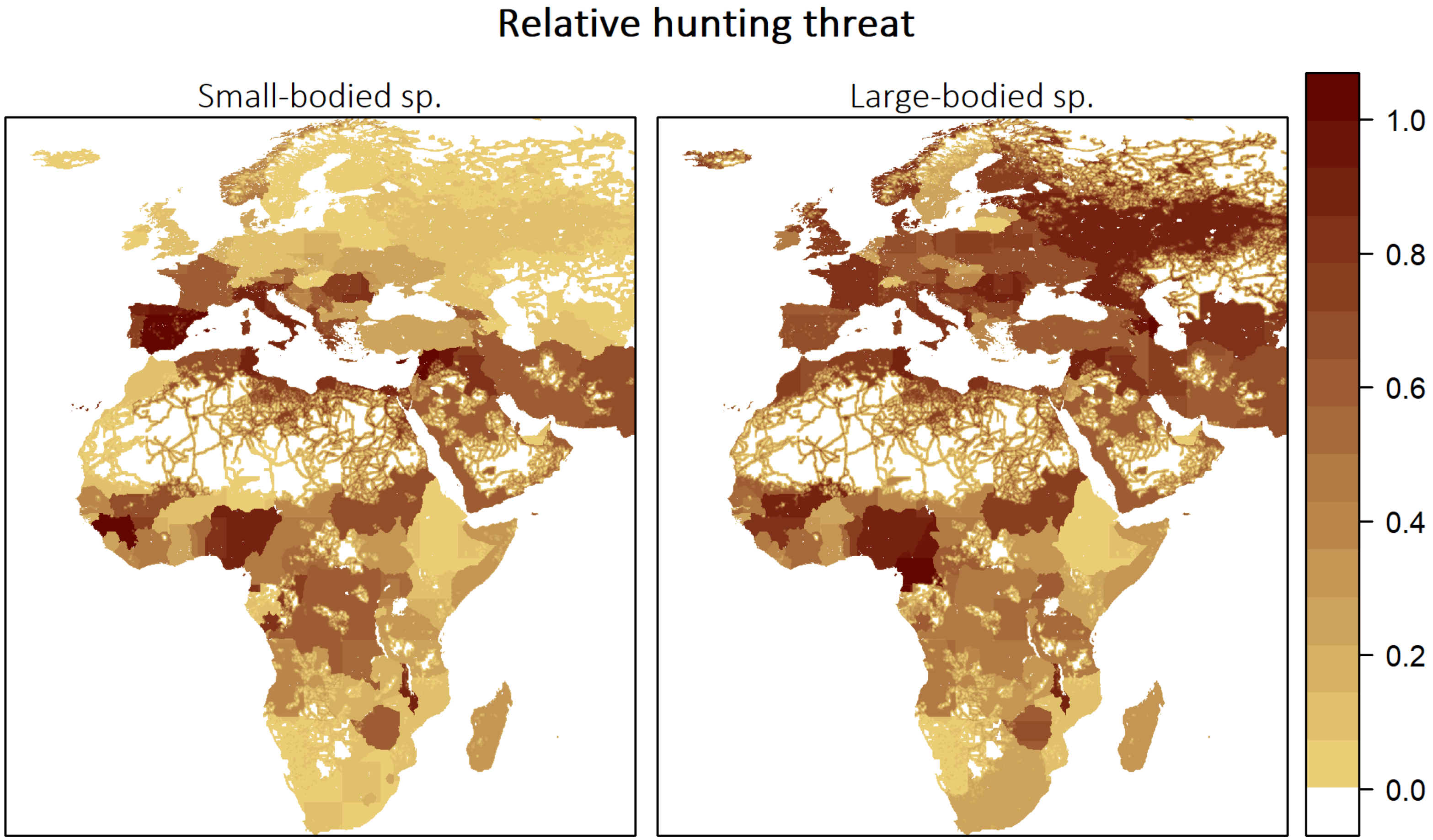

Figure 4.2 – Relative levels of hunting of small- and large-bodied birds across the study region, where 0 represents no hunting threat and 1 represents the maximum relative threat.

Habitat change

Conversion of natural habitat to agricultural land has previously been linked to declines in migratory birds (Adams et al., 2014; Cresswell et al., 2007; Vickery et al., 2014; Walther, 2016), as has afforestation for farmland, steppe and wetland specialists (Butler et al., 2010; Goriup & Tucker, 2007; Gunnarsson et al., 2006; Voříšek et al., 2010). We mapped agricultural expansion using cropland and grazing layers produced by Klein Goldewijk et al. (2017), and mapped anthropogenic afforestation as the positive change in forest land cover between a 1985 baseline map (Meiyappan & Jain, 2012) and a 2017 forest layer created from MODIS land cover data (Friedl & Sulla-Menashe, 2015). We used the urbanisation layer created for the direct mortality threats (see above) to map natural habitat converted to urban land, to which fewer avian species can adapt (Chace & Walsh, 2006).

The use of agrochemicals (particularly pesticides and fertilizers) associated with agricultural intensification may also affect species through toxicity (Calvert et al., 2013; Mineau & Whiteside, 2013), reduction in prey availability (Bright et al., 2008; MacDonald, 2006), and habitat degradation (Vickery et al., 2001). We mapped pesticide and fertilizer use within agricultural lands (see above) using United Nations estimates of mean per-country tonnage per km^2 for the years 2009-2017 (masked to cropland only for pesticides, cropland and grazing land for fertilizers) (FAO, 2019a, 2019b).

Climate change

Climate change, including more frequent extreme climatic events (Ummenhofer & Meehl, 2017), can have a range of negative demographic impacts on birds (Both et al., 2006, 2010; Møller et al., 2008; Szép, 1995; Tøttrup et al., 2012; Van Gils et al., 2016), but the speed and magnitude of climatic change varies considerably in space (IPCC, 2013). We mapped climate change threats using CRU TS Version 4.03 (Harris et al., 2020), generating monthly temperature and precipitation anomalies for each grid cell by subtracting monthly mean values for 2009–2018 (modern period) from mean values for 1961–1990 (baseline period). We also mapped the standard error around the mean monthly values to yield monthly series of temperature and precipitation variability anomalies as a metric of changes in climatic volatility (Foden et al., 2013; IPCC, 2013). We converted each monthly series (temperature anomaly, temperature variability anomaly, precipitation anomaly, precipitation variability anomaly) to absolute anomalies (larger values indicating size of anomaly in either direction), and finally averaged these for the temperate breeding season (March–August) and non-breeding season (September–February).

4.2.2 Relating risk exposure to population trends

The Pan-European Common Bird Monitoring Scheme (PECBMS) collates national survey data to create population trends and indices for 170 bird species breeding in Europe (EBCC/BirdLife/RSPB/CSO, Brlík et al., 2021; Gregory et al., 2005). We obtained the European Long-term Trends (calculated up to 2016 from a median base year of 1980, https://pecbms.info/trends-and-indicators/species-trends/) for the 124 PECBMS species classified as migrants by BirdLife International (BirdLife International, 2020), together with their seasonal range polygons (BirdLife International & Handbook of the Birds of the World, 2019), which we then filtered to 103 non-pelagic migratory species with extant breeding and non-breeding ranges within the Afro-Palaearctic region (Figure 4.3, see Appendix S4.3 for species exclusion criteria). We used the PECBMS Long-term Trends as these are temporally representative of the impacts captured in our risk layers, which are measured relative to a long-term baseline or unmodified landscape (see *2.1 Data layers*).

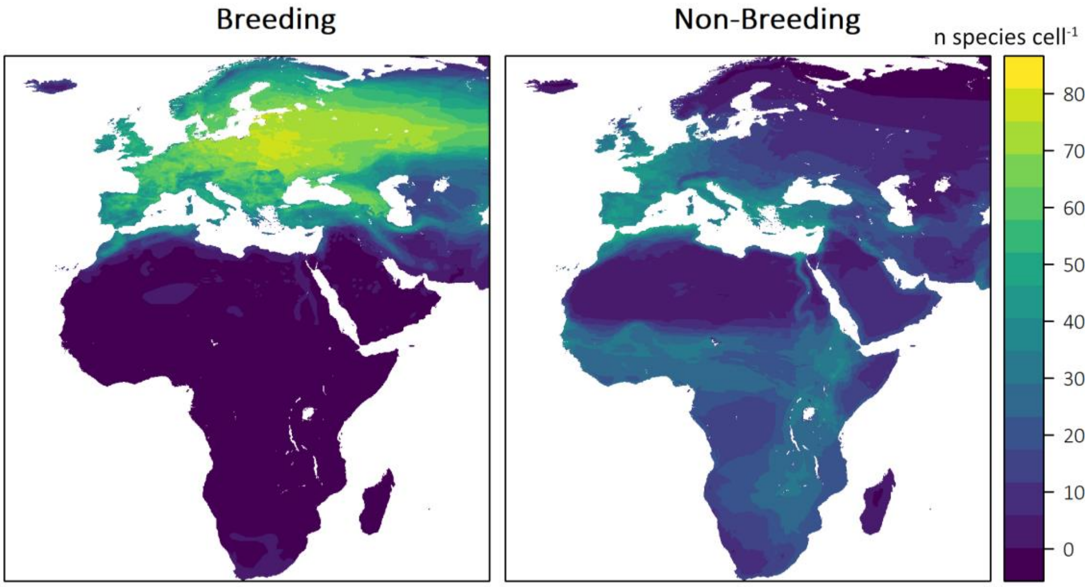

Figure 4.3 – Species richness of breeding and non-breeding ranges of the 103 species included in the analysis across the Afro-Palaearctic study area.

4.2.3 Species' threat-vulnerability weightings

We generated species vulnerability weightings for each of the sixteen threat layers (Figure 4.1) to account for between-species variation in threat relevance. Each layer was min-max bounded so that values fell between 0 (lowest/no threat) to 1 (maximum threat). For each threat, weightings were also min-max bounded, with 0 representing the lowest susceptibility to a given threat, and 1 the highest susceptibility across our species pool. Resulting maps therefore reflect relative risk exposure, rather than absolute risk magnitude – where risk is the combination of threat with vulnerability.

Direct mortality

We weighted species sensitivities to collisions with buildings using vulnerability scores previously calculated by Loss, Will, Loss, et al. (2014) as a function of morphology and behavioural traits, assigning the values of the nearest ecological and morphological equivalents to species not included in their dataset (Appendix S4.4, Table S4.7). For susceptibility to nocturnal lights, we used these same building collision weightings, but reduced the weighting to zero for species groups that do not migrate at night (Families: Accipitridae (minus *Circus* sp. (Spaar & Bruderer, 1997)), Ciconidae and Gruidae). Species that regularly persist in urban areas are considered less vulnerable to negative effects of human disturbance (Bonier et al., 2007; Samia et al., 2015), while flocking species are thought more vulnerable to disturbance. To reflect this, we weighted species sensitivity to roads and human population density as the natural log of the product of two binary traits indicating whether a species exhibits flocking behaviour and whether it exploits urban areas.

To weight direct risks from powerlines and windfarms, we used a combination of morphological and behavioural traits considered indicative of collision vulnerability (e.g. wingload proxy, vision and flight characteristics), adapted from the powerline collision susceptibility weightings developed by D'Amico et al. (2019) – see Appendix S4.4. We did not create species-specific weightings for hunting susceptibility as many of the most widely-used methods (e.g. mist netting) are indiscriminate. For each species, we therefore used mass to determine the relevant hunting layer (small- or large-bodied); corvids (Family: Corvidae), raptors (Order: Accipitriformes) and waders (Order: Charadriiformes) were all considered 'large-bodied' species, regardless of mass.

Habitat change

Anthropogenic conversion of habitats only poses a significant risk to species that are unable to exploit the novel habitat. We therefore extracted habitat-use traits for each species from Cramp et al. (1994) and weighted each anthropogenic land-use according to binary indices indicating whether or not they are used by the species (cropland, grazing, afforestation and urbanisation). For agrochemicals, only species that use cropland habitats were assumed to be vulnerable to pesticides, whereas vulnerability to fertilizers was also extended to species that use pastoral habitat (Vickery et al., 2001). For species whose use of anthropogenic habitat varies between seasons (Cresswell, 2014; Pérez-Tris & Tellería, 2002), we created separate season-specific habitat vulnerability maps. Finally, evidence indicates that habitat generalist species are less susceptible to the effects of land-use change (Blackburn & Cresswell, 2015; Hewson & Noble, 2009). We therefore multiplied the overall combined habitat change risk surface for each species by a habitat specialism score (min-max bounded within the subset of our species) extracted from Morelli et al. (2019).

Climate change

Ecological specialism can influence species vulnerability to climate change (Foden et al., 2008; Pearce-Higgins et al., 2015), as can dispersal ability (Foden et al., 2013). We used ordinal dispersal scores for each species created by Foden et al. (2013) to give more dispersal-limited species higher vulnerability weightings to climate change. We extracted the dietary and habitat specialism scores from Morelli et al. (2019) to calculate the final climate risk weighting for each species as the natural log of the product of degree of dietary specialism, degree of habitat specialism and dispersal vulnerability.

4.2.4 Composite risk-mapping algorithm

Composite risk mapping is complicated by the possibility that risks posed by certain threat layers might be increasive but non-additive, meaning that the presence of multiple spatially contiguous threats may increase the total risk, but to a lesser degree than would be implied by direct summation of threat values (Kennedy et al., 2019). To account for this, we grouped risk layers whose threats were likely to be correlated or non-independent (e.g. human population density, roads and urbanisation), and combined them using fuzzy algebraic sums (Theobald 2013). In cases where threats were independent and thus truly additive (e.g. threat posed by hunting pressure) we used simple summation. As the structure of independent and non-independent threats varied between the three risk types (Figure S4.2), final risk surfaces were given by three different formulae. In all cases, where s is species and i is a cell:

$$Direct\ mortality\ risk_{s,i} = [1 - \prod_{j=1}^{5}\left(1 - M_{i,j}C_{s,j}\right)] + \frac{N_i D_s}{n(j)} + \frac{H_{i,s}}{n(j)}$$

Where j $(1 \leq j \leq 5)$ is indicates one of five non-independent direct mortality layers: {urbanisation, population density, roads, windfarms, powerlines}. $M_{i,j}$ is therefore the value for threat layer *j* in cell i. $C_{s,j}$ is the vulnerability weighting (between 0 and 1) for species s

with respect to layer j. N is the nocturnal lights layer, and D_s is the nocturnal lights weighting coefficient for species s. $H_{i,s}$ is the hunting risk for species s in cell i, which varies spatially and between species (see *2.3 Species' threat-vulnerability weightings*). $n(j)$ denotes the number of layers within j, in this case five.

$$Habitat\ change\ risk_{s,i} = \left\{1 - [1 - \sum_{h=1}^{5}\left(A_{i,h}E_{i,s,h}\right)][1 - \frac{F_i G_{i,s}}{n(h)}]\right\} \times W_s$$

Where h ($1 \leq h \leq 5$) indicates one of five independent habitat layers: {pesticides, cropland, afforestation, urbanisation, grazing}, with $A_{i,j}$ being the value for layer *j* in cell i. $E_{i,s,h}$ is a season-specific weighting coefficient for species s in cell i with respect to layer h. F is fertilizer and $G_{i,s}$ the season-specific fertilizer weighting coefficient for species s in cell i. W_s is the habitat specialism weighting for species s. $n(h)$ denotes the number of layers within h, in this case five.

$$Climate\ change\ risk_{s,i} = [2 - \left(1 - P_{s,i}\right)\left(1 - V_{s,i}\right) - \left(1 - T_{s,i}\right)\left(1 - Y_{s,i}\right)]\ Z_s$$

Where $P_{s,i}$ is precipitation, $V_{s,i}$ is precipitation variability, $T_{s,i}$ is temperature and $Y_{s,i}$ is temperature variability. Z_s is the climate sensitivity weighting for species s.

We clipped the resulting risk surfaces to the relevant species' breeding and non-breeding distribution polygons (BirdLife International & Handbook of the Birds of the World, 2019), using these to calculate mean season-specific exposure for direct mortality risk, habitat change risk and climate change risk for each species.

4.2.5 Statistical analysis

We used linear models with a Gaussian distribution to assess the influence of direct mortality, habitat change and climate change risk exposure on species population trends. We weighted population trends by their inverse standard error, thereby giving greater emphasis in the model to more accurate trend estimates. We also included migratory distance and (logged) body size in all models to control for trend variation attributable to life history characteristics outside those captured in our threat maps. Migratory distance was calculated as the great circle distance between the centroids of the breeding and nonbreeding ranges (Vágási et al., 2016). We created a series of global models, each considering the effects of biologically relevant two-way interactions between variables. We did not examine for any phylogenetic signal in the population trends, as elsewhere little evidence has been found for a phylogenetic structure to the PECBMS population trends (Morelli et al., 2020).

We followed an information theoretic approach (Burnham & Anderson, 2002), in which for each global model, a set of reduced models are ranked using Akaike's Information Criterion adjusted for small sample size (AICc) – considering models within two AICc units competitive. To avoid model-averaging over interaction terms (Cade, 2015), we based inference on the model with the fewest parameters within two AICc units of the top model (Burnham & Anderson, 2002). We scaled and centred all continuous variables prior to analysis.

Statistical and spatial analyses were undertaken using R (R Core Team, 2018), with particular reliance on packages 'MuMIn' (Bartoń, 2019) and 'raster' (Hijmans, 2020).

4.3 RESULTS

Spatial threat patterns

At broad spatial scales, Western and Central Europe consistently emerged as having higher levels of most threat categories than elsewhere within the Afro-Palearctic region; all threat layers showed considerable local-scale variation (Figure 4.4). Habitat change threats were strongly related to elevation, with the Alps, Carpathians, Cantabrians and Dinarides mountain ranges all having noticeably lower levels of habitat change than surrounding regions (Figure 4.4, Figure S4.3, (Danielson & Gesch, 2010)). The reverse was true for climate change threats, where higher elevation regions generally coincided with more extreme anomalies, particularly in the breeding season (Figure 4.4, Figure S4.4). Hotspots of high composite threat levels also exist in the Nile delta, Western Levant and Indus valley, where concentrated human population density, associated infrastructure and intensive land-use also notably coincide with high species richness of migratory birds (Figure 4.3, Figure S4.5).

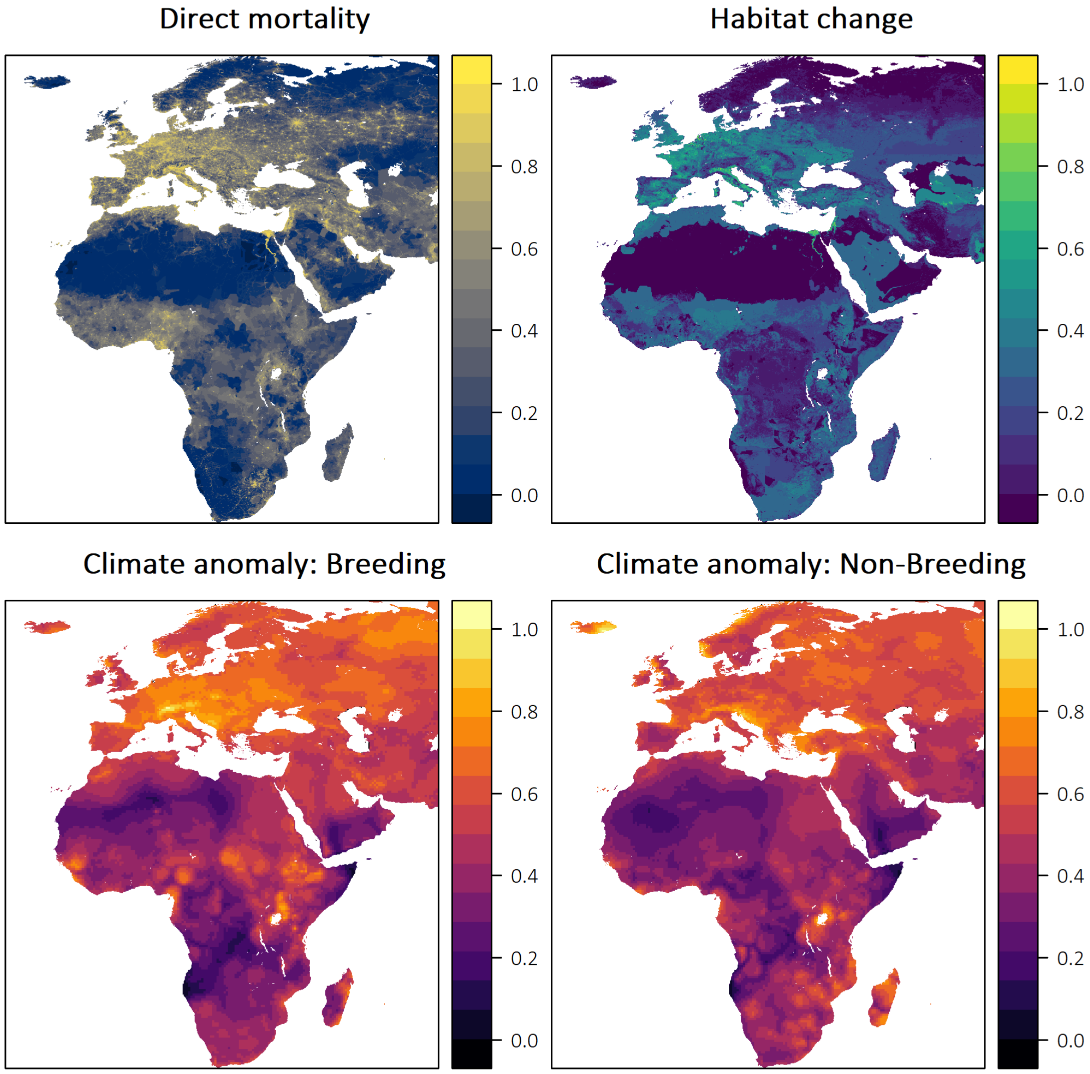

Figure 4.4 – Composite maps for the three risk layer groups. In all cases, 1 indicates the maximum relative risk level and 0 indicates minimum relative risk level. Climate anomalies vary seasonally, so we created separate risk surfaces for the breeding and non-breeding seasons. Maps represent the unweighted combination of their constituent layers, i.e. with no species-specific information fed into their creation.

Population trend analysis

The population trend analysis yielded two similarly well-performing models, reduced from different global models and indistinguishable by AICc (Tables S4.8 and S4.9). In both models, population trends increased with body size, and decreased with migratory distance and exposure to non-breeding range direct mortality (Figures 4.5a and 4.5c); coefficient size and direction for these parameters were similar between the models (Table 4.2). Both competitive models retained an additional (but different) two-way interaction. Model1 retained a negative influence of non-breeding climate change that weakened with increasing migratory distance (Figure 4.5b). Model2 retained a negative effect of direct mortality risk exposure in the breeding range, mediated by the extent of breeding range habitat change (weaker for species whose ranges had lower levels of habitat loss; Figure 4.5d). We generated bivariate maps to show the relative co-occurrence of each risk type in space (Figure 4.6). These maps highlight the relatively low exposure to climate change for long-distance migrants wintering in parts of central Africa (yellow cells in Figure 4.6a) relative to those travelling to eastern and southern Africa where composite climate anomalies are greater (purple tones in Figure 4.6a). They also highlight the high congruence of direct mortality and habitat change threats for species wintering in the Sahel region (purple tones in Figure 4.6b), with humid zones of central Africa showing higher direct mortality risks but lower habitat change (blue tones in Figure 4.6b) and the opposite in southern Africa (yellow tones in Figure 4.6b).

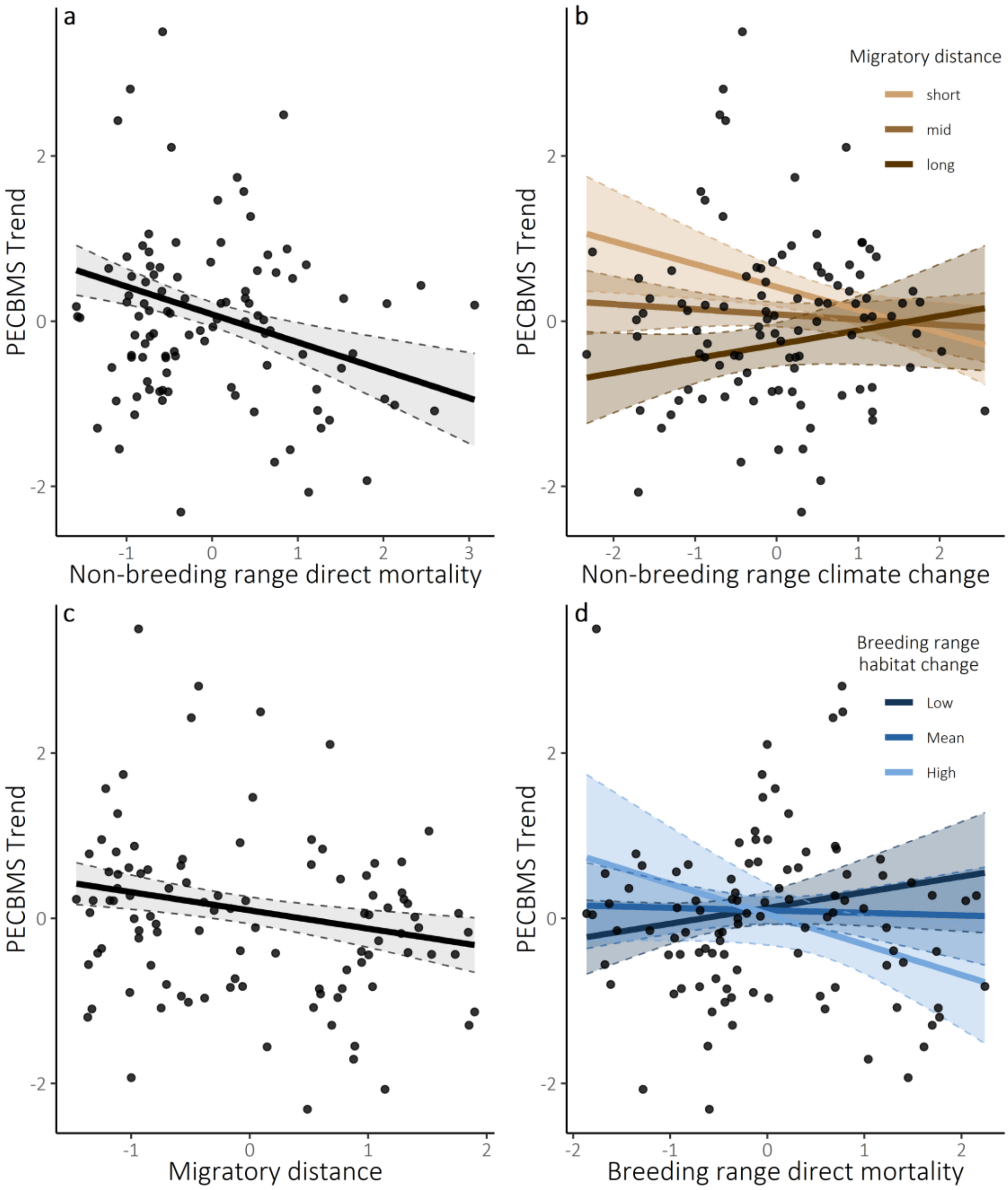

Figure 4.5 – Effects of spatially quantified threats on species population trends: a) Non-breeding direct mortality risk exposure; b) non-breeding climate change risk exposure, with model-predicted slopes for short (10th percentile), mean and long (90th percentile) migration distances; c) Migratory distance; d) Breeding range direct mortality risk exposure, with slopes predicted for low (10th percentile), mean and high (90th percentile) levels of breeding range habitat change. Dashed lines represent associated 95% confidence intervals, and points indicate raw values for each species.

Table 4.2 – Coefficient estimates (β) and associated standard errors (SE), 95% confidence intervals (L95 and U95) and P*-values for the two best-supported models to explain species population trends. Bold text indicates variables significant/important in the model (alpha level = 0.05/confidence intervals excluding zero).*

	Coefficient	Figure	β	SE	L95	U95	*t*	*P-value*
Model1 (adj. R^2: 0.19)								
	Intercept	-	0.08	0.08	-0.07	0.23	1.09	0.280
	Migratory distance	**-**	**-0.27**	**0.08**	**-0.44**	**-0.11**	**-3.38**	**0.001**
	Body mass	**-**	**0.24**	**0.09**	**0.07**	**0.41**	**2.79**	**0.006**
	Non-breeding season direct mortality	**4.5a**	**-0.34**	**0.09**	**-0.51**	**-0.16**	**-3.83**	**< 0.001**
	Non-breeding season climate change	-	-0.06	0.08	-0.22	0.09	-0.80	0.427
	Non-breeding season climate change : Migratory distance	**4.5b**	**0.18**	**0.07**	**0.03**	**0.32**	**2.42**	**0.017**
Model2 (adj. R^2: 0.20)								
	Intercept	-	0.10	0.08	-0.07	0.26	1.15	0.251
	Migratory distance	**4.5c**	**-0.22**	**0.07**	**-0.37**	**-0.08**	**-3.02**	**0.003**
	Body mass	**-**	**0.28**	**0.09**	**0.11**	**0.45**	**3.23**	**0.002**
	Direct mortality	**-**	**-0.31**	**0.13**	**-0.57**	**-0.05**	**-2.34**	**0.021**
	Breeding season habitat change	-	-0.03	0.10	-0.24	0.17	-0.32	0.751
	Breeding season direct mortality	-	-0.03	0.13	-0.29	0.23	-0.23	0.816
	Breeding season direct mortality : Breeding season habitat change	**4.5d**	**-0.24**	**0.09**	**-0.42**	**-0.06**	**-2.67**	**0.009**

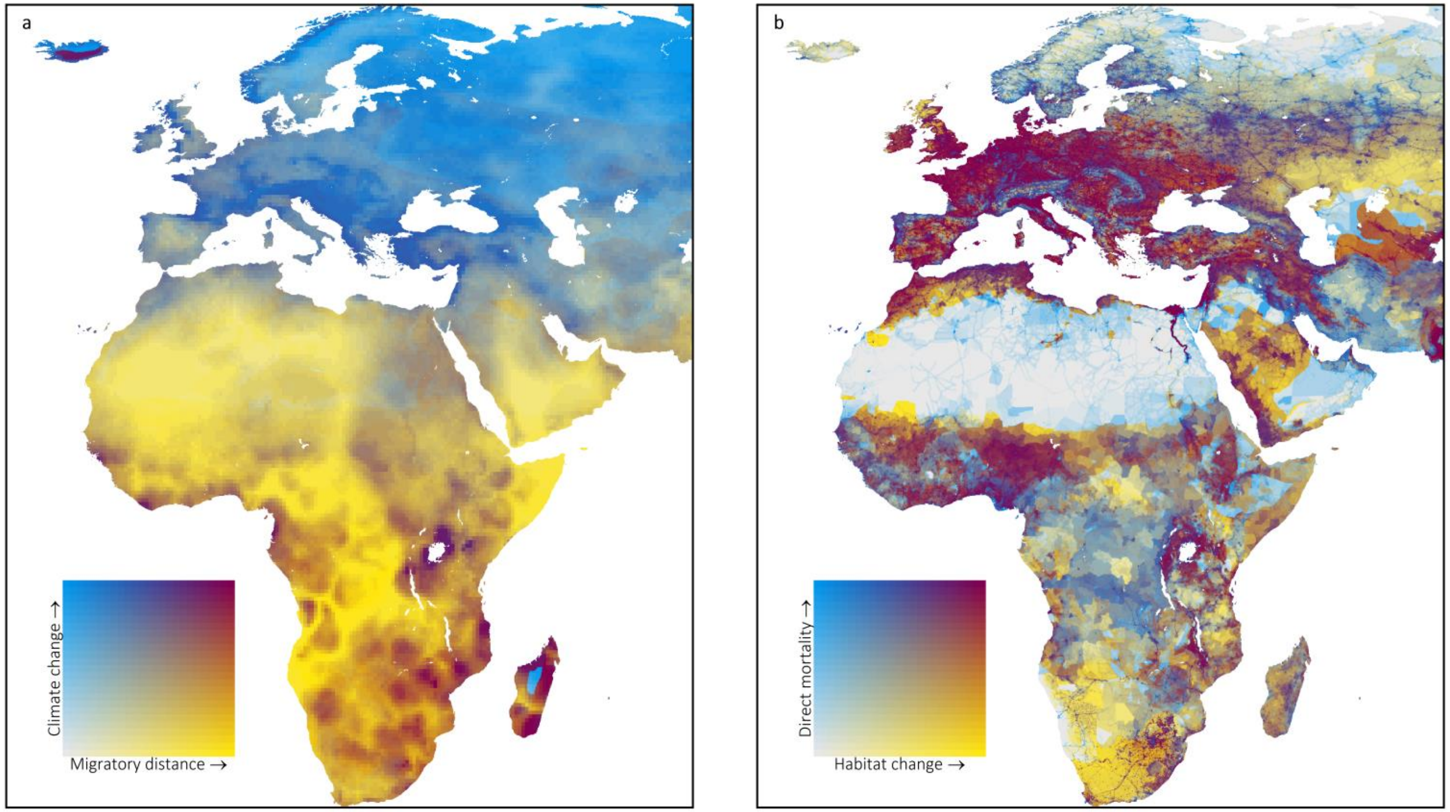

Figure 4.6 – a) Bivariate map showing the unweighted climate change risk surface for the non-breeding season (grey to blue y-axis) and the mean migratory distance undertaken by PECBMS species occurring in each cell in the non-breeding season (grey to yellow x-axis). Purple regions indicate where high levels of non-breeding climate change coincide with longer-distance migratory species; b) Bivariate map showing the unweighted risk surface for habitat change (grey to yellow x-axis) and unweighted risk surface for direct mortality (grey to blue y-axis). Purple regions indicate where high levels of both direct mortality risk and habitat change risk coincide.

4.4 DISCUSSION

Our composite threat maps demonstrate the variation in intensity and spatial distribution of threats to migratory birds across species' seasonal ranges. Range-scale species risk exposure had significant power in explaining variation in population trends across species. We found a consistent negative relationship between population trends and range-scale exposure to direct mortality risks during the non-breeding season, suggesting that anthropogenic factors influencing survival during winter and on migration (including hunting, nocturnal lights and infrastructure) play an important role in driving declines. We also found some evidence for a negative effect of non-breeding range climate change, mediated by migratory distance, and a negative effect of breeding range direct mortality risk, mediated by extent of habitat change.

Non-breeding season direct mortality

Our results represent the first evidence for overarching population-scale effects of anthropogenic sources of mortality on avian migrants at a continental scale (see also US bird mortality estimates presented in Loss et al. (2012; 2015)). Despite relative threat levels being lower across non-breeding range areas than breeding ranges on average (Figure 4.4), non-breeding season direct mortality risk exposure more consistently explained variation in population trends than that for the breeding season (Table 4.2). As our models accounted for a negative effect of migratory distance on population trends, this result indicates that exposure to direct mortality risks may have particularly acute effects on individuals in the non-breeding season. This could be related to differences in behaviour, movement or local habitat use between seasons – for example, as birds are generally central place foragers in the breeding season (with movements limited by proximity to nest), their vulnerability to direct mortality risks such as infrastructure collision and hunting may be reduced relative to the non-breeding season. Birds are typically more itinerant outside of the breeding season, possibly putting them at greater risk of exposure to direct mortality threats within their surroundings (Silva et al., 2014; Thaxter et al., 2019).

Climate change effects mediated by migratory distance

We found a negative effect of climate change risk exposure on the non-breeding grounds, but only for short distance migratory birds (Figure 4.5b). The shorter-distance migrants within our dataset largely remain within Europe year-round; these species therefore generally face greater exposure to climate anomalies than those reaching sub-Saharan Africa in the temperate winter (Figure 4.6a). Population trends of the longest distance migrants in our dataset were less negatively influenced by non-breeding climate change (although with considerable uncertainty around these slopes). Many long-distance migrants have previously shown to be highly sensitive to non-breeding season climate, particularly rainfall levels within the Sahel (Szép, 1995; Winstanley et al., 1974). There is some evidence for increased rainfall and greening in the Sahel in recent decades (Biasutti, 2019; Maidment et al., 2015; Olsson et al., 2005), potentially improving wintering conditions for migrants to these regions. This result contrasts with that of Howard et al. (2020), who found population trends of short-distance migrants were better explained by breeding season climate than non-breeding season. This divergence may relate to our inclusion of direct mortality threats as a predictor (not accounted for in the models of Howard et al. (2020)), as this variable explains a significant amount of trend variation, and may therefore influence the direction or magnitude of patterns detected for other variables.

Breeding season direct mortality mediated by habitat change

We found a negative effect of exposure to direct mortality risks within the breeding range, particularly for species exposed to increased habitat change (Figure 4.5d). This is unsurprising, as populations inhabiting low-quality habitats may be more vulnerable to stochastic mortality, while those in high quality sites may be buffered from population-level effects of direct mortality (Morrison et al., 2013). Species whose breeding ranges have undergone high levels of habitat change may also be more vulnerable to direct mortality, via, for instance, increased foraging distance (Tremblay et al., 2004) leading to greater exposure to sources of direct mortality such as human infrastructure within home ranges.

This between-threat interaction was not detected for the non-breeding range, again potentially indicating seasonal differences in threat relevance, as detected elsewhere (Howard et al., 2020; Vickery et al., 2014). Our findings contrast with recent evidence for the importance of non-breeding season land-cover for population trends (Howard et al., 2020), but again this may be explained by the inclusion of non-breeding direct mortality threats in our analysis. Our risk surfaces suggest that habitat in sub-Saharan Africa has generally undergone less drastic habitat degradation than in Europe (Figure 4.4), perhaps explaining the weaker interaction with direct mortality. Also, avian habitat requirements during the non-breeding season are typically more generalist than in the breeding season (Blackburn & Cresswell, 2015), potentially making migrants less vulnerable to habitat change outside the breeding season.

Hunting patterns

Hunting is a complex and sensitive cultural issue, with a wide variety of drivers (subsistence/bushmeat, sport, tradition/heritage, magic/fetish), each varying and interacting with culture and geography (Buij et al., 2016; Hirschfeld & Heyd, 2005; Milner-Gulland et al., 2003). Our relative bird hunting pressure maps (Figure 4.2) broadly align with local patterns identified elsewhere (Brochet et al., 2016; Brochet, Jbour, et al., 2019; Brochet, Van Den Bossche, et al., 2019; Schneider-Jacoby & Spangenberg, 2010), including relatively low levels of hunting in Israel and Palestine in contrast to Lebanon, Syria and (for small-bodied birds) Egypt, notably low levels of hunting in Switzerland, high levels of hunting large-bodied birds in Azerbaijan, and the prominence of Italy and Cyprus for the hunting of small-bodied birds, with respondents highlighting trade to Italy as a driver of passerine hunting in the Balkans. In sub-Saharan Africa, demand for bushmeat is increasing (Whytock et al., 2016), as is accessibility through construction of roads (Milner-Gulland et al., 2003). We show Nigeria, Malawi and Guinea-Conakry to be particular hotspots for bird hunting, with survey respondents noting drivers relating to subsistence, fetish (see Buij et al. (2016)), increasing availability of guns, and a particularly significant culture of hunting in Guinea-Conakry. In contrast, our survey revealed low relative levels of bird hunting in Eritrea and Djibouti, and respondents pointed to the demilitarisation of Mozambique as contributing to low hunting pressure there. Medium- to large-scale variation in hunting pressure may to some extent be driven by abundance of migratory birds, and therefore flyways – for instance Tunisia, Cyprus and the Black Sea–Mediterranean flyway, the Balkans and the Adriatic flyway, Egypt and the Red Sea migration bottleneck. Ultimately, our findings reinforce that drivers of hunting pressure are complex interactions of geographical, cultural, political, and socioeconomic factors.

Study limitations

The results presented here are only as reliable as the underlying data. Greater knowledge of species' ecology outside breeding ranges could improve the fine-tuning of threat exposure (Faaborg et al., 2010), particularly for non-breeding season ecological requirements, as well as better-defined wintering areas and migratory routes / connectivity (Martin et al., 2007). Indeed, other studies have identified high rates of mortality on migration (Klaassen et al., 2014; Sillett & Holmes, 2002), and strong links between migratory route and population trends (Hewson et al., 2016; Lisovski et al., 2020). Explicitly combining the threat layers assembled here with detailed tracking data will shed light on the processes underlying declines of migratory species.

Our threat layers almost certainty under-estimate some risks, particularly in regions outside of Europe where non remote-sensed data is often more coarse. While our hunting layer is the first assessment of pan-continental bird hunting pressure, it relies on expert opinion and may therefore be vulnerable to bias. Finally, our trend analyses may be sensitive to the timescale over which impacts have occurred. Certain threats, particularly energy infrastructure, have accelerated in recent years, the effects of which may be only weakly reflected (if at all) in the c. 35-year PECBMS trends. The inverse may also be the case, if PECBMS trends suffer ‘shifting baseline syndrome’ (Papworth et al., 2009). The period over which the PECBMS trends are calculated begins in 1980; elsewhere, analysis of species breeding in England has found that the greatest declines in trans-Saharan migrants occurred prior to 1986, particularly in those migrants to arid-savannah regions (Thaxter et al., 2010). In general, species’ responses to anthropogenic threats may be non-linear, idiosyncratic, and suffer from time-lag effects (Bonnet-Lebrun et al., 2020; Buchanan et al., 2020; Menéndez et al., 2006), weakening our ability to detect overarching population-scale effects.

4.5 CONCLUSIONS

We present a macroecological approach to comprehensive risk mapping for migratory species. Spatially explicit risk mapping allowed us to detect novel evidence for population-level effects of direct mortality risks among Afro-Palaearctic migratory birds, and novel patterns of between-risk synergy. Our results point to the potential for cumulative and interactive effects of different direct mortality threats, with both habitat loss and climate change being important in mediating more direct threats such as hunting and infrastructure development. Risks posed by direct mortality threats may be both the easiest to detect and the easiest to mitigate, due to the ‘acute’ nature of immediate mortality threats in contrast to chronic, insidious effects of changes to habitat and climate (Doherty et al., 2021). Successful mitigation of threats to migratory species will rely on comprehensive understanding of potentially complex interactions between threats; our results emphasise the importance of full-season and spatially explicit approaches to quantifying anthropogenic drivers of population declines.

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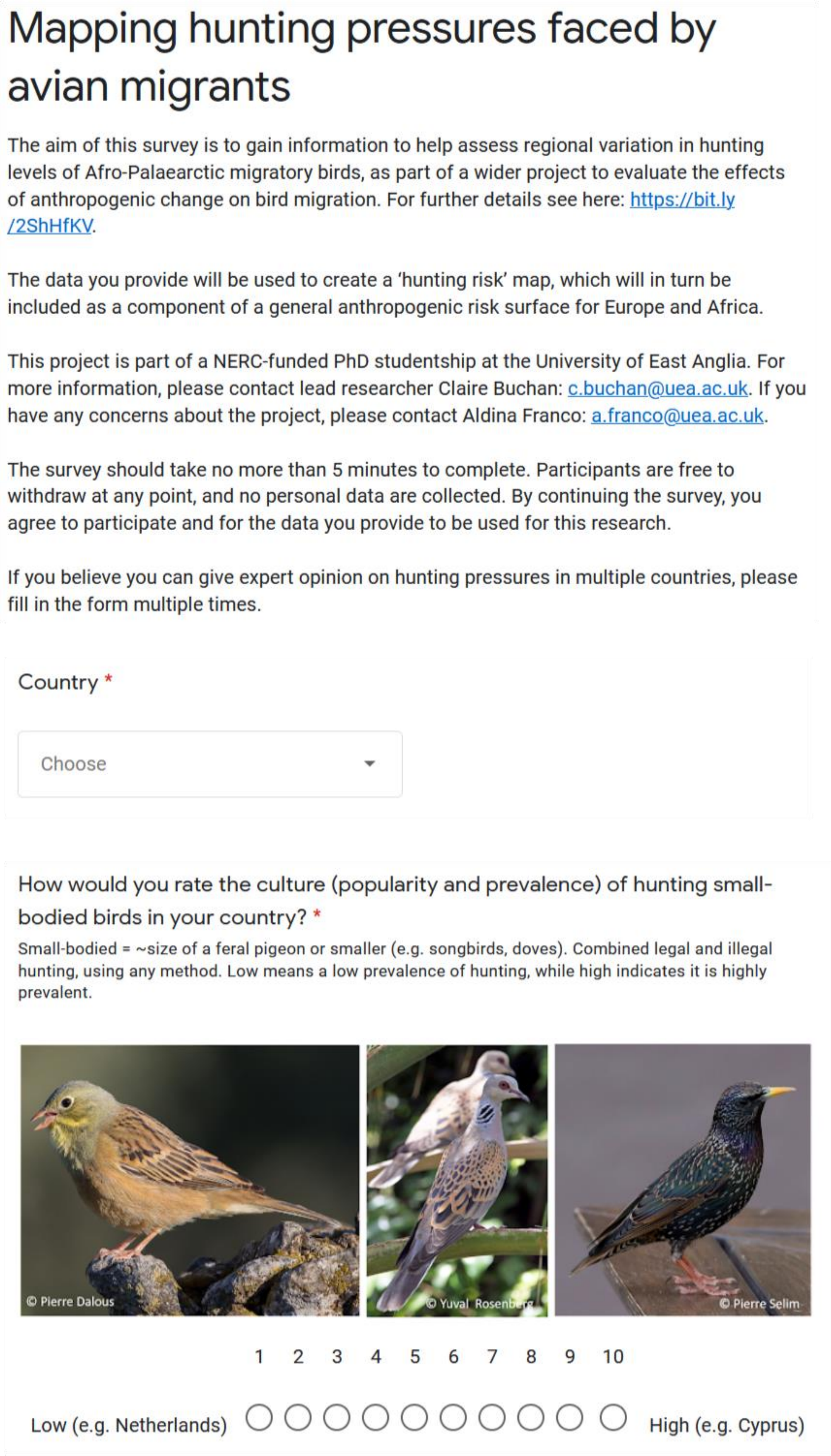
Chapter 4 Supplementary Materials

Appendix S4.1 Bird hunting survey



Mapping hunting pressures faced by avian migrants

The aim of this survey is to gain information to help assess regional variation in hunting levels of Afro-Palaearctic migratory birds, as part of a wider project to evaluate the effects of anthropogenic change on bird migration. For further details see here: https://bit.ly/2ShHfKV.

The data you provide will be used to create a 'hunting risk' map, which will in turn be included as a component of a general anthropogenic risk surface for Europe and Africa.

This project is part of a NERC-funded PhD studentship at the University of East Anglia. For more information, please contact lead researcher Claire Buchan: c.buchan@uea.ac.uk. If you have any concerns about the project, please contact Aldina Franco: a.franco@uea.ac.uk.

The survey should take no more than 5 minutes to complete. Participants are free to withdraw at any point, and no personal data are collected. By continuing the survey, you agree to participate and for the data you provide to be used for this research.

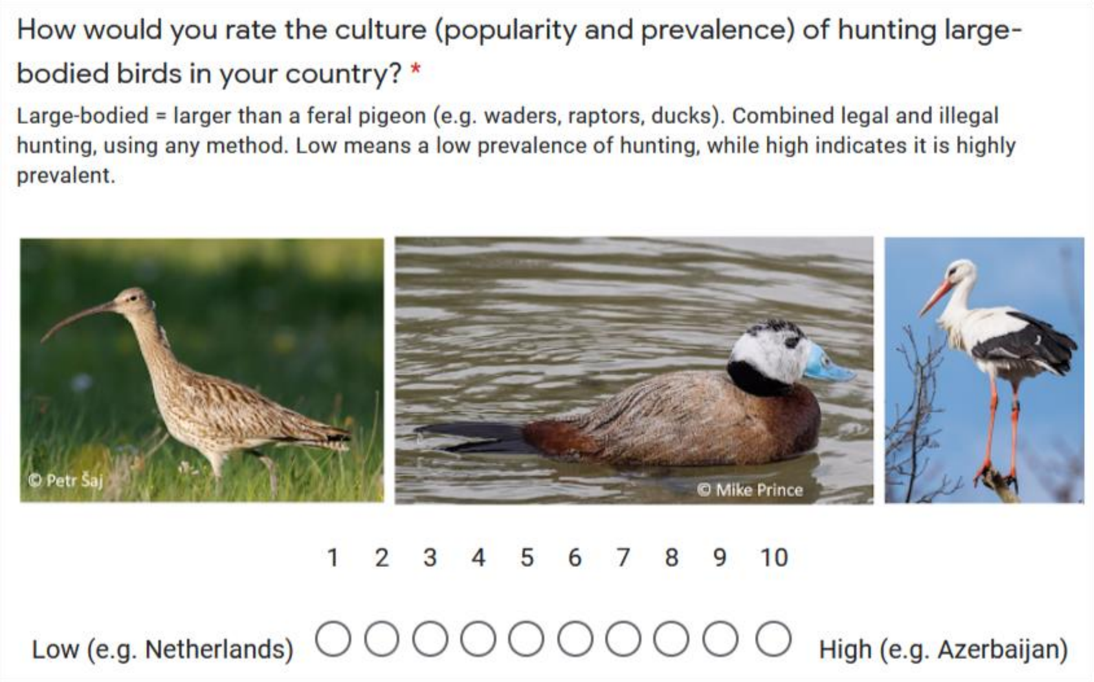
If you believe you can give expert opinion on hunting pressures in multiple countries, please fill in the form multiple times.

Country *

How would you rate the culture (popularity and prevalence) of hunting small-bodied birds in your country? *

Small-bodied = ~size of a feral pigeon or smaller (e.g. songbirds, doves). Combined legal and illegal hunting, using any method. Low means a low prevalence of hunting, while high indicates it is highly prevalent.

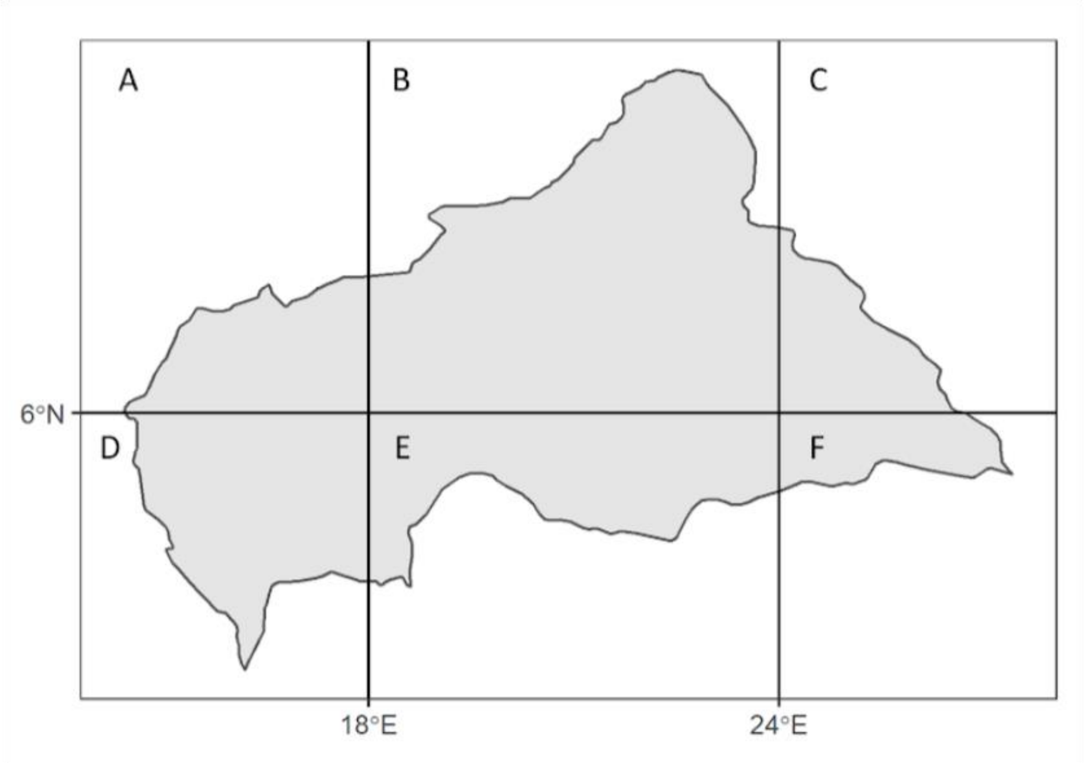
	1	2	3	4	5	6	7	8	9	10	
Low (e.g. Netherlands)	○	○	○	○	○	○	○	○	○	○	High (e.g. Cyprus)



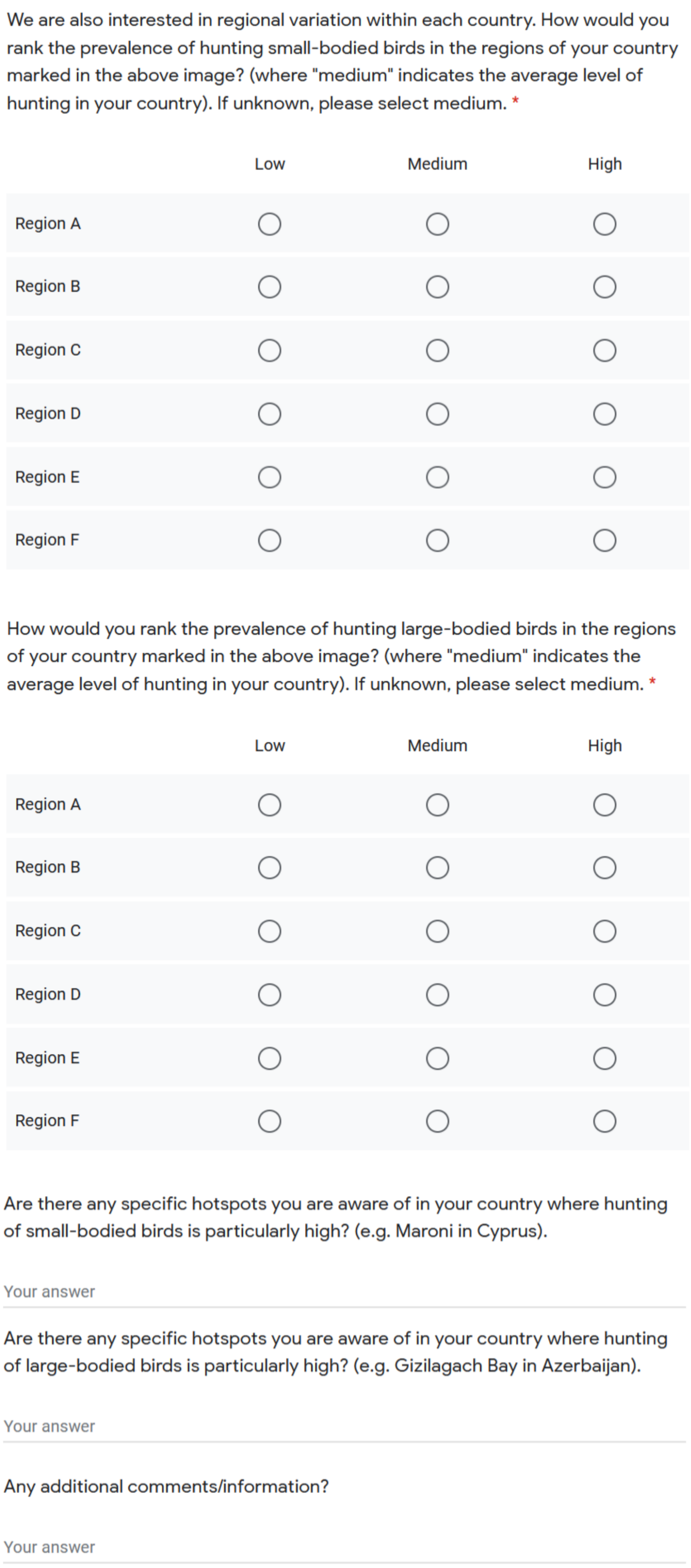
How would you rate the culture (popularity and prevalence) of hunting large-bodied birds in your country? *

Large-bodied = larger than a feral pigeon (e.g. waders, raptors, ducks). Combined legal and illegal hunting, using any method. Low means a low prevalence of hunting, while high indicates it is highly prevalent.

	1	2	3	4	5	6	7	8	9	10	
Low (e.g. Netherlands)	○	○	○	○	○	○	○	○	○	○	High (e.g. Azerbaijan)



(Map and regions generated according to respondent's country selection.)



We are also interested in regional variation within each country. How would you rank the prevalence of hunting small-bodied birds in the regions of your country marked in the above image? (where "medium" indicates the average level of hunting in your country). If unknown, please select medium. *

	Low	Medium	High
Region A	○	○	○
Region B	○	○	○
Region C	○	○	○
Region D	○	○	○
Region E	○	○	○
Region F	○	○	○

How would you rank the prevalence of hunting large-bodied birds in the regions of your country marked in the above image? (where "medium" indicates the average level of hunting in your country). If unknown, please select medium. *

	Low	Medium	High
Region A	○	○	○
Region B	○	○	○
Region C	○	○	○
Region D	○	○	○
Region E	○	○	○
Region F	○	○	○

Are there any specific hotspots you are aware of in your country where hunting of small-bodied birds is particularly high? (e.g. Maroni in Cyprus).

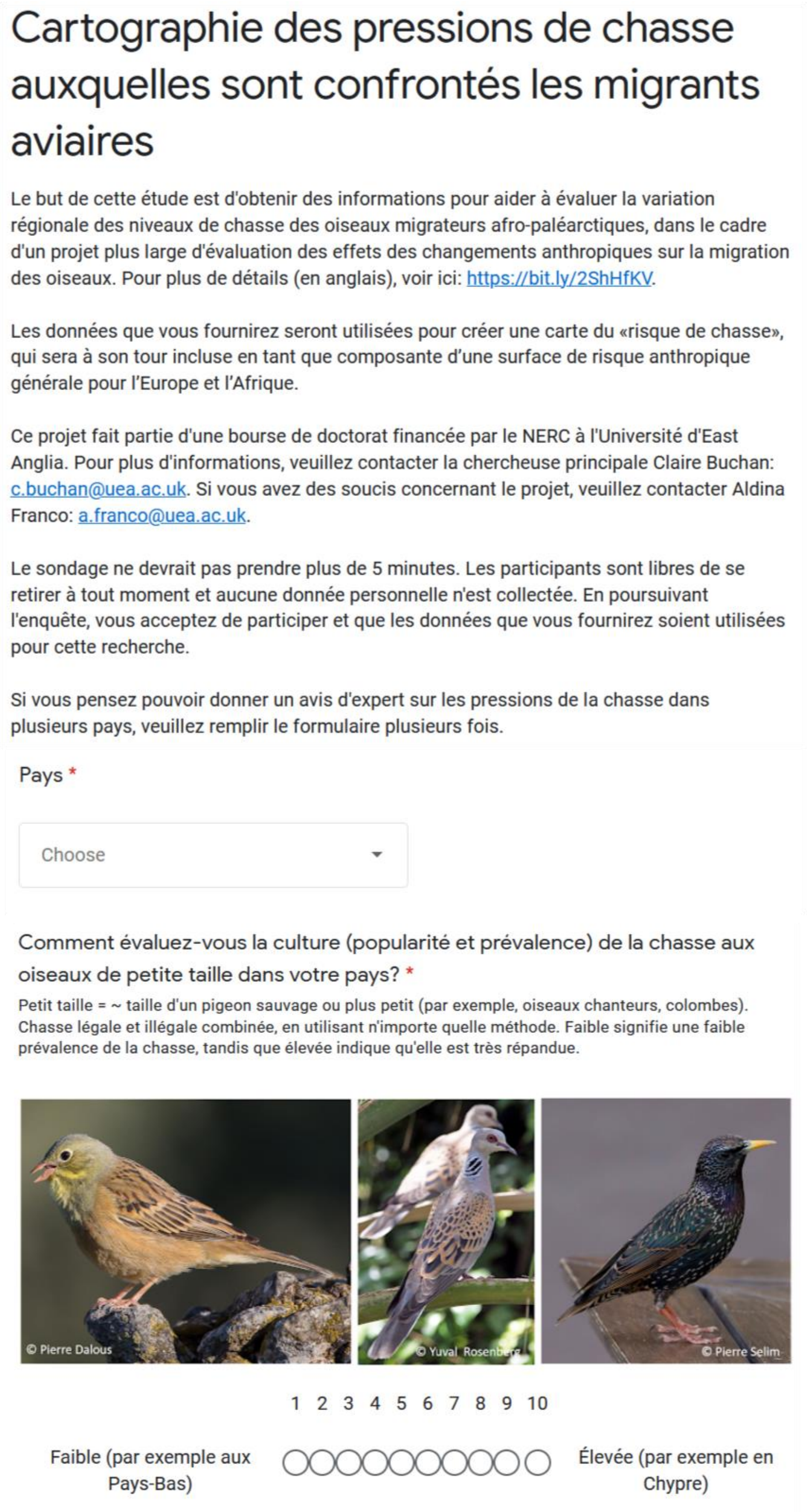
Your answer

Are there any specific hotspots you are aware of in your country where hunting of large-bodied birds is particularly high? (e.g. Gizilagach Bay in Azerbaijan).

Your answer

Any additional comments/information?

Your answer



Cartographie des pressions de chasse auxquelles sont confrontés les migrants aviaires

Le but de cette étude est d'obtenir des informations pour aider à évaluer la variation régionale des niveaux de chasse des oiseaux migrateurs afro-paléarctiques, dans le cadre d'un projet plus large d'évaluation des effets des changements anthropiques sur la migration des oiseaux. Pour plus de détails (en anglais), voir ici: https://bit.ly/2ShHfKV.

Les données que vous fournirez seront utilisées pour créer une carte du «risque de chasse», qui sera à son tour incluse en tant que composante d'une surface de risque anthropique générale pour l'Europe et l'Afrique.

Ce projet fait partie d'une bourse de doctorat financée par le NERC à l'Université d'East Anglia. Pour plus d'informations, veuillez contacter la chercheuse principale Claire Buchan: c.buchan@uea.ac.uk. Si vous avez des soucis concernant le projet, veuillez contacter Aldina Franco: a.franco@uea.ac.uk.

Le sondage ne devrait pas prendre plus de 5 minutes. Les participants sont libres de se retirer à tout moment et aucune donnée personnelle n'est collectée. En poursuivant l'enquête, vous acceptez de participer et que les données que vous fournirez soient utilisées pour cette recherche.

Si vous pensez pouvoir donner un avis d'expert sur les pressions de la chasse dans plusieurs pays, veuillez remplir le formulaire plusieurs fois.

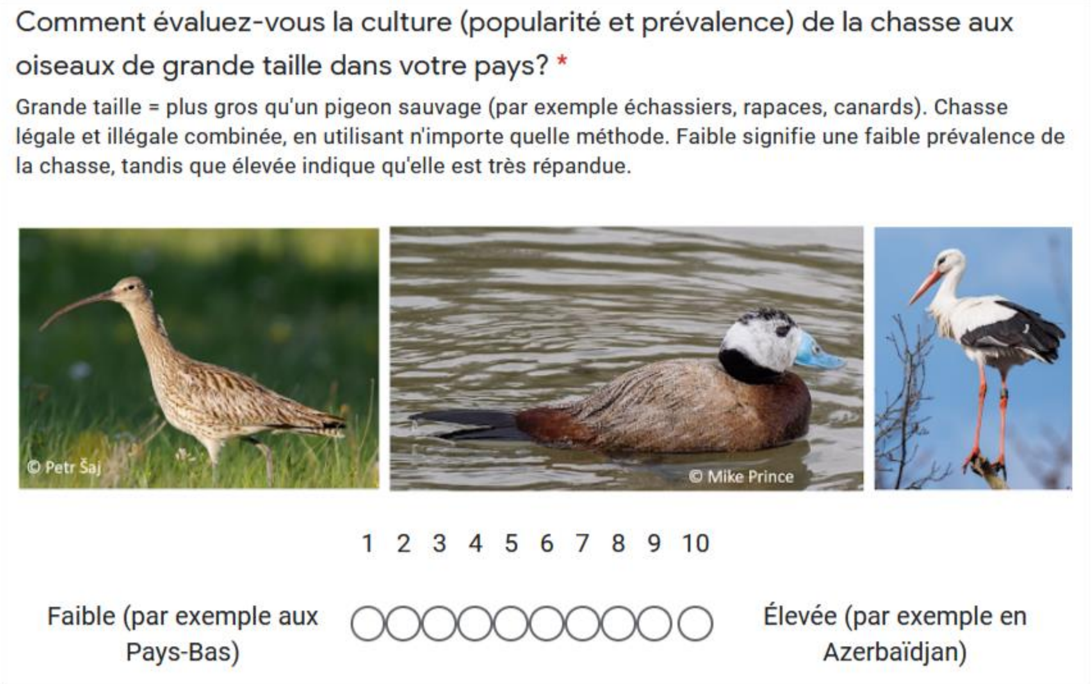
Pays *

Choose ▾

Comment évaluez-vous la culture (popularité et prévalence) de la chasse aux oiseaux de petite taille dans votre pays? *

Petit taille = ~ taille d'un pigeon sauvage ou plus petit (par exemple, oiseaux chanteurs, colombes). Chasse légale et illégale combinée, en utilisant n'importe quelle méthode. Faible signifie une faible prévalence de la chasse, tandis que élevée indique qu'elle est très répandue.

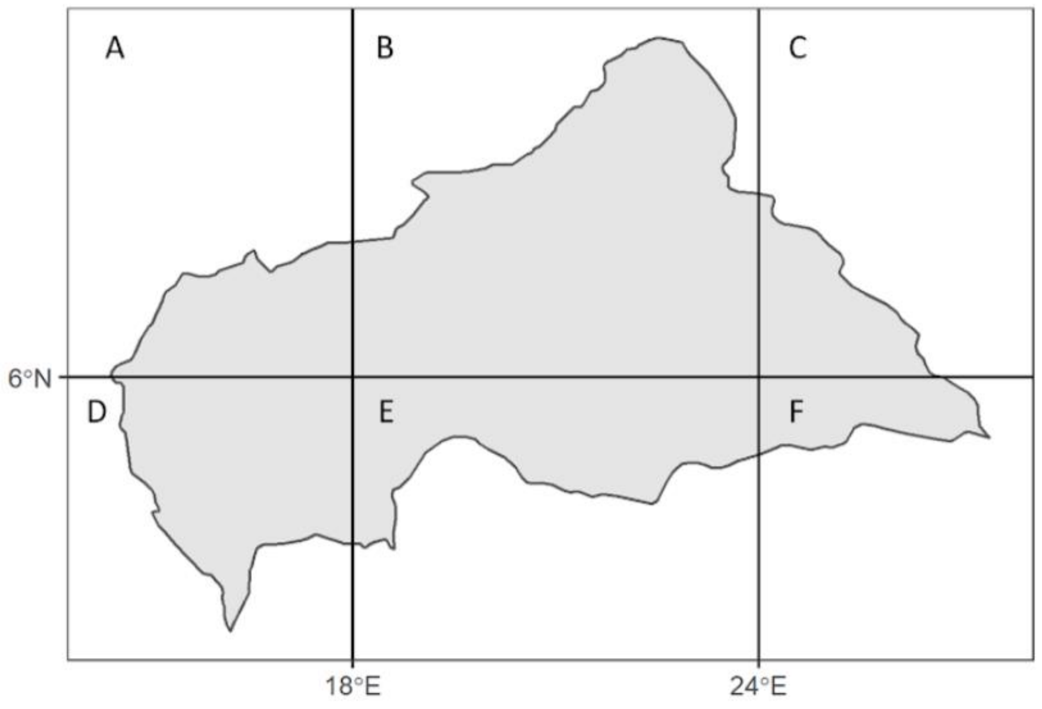
	1	2	3	4	5	6	7	8	9	10	
Faible (par exemple aux Pays-Bas)	○	○	○	○	○	○	○	○	○	○	Élevée (par exemple en Chypre)



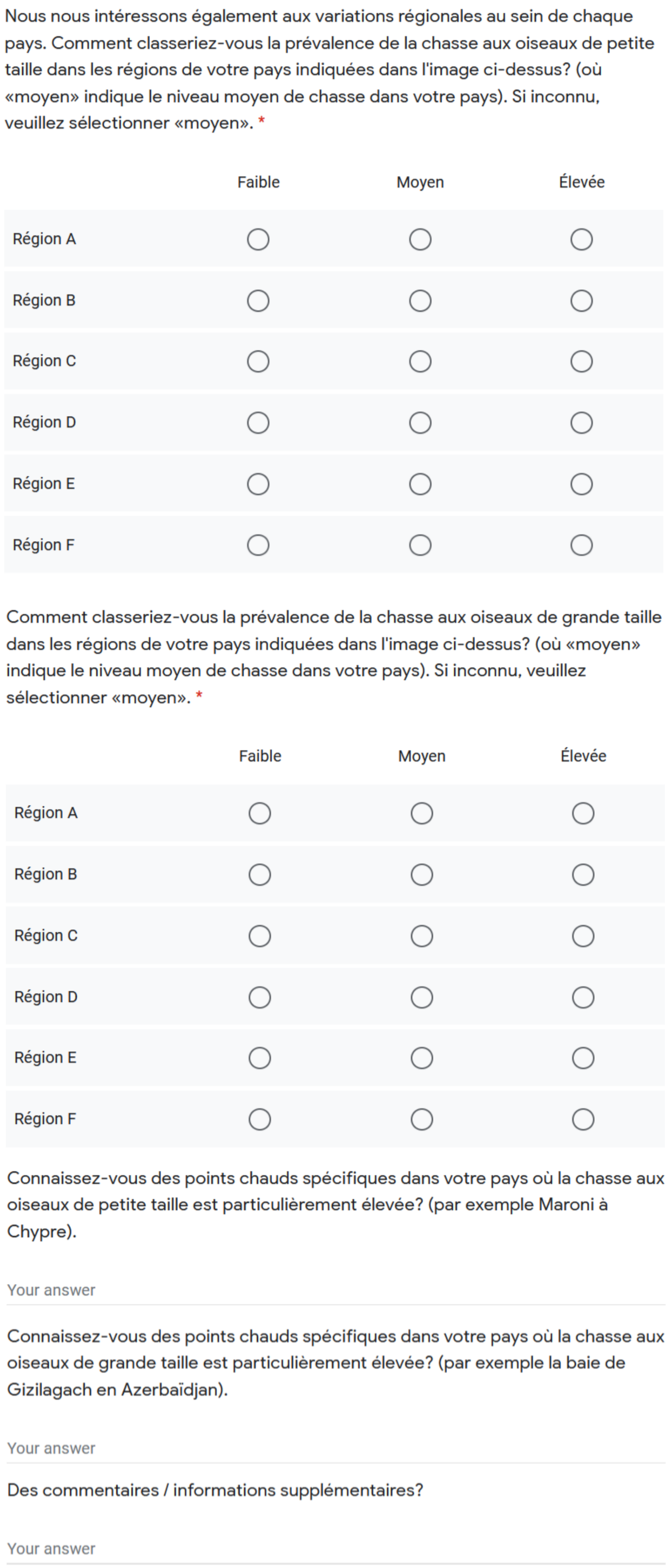
Comment évaluez-vous la culture (popularité et prévalence) de la chasse aux oiseaux de grande taille dans votre pays? *

Grande taille = plus gros qu'un pigeon sauvage (par exemple échassiers, rapaces, canards). Chasse légale et illégale combinée, en utilisant n'importe quelle méthode. Faible signifie une faible prévalence de la chasse, tandis que élevée indique qu'elle est très répandue.

	1	2	3	4	5	6	7	8	9	10	
Faible (par exemple aux Pays-Bas)	○	○	○	○	○	○	○	○	○	○	Élevée (par exemple en Azerbaïdjan)



(Map and regions generated according to respondent’s country selection.)



Nous nous intéressons également aux variations régionales au sein de chaque pays. Comment classeriez-vous la prévalence de la chasse aux oiseaux de petite taille dans les régions de votre pays indiquées dans l'image ci-dessus? (où «moyen» indique le niveau moyen de chasse dans votre pays). Si inconnu, veuillez sélectionner «moyen». *

	Faible	Moyen	Élevée
Région A	○	○	○
Région B	○	○	○
Région C	○	○	○
Région D	○	○	○
Région E	○	○	○
Région F	○	○	○

Comment classeriez-vous la prévalence de la chasse aux oiseaux de grande taille dans les régions de votre pays indiquées dans l'image ci-dessus? (où «moyen» indique le niveau moyen de chasse dans votre pays). Si inconnu, veuillez sélectionner «moyen». *

	Faible	Moyen	Élevée
Région A	○	○	○
Région B	○	○	○
Région C	○	○	○
Région D	○	○	○
Région E	○	○	○
Région F	○	○	○

Connaissez-vous des points chauds spécifiques dans votre pays où la chasse aux oiseaux de petite taille est particulièrement élevée? (par exemple Maroni à Chypre).

Your answer

Connaissez-vous des points chauds spécifiques dans votre pays où la chasse aux oiseaux de grande taille est particulièrement élevée? (par exemple la baie de Gizilagach en Azerbaïdjan).

Your answer

Des commentaires / informations supplémentaires?

Your answer

Appendix S4.2 Data layers

Layers cover terrestrial surfaces in the region bounded by (-28.3°, 69.5°, -34.92°, 71.17°) – hereafter referred to as the Afro-Palaearctic region. This boundary was set by the maximum extents of two datasets for which global-scale coverage was not available (powerlines and hunting), and includes the major flyways and seasonal ranges of most migratory bird species in the Afro-Palaearctic system. Each layer measured the current extent of human modification of the natural environment, relative either to a baseline period (climate variables and afforestation) or to an equivalent un-modified landscape (land-use and infrastructure). All layers were min-max bounded prior to use in our algorithms, such that all values fell between 0 and 1, with 0 indicating the lowest level of modification, and 1 indicating the highest level of modification.

Human population density

We used the CIESIN Gridded Population of the World (GPW v4.11) human population density layer for 2015 (CIESIN, 2018), in which the value for each cell is an estimate of number of persons per km^2. We aggregated this from a resolution of 2.5 arcminutes to 5 arcminutes, clipped to the Afro-Palaearctic region, collapsed the top 0.1%, and log(x+1) transformed the layer (Kennedy et al., 2019).

Land use

To map habitat conversion to agriculture, we used the HYDE 3.2.1 cropland and grazing land layers created by Klein Goldewijk et al. (2017) for the year 2017. The cell values in these rasters represent the area per cell of land devoted to the respective land use (cropland and grazing land), as defined by the UN FAO as 'Arable land and permanent crops' and 'Permanent pasture' respectively (http://www.fao.org/ag/agn/nutrition/Indicatorsfiles/Agriculture.pdf). To map anthropogenic afforestation, we quantified gains in forest cover between 1985 and 2017. We used a baseline land-cover map created by Meiyappan & Jain (2012) for 1985, from which we extracted and summed the all forest land-cover classes (Table S4.1) to create a single percentage forest cover for 1985. To create a modern forest cover layer, we repeated this process for the MODIS MCD12C1 multiband percentage land cover for 2017 (median year of our risk layers) (Friedl & Sulla-Menashe, 2015), summing the values of land cover classifications given in Table S4.1. The historic land-cover layer was at a resolution of 30 arcminutes, so we disaggregated this by a factor of 10 to match the 3-arcminute resolution of the 2017 forest layer, and reprojected both layers to EPSG: 4326. Finally, to create the afforestation layer, we subtracted the baseline forest cover layer from the modern forest cover layer, thereby obtaining gridded data on the proportion of each cell converted from non-forest to forest. We assigned all cells with negative values (deforestation) a value 0. We aggregated the layer to a final resolution of 5 arcminutes to match other datasets, and clipped it to the Afro-Palaearctic extent.

Table S4.1 – Land cover categories included in the creation of a single forest layer for the baseline (1985) and modern (2017) periods.

Historic land cover 1985	MODIS Land Cover Type 1 2017
Tropical Deciduous Broadleaf Forest	Evergreen Needleleaf Forests
Temperate Evergreen Needleleaf Forest	Evergreen Broadleaf Forest
Boreal Evergreen Needleleaf Forest	Deciduous Needleleaf Forest
Secondary Tropical Evergreen Broadleaf Forest	Deciduous Broadleaf Forest
Secondary Temperate Evergreen Broadleaf Forest	Mixed Forest
Secondary Temperate Deciduous Broadleaf Forest	
Secondary Boreal Deciduous Needleleaf Forest	
Tropical Evergreen Broadleaf Forest	
Temperate Evergreen Broadleaf Forest	
Temperate Deciduous Broadleaf Forest	
Boreal Deciduous Needleleaf Forest	
Secondary Tropical Deciduous Broadleaf Forest	
Secondary Temperate Evergreen Needleleaf Forest	
Secondary Boreal Evergreen Needleleaf Forest	

Agrochemicals

We obtained the UN Food and Agriculture Organisation datasets on yearly estimates (tonnes per country) of the agricultural use of pesticides and fertilizers (nitrogen, potash and phosphates) available for 2009–2017 (FAO, 2019a, 2019b). We summed the three fertilizer estimates to obtain yearly estimates of overall fertilizer use in tonnes per country. As there can be high variation between years in estimated agrochemical use, we took the mean of the yearly values to obtain per-country estimates of annual fertilizer use and pesticide use.

To map agrochemical use spatially, we used the 2017 agricultural land use layers for cropland and grazing (see above) to calculate the total area in km^2 of cropland and grazing land in each country, and used these to convert the estimates of total agrochemical use in tonnes per country to use of pesticides per km^2 of cropland per country and use of fertilizers per km^2 of agricultural land per country. Of the approximately 50.2 million km^2 terrestrial surface within the Afro-Palaearctic extent, the UN FAO dataset provided fertiliser use data covering 45.8 million km^2 (91.2%) and pesticide use data covering 43.76 million km^2 (87.2%). Dependencies, autonomous regions, microstates and disputed territories missing agrochemical data accounted for 642,376 km^2 (1.3% of the area), and were assigned the estimates of a relevant nation with data (see Table S4.2). Nations with no agricultural land (Monaco and Vatican) were given a value of zero (representing < 0.00001% of the total area).

Eight nations were absent from the UN FAO fertilizer dataset, but present in the pesticide dataset, covering a region of approximately 2.9 million km^2 (5.7% of the total area). We predicted the fertilizer per km^2 of relevant agricultural land for these nations using a linear model of fertilizer use as a function of pesticide use interacting with continent (r^2: 0.5). Ten nations were absent from the UN FAO pesticide dataset, but present in the fertilizer dataset, covering a region of approximately 4.9 million km^2 (9.7% of the total area). We predicted the pesticide per km^2 of relevant agricultural land for these nations using a linear model of pesticide use as a function of fertilizer use interacting with continent (r^2: 0.5). Eight remaining nations were missing both pesticide and fertilizer data, covering a region of 877,918 km^2 (1.7% of the total area). We predicted the agrochemical use for these nations using linear models of pesticide use as a function of GDP interacting with continent (r^2: 0.3) and fertilizer use as a function of GDP interacting with continent (r^2: 0.4).

To convert the country-level agrochemical use per km^2 of relevant agricultural land to a threat layer with within-country variation, we converted the cropland and agricultural land (cropland and grazing land) layers described above to 0-1 bounded proportion layers. We then multiplied the country-level pesticide use per km^2 by the cropland proportion raster (to scale pesticide use by the proportion of land on which it is used), and multiplied country-level fertilizer use per km^2 by the agricultural land proportion raster (to scale pesticide use by the proportion of land on which it is used).

We rasterised the resulting shapefile to a resolution of 5 arcminutes to match other layers, and ensured a coordinate reference system of EPSG:4326. Finally, we ensured the layers were cropped to the Afro-Palaearctic extent used throughout, then collapsed top 0.1% and log(x+1) transformed both layers.

Table S4.2 – Summary of nations and territories missing from one or both UN FAO agrochemical datasets, and the means by which these values were interpolated.

	Nation/Territory
Pesticide use predicted from fertilizer use	
	Afghanistan
	Benin
	Bosnia and Herzegovina
	Democratic Republic of the Congo
	Gabon
	Georgia
	Nigeria
	Serbia
	United Arab Emirates
	Uzbekistan
Fertilizer use predicted from pesticide use	
	Cabo Verde
	Chad
	Comoros
	Guinea-Bissau
	Lesotho
	Mauritania
	Palestine
	Turkmenistan
Fertilizer and pesticide use predicted from GDP	
	Djibouti
	Equatorial Guinea
	eSwatini
	Liberia
	São Tomé and Principe
	Sierra Leone
	Somalia
	Somaliland

Nation/Territory	
Assigned fertilizer and pesticide use of relevant nation	Matched nation
Isle of Man	UK
Liechtenstein	Switzerland
South Sudan	Sudan
Andorra	Spain
Kosovo	Serbia
Western Sahara	Morocco
San Marino	Italy
Guernsey	France
Jersey	France
Åland	Finland
Faeroe Islands	Denmark
Northern Cyprus	Cyprus

Urbanisation

We used the Global Human Settlement built-up areas layer (Corbane et al., 2018) for the year 2014 (layer ID: GHS_BUILT_LDS2014_GLOBE_R2018A_54009_250_V2_0), which we reprojected to EPSG:4236 at a resolution of 5 arcminutes and clipped to the Afro-Palaearctic region used throughout.

Windfarms

The dataset created by Dunnett et al. (2020) contains the centroid coordinates of operational windfarms in 2020 and the estimated area of the farm (inferred from the number of turbines and appropriate turbine spacing). We reprojected the data to Mollweide (ESRI:54009) (to match the projection used throughout for manipulations requiring a projected CRS), and created a circular buffer around each windfarm centroid, sized according to the windfarm area given in the dataset. We reprojected this to EPSG:4326 to match other layers, and rasterized the resulting shapefile to a resolution of 30 arcseconds, giving any cell the centroid of which was covered by a windfarm buffer a value of 1. We then aggregated this high-resolution raster by a factor of ten to our final target resolution of five arcminutes, using the 'mean' function such that the value each cell was equal to the mean value of the 100 composite cells. The resulting raster therefore represents the approximate proportion of each cell covered by windfarms, which we cropped to the Afro-Palaearctic extent to yield the final risk layer.

Powerlines

We combined the World Bank Africa Electricity Distribution and Transmission (existing only) last updated in 2017 (World Bank, 2017) – which covers sub-Saharan Africa, North Africa and the Middle East – with the powerline data for Europe collated by the OpenInfra project (Garrett, 2018). We projected these vector datasets to ESRI:54009, created a vector grid with a cell size matching that of a five arcminute resolution raster, and assigned each cell the length in metres of powerlines within the cell. We reprojected this to EPSG:4326, rasterised it to a resolution of five arcminutes and collapsed the top 0.1%.

Hunting

Respondents to the hunting survey (Appendix S4.1) were asked to score the country between 1 (low relative levels of hunting) and 10 (high relative levels of hunting) for both small- and large-bodied species (based on size relative to a feral pigeon) in terms of hunting prevalence relative to other countries in the study region. To map finer-scale patterns, each country was overlaid with a 3°, 6°, 9° or 12° grid, depending on country size, and respondents were then asked to assign a three-level 'high', 'low', or 'medium' value for each gridsquare, as a measure of relative within-country variation in hunting intensity. We georeferenced the responses, and quantified the regional variation scores such that 'medium' gridsquares received the initial overall country-level score, while those marked as 'high' and 'low' were assigned the country-level score ±0.5. Scores across the entire study region therefore varied between 0.5 and 10.5. We received 137 responses for 98 countries (mean responses per country: 1.40); for countries in the Afro-Palaearctic region for which we did not receive a response (n=21), we assigned the mean values calculated across neighbouring countries, given by the relevant UN-defined subregion (Table S4.3).

We rasterised the georeferenced survey responses to EPSG:4326 at a resolution of five arcminutes, and then modified the resulting hunting maps using high-resolution datasets capturing local accessibility, urbanisation and protection (Benítez-López et al., 2019; Milner-Gulland et al., 2003; Venter et al., 2016). Because hunting is only likely to occur in cells that are accessible to humans, we downweighted hunting scores in cells with very low surrounding population density and road access: if a cell had fewer than five people per km^2 (CIESIN, 2018) *and* no roads (Meijer et al., 2018), we assigned it a hunting risk score of zero, and applied this negative effect of low accessibility to surrounding cells – across a second order queen's case (approximately 20-km radius) – assuming a sublinear decay function. We also masked the hunting layers by urbanisation (Corbane et al., 2018) and protected area status (UNEP-WCMC and IUCN, 2019), assigning cells a hunting risk of zero if they had >90% urban cover, or fell within established protected areas of the highest levels of protection (IUCN designations: Strict Reserves (1a) and Wilderness Areas (1b)), reflecting the low likelihood of hunting taking place in these areas.

Table S4.3 – Nations for which we did not receive hunting survey responses and which we therefore assigned the mean hunting scores of the relevant subregion.

Nation/Territory	UN subregion
Afghanistan	Southern Asia
Algeria	Northern Africa
Bahrain	Western Asia
Burundi	Eastern Africa
Central African Republic	Middle Africa
Cote d'Ivoire	Western Africa
Faeroe Islands	Northern Europe
Georgia	Western Asia
Kuwait	Western Asia
Lesotho	Southern Africa
Madagascar	Eastern Africa
Oman	Western Asia
Pakistan	Southern Asia
Qatar	Western Asia
Saudi Arabia	Western Asia
Somalia	Eastern Africa
South Sudan	Eastern Africa
Sudan	Northern Africa
Togo	Western Africa
Turkmenistan	Central Asia
Ukraine	Eastern Europe
Yemen	Western Asia

Validating hunting survey

To validate the results of our hunting survey, we compared our per-country estimates of relative bird hunting intensity to published per-country estimates of illegally killed birds. We extracted estimates of total number of birds killed, birds killed per km^2, and birds killed per capita for the Mediterranean (Brochet et al. (2016), Table 1), North and Central Europe (Brochet, Van Den Bossche, et al. (2019), Table 1) and the Arabian peninsula (Brochet, Jbour, et al. (2019), Table 1).

Forty-eight countries were both present in these published datasets and were nations for which we had received survey responses. Of these, three were included in the published estimate data (Israel in Brochet et al. (2016), Switzerland and Luxembourg in Brochet, Van Den Bossche, et al. (2019)) but not assigned numerical estimates, instead noted for having 'trivial numbers' of birds killed. In order to include these in the validation, we assigned these nations an estimate one order of magnitude smaller than the next lowest estimate within the dataset (although results were robust to varying this value).

We used univariate linear models to assess the relationship between country-level relative hunting scores obtained by our survey and the published estimates of total birds killed, birds killed per km^2 and birds killed per capita. As our survey solicited responses specific to body size, we modelled survey responses for small-bodied and for large-bodied species separately, as a function of each of the three published metrics of illegal bird hunting (logged to achieve a normal distribution). We assessed predictor significance using likelihood ratio tests with Bonferroni-corrected p-values at a significance level of 0.05. We also assessed the correlation of the hunting survey scores and the untransformed published estimated hunting metrics using Spearman's ρ.

All three per-country metrics of illegally killed birds extracted from the literature significantly predicted the per-country relative hunting scores obtained by our survey, for both large- and small-bodied species, explaining between 18% and 39% of variation in the survey scores (Table S4.4, Figure S4.1). The total number of birds killed explained slightly more variance than birds killed per km^2 or birds killed per capita, and all three published metrics explained slightly more variation in scores for small-bodied species than for large-bodied. Spearman's ρ tests also revealed significant correlations between the survey response scores for both large- and small-bodied species and all three published metrics of illegally killed birds, with ρ varying between 0.43 and 0.64 (Table S4.5).

Table S4.4 – Summaries of six univariate linear models and associated likelihood ratio tests assessing the relationship between the published country-level estimates of illegally killed birds and the per-country relative hunting scores obtained by our survey.

					Likelihood ratio test statistics			
Survey response	Published estimate	Intercept	β	r^2	χ^2	χ^2 df	*P*-value	Bonferroni-corrected *P*-value
Small- bodied	total n killed (log)	-3.88	0.77	0.39	23.99	1	< 0.001	< 0.001
	n killed per km^2 (log)	4.81	0.66	0.37	22.24	1	< 0.001	< 0.001
	n killed per capita (log)	4.75	0.68	0.34	20.16	1	< 0.001	< 0.001
Large-bodied	total n killed (log)	1.02	0.49	0.26	14.44	1	< 0.001	< 0.001
	n killed per km^2 (log)	6.49	0.36	0.18	9.40	1	0.002	0.006
	n killed per capita (log)	6.51	0.44	0.24	12.90	1	< 0.001	< 0.001

Table S4.5 – Summary statistics from six Spearman's ρ correlation tests conducted on the datatset of 48 countries relating survey responses to published estimates of illegally killed birds.

Survey response	Published estimate	ρ	*P*-value
Small-bodied	total n killed	0.63	< 0.001
	n killed per km^2	0.64	< 0.001
	n killed per capita	0.57	< 0.001
Large-bodied	total n killed	0.47	< 0.001
	n killed per km^2	0.43	0.002
	n killed per capita	0.51	< 0.001

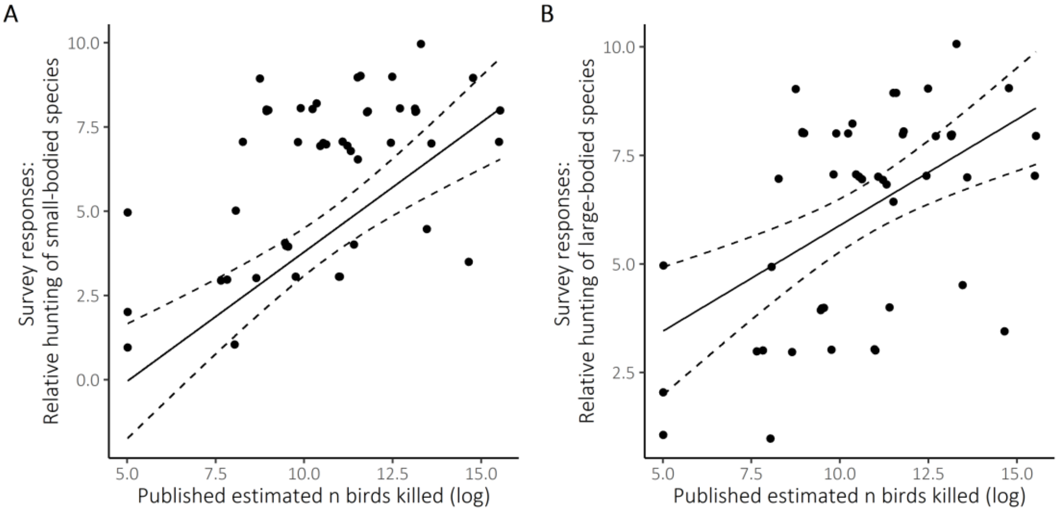


Figure S4.1 – Plots showing the relationship between published country-level estimates of illegally killed birds and the country-level relative hunting intensity scores obtained by our survey for (A) small-bodied and (B) large-bodied birds. Points represent raw data, solid and dashed lines represent model-predicted mean survey response and associated 95% confidence intervals.

Roads

We clipped the Global Roads Inventory Project (GRIP) version 4 total roads density (m/km^2) layer (Meijer et al., 2018) to the Afro-Palaearctic extent used throughout and collapsed the top 0.1%.

Nocturnal lights

We used the National Oceanic and Atmospheric Administration Defense Meteorological Progam Operation Linescan System (NOAA DMPS OLS), version 4: Nighttime Lights Time Series 'stable lights' data for 2013 (the most recent available) ((NOAA, 2013), image ID: F182013). Cell values in this layer were in raw digital number (DN) – ranging from 0-63 (the instrument takes 6-bit measurements) – representing the intensity of visible and near-infrared light emission. We aggregated this layer from a resolution of 0.5 arcminutes to 5 arcminutes, cropped the resulting layer to the Afro-Palaearctic extent and finally log(x+1) transformed the data (Kennedy et al., 2019).

Climate anomalies

We obtained the CRU TS version 4.03 global monthly precipitation and temperature data for the years 1961 to 1990 (baseline period) and 2009 to 2018 (modern period) (Harris et al., 2020), and used these to calculate monthly mean temperature and monthly mean precipitation for both the baseline period and the modern period. To map spatial variation in the magnitude of climate change in each month, we subtracted the baseline monthly means from the modern monthly means to create a series of monthly temperature and precipitation anomalies. To map changes in the level of climatic variability, we also calculated the monthly standard error for temperature and precipitation values for the baseline period and the modern decade; we subtracted the baseline monthly standard errors from the modern monthly standard errors to create a series of monthly temperature and precipitation variability anomalies.

We converted each of the four resulting monthly series (temperature anomaly, temperature variability anomaly, precipitation anomaly, precipitation variability anomaly) to absolute anomalies (i.e. values indicate the magnitude of anomaly in either direction). We then summarised these monthly series into the mean for the temperate breeding season (March–August) and non-breeding season (September–February). The data was provided in EPSG:4326 at a resolution of 30 arcminutes, so we disaggregated the final layers by a factor of six, to achieve a resolution of 5 arcminutes to match other layers. Finally, we cropped these to the Afro-Palaearctic extent and min-max bounded each raster using the minimum and maximum values for the entire monthly series to which it belonged, thereby taking into account monthly temporal variability within climate anomalies as well as spatial variability.

Appendix S4.3 Population trends and ranges

Of the species for which PECBMS (Brlík et al., 2021) provides population trends, 124 are classified as migratory by BirdLife International (BirdLife International, 2020); we filtered these to 103 non-pelagic migratory species with extant breeding and non-breeding ranges within the Afro-Palaearctic region (Table S4.4). We did not exclude those with small resident ranges in South Africa (*Ciconia ciconia*, *Meriops apiaster*, and *Sturnus vulgaris* (introduced)), nor those with resident ranges along the Nile delta. Taxonomy and nomenclature follow that used in the (BirdLife International & Handbook of the Birds of the World, 2019) dataset.

Table S4.6 – Rationales for the exclusion of 21 migratory PECBMS species. A-P: Afro-Palaearctic region.

Species	Exclusion rationale
Acrocephalus scirpaceus	Resident range in sub-Saharan Africa
Ardea cinerea	Resident range in sub-Saharan Africa
Bubulcus ibis	Resident range in sub-Saharan Africa
Carduelis citrinella	Lacks breeding range within A-P
Carpodacus erythrinus	Lacks non-breeding range within A-P
Clamator glandarius	Resident and breeding range in sub-Saharan Africa
Corvus corone	Lacks non-breeding range within A-P
Egretta garzetta	Resident range in sub-Saharan Africa
Emberiza melanocephala	Lacks non-breeding range within A-P
Emberiza rustica	Lacks non-breeding range within A-P
Falco tinnunculus	Resident range in sub-Saharan Africa
Fulica atra	Resident range in Africa
Galerida cristata	Resident range in sub-Saharan Africa; lacks non-breeding range within A-P
Gallinula chloropus	Resident range in sub-Saharan Africa
Larus ridibundus	Large pelagic non-breeding range
Oenanthe cypriaca	Very small breeding range; no specialisation data
Podiceps cristatus	Resident range in sub-Saharan Africa; non-breeding range largely coastal
Saxicola torquatus	Resident range in sub-Saharan Africa
Sylvia melanothorax	Lacks breeding range within A-P
Tachybaptus ruficollis	Resident range in sub-Saharan Africa
Upupa epops	Resident range in sub-Saharan Africa

Appendix S4.4 Species' threat-vulnerability weightings

Urbanisation and nocturnal lights

To create species-specific bird-building collision risk susceptibility scores by which to weight the urbanisation and nocturnal lights threat, we used the risk values calculated by Loss et al. (2014) for US species. Loss et al. present risk scores for US species groups in Table 5 of their publication; for the majority (n=93) of our species dataset, we assigned our species these values according to ecologically equivalent groups. In the case of the common swift (*Apus apus*), the relevant ecologically equivalent group in Loss et al. (2014) was “Hummingbirds and swifts” (Order: Apodiformes), the risk score of which was influenced by the high collision risks associated with a single hummingbird species (*Calypte anna*). We therefore assigned the value of the closest ecologically equivalent individual species, the chimney swift (*Chaetura pelagica*). For species present in both our Afro-Palaearctic dataset and their US dataset (n=3) we used the exact species risk score given in Appendix D of Loss et al. (2014). For species in the Family Motacillidae (n=6) there was no suitable ecological equivalent, so we assigned these the mean risk score for all passerines (Order: Passeriformes, n=72) in our dataset. We min-max bounded the resulting risk weightings within our dataset.

Table S4.7 – Ecological equivalents from Loss et al. 2014 for our 103 Afro-Palaearctic species from which we extracted collision risk scores

Species	Family	Order	Collision risk value source
			US species groups in Loss et al. 2014: Table 5
Accipiter nisus	Accipitridae	ACCIPITRIFORMES	Diurnal raptors
Acrocephalus arundinaceus	Sylviidae	PASSERIFORMES	Warblers
Acrocephalus palustris	Sylviidae	PASSERIFORMES	Warblers
Acrocephalus schoenobaenus	Sylviidae	PASSERIFORMES	Warblers
Actitis hypoleucos	Scolopacidae	CHARADRIIFORMES	Shorebirds
Alauda arvensis	Alaudidae	PASSERIFORMES	Blackbirds, meadowlarks and orioles
Alcedo atthis	Alcedinidae	CORACIIFORMES	Kingfishers
Burhinus oedicnemus	Burhinidae	CHARADRIIFORMES	Shorebirds
Buteo buteo	Accipitridae	ACCIPITRIFORMES	Diurnal raptors
Calandrella brachydactyla	Alaudidae	PASSERIFORMES	Blackbirds, meadowlarks and orioles
Calcarius lapponicus	Emberizidae	PASSERIFORMES	Sparrows
Carduelis carduelis	Fringillidae	PASSERIFORMES	Cardueline finches
Cettia cetti	Sylviidae	PASSERIFORMES	Warblers
Ciconia ciconia	Ciconiidae	CICONIIFORMES	Herons
Circus aeruginosus	Accipitridae	ACCIPITRIFORMES	Diurnal raptors
Coccothraustes coccothraustes	Fringillidae	PASSERIFORMES	Cardueline finches

Species	Family	Order	Collision risk value source
Columba oenas	Columbidae	COLUMBIFORMES	Doves and pigeons
Columba palumbus	Columbidae	COLUMBIFORMES	Doves and pigeons
Corvus frugilegus	Corvidae	PASSERIFORMES	Corvids
Corvus monedula	Corvidae	PASSERIFORMES	Corvids
Cuculus canorus	Cuculidae	CUCULIFORMES	Cuckoos
Cygnus olor	Anatidae	ANSERIFORMES	Ducks and geese
Delichon urbicum	Hirundinidae	PASSERIFORMES	Swallows
Emberiza cia	Emberizidae	PASSERIFORMES	Sparrows
Emberiza citrinella	Emberizidae	PASSERIFORMES	Sparrows
Emberiza hortulana	Emberizidae	PASSERIFORMES	Sparrows
Emberiza schoeniclus	Emberizidae	PASSERIFORMES	Sparrows
Erithacus rubecula	Muscicapidae	PASSERIFORMES	Flycatchers
Ficedula albicollis	Muscicapidae	PASSERIFORMES	Flycatchers
Ficedula hypoleuca	Muscicapidae	PASSERIFORMES	Flycatchers
Fringilla coelebs	Fringillidae	PASSERIFORMES	Cardueline finches
Fringilla montifringilla	Fringillidae	PASSERIFORMES	Cardueline finches
Gallinago gallinago	Scolopacidae	CHARADRIIFORMES	Shorebirds
Grus grus	Gruidae	GRUIFORMES	Herons
Haematopus ostralegus	Haematopodidae	CHARADRIIFORMES	Shorebirds

Species	Family	Order	Collision risk value source
Hippolais icterina	Sylviidae	PASSERIFORMES	Warblers
Hippolais polyglotta	Sylviidae	PASSERIFORMES	Warblers
Hirundo rustica	Hirundinidae	PASSERIFORMES	Swallows
Jynx torquilla	Picidae	PICIFORMES	Woodpeckers
Lanius collurio	Laniidae	PASSERIFORMES	Flycatchers
Lanius minor	Laniidae	PASSERIFORMES	Flycatchers
Lanius senator	Laniidae	PASSERIFORMES	Flycatchers
Limosa limosa	Scolopacidae	CHARADRIIFORMES	Shorebirds
Locustella fluviatilis	Sylviidae	PASSERIFORMES	Warblers
Locustella naevia	Sylviidae	PASSERIFORMES	Warblers
Lullula arborea	Alaudidae	PASSERIFORMES	Blackbirds, meadowlarks and orioles
Luscinia luscinia	Muscicapidae	PASSERIFORMES	Flycatchers
Luscinia megarhynchos	Muscicapidae	PASSERIFORMES	Flycatchers
Melanocorypha calandra	Alaudidae	PASSERIFORMES	Blackbirds, meadowlarks and orioles
Merops apiaster	Meropidae	CORACIIFORMES	Kingfishers
Muscicapa striata	Muscicapidae	PASSERIFORMES	Flycatchers
Numenius arquata	Scolopacidae	CHARADRIIFORMES	Shorebirds
Numenius phaeopus	Scolopacidae	CHARADRIIFORMES	Shorebirds
Oenanthe hispanica	Muscicapidae	PASSERIFORMES	Flycatchers

Species	Family	Order	Collision risk value source
Oenanthe oenanthe	Muscicapidae	PASSERIFORMES	Flycatchers
Oriolus oriolus	Oriolidae	PASSERIFORMES	Blackbirds, meadowlarks and orioles
Phoenicurus ochruros	Muscicapidae	PASSERIFORMES	Flycatchers
Phoenicurus phoenicurus	Muscicapidae	PASSERIFORMES	Flycatchers
Phylloscopus bonelli	Sylviidae	PASSERIFORMES	Warblers
Phylloscopus collybita	Sylviidae	PASSERIFORMES	Warblers
Phylloscopus sibilatrix	Sylviidae	PASSERIFORMES	Warblers
Phylloscopus trochilus	Sylviidae	PASSERIFORMES	Warblers
Pluvialis apricaria	Charadriidae	CHARADRIIFORMES	Shorebirds
Prunella modularis	Prunellidae	PASSERIFORMES	Wrens
Pyrrhula pyrrhula	Fringillidae	PASSERIFORMES	Cardueline finches
Regulus ignicapilla	Reguliidae	PASSERIFORMES	Kinglets
Regulus regulus	Reguliidae	PASSERIFORMES	Kinglets
Saxicola rubetra	Muscicapidae	PASSERIFORMES	Flycatchers
Serinus serinus	Fringillidae	PASSERIFORMES	Cardueline finches
Streptopelia turtur	Columbidae	COLUMBIFORMES	Doves and pigeons
Sylvia atricapilla	Sylviidae	PASSERIFORMES	Warblers
Sylvia borin	Sylviidae	PASSERIFORMES	Warblers
Sylvia cantillans	Sylviidae	PASSERIFORMES	Warblers

Species	Family	Order	Collision risk value source
Sylvia communis	Sylviidae	PASSERIFORMES	Warblers
Sylvia curruca	Sylviidae	PASSERIFORMES	Warblers
Sylvia hortensis	Sylviidae	PASSERIFORMES	Warblers
Sylvia melanocephala	Sylviidae	PASSERIFORMES	Warblers
Sylvia nisoria	Sylviidae	PASSERIFORMES	Warblers
Tadorna tadorna	Anatidae	ANSERIFORMES	Ducks and geese
Tetrax tetrax	Otididae	OTIDIFORMES	Upland game birds
Tringa erythropus	Scolopacidae	CHARADRIIFORMES	Shorebirds
Tringa glareola	Scolopacidae	CHARADRIIFORMES	Shorebirds
Tringa nebularia	Scolopacidae	CHARADRIIFORMES	Shorebirds
Tringa ochropus	Scolopacidae	CHARADRIIFORMES	Shorebirds
Tringa totanus	Scolopacidae	CHARADRIIFORMES	Shorebirds
Troglodytes troglodytes	Troglodytidae	PASSERIFORMES	Wrens
Turdus iliacus	Turdidae	PASSERIFORMES	Thrushes
Turdus merula	Turdidae	PASSERIFORMES	Thrushes
Turdus philomelos	Turdidae	PASSERIFORMES	Thrushes
Turdus pilaris	Turdidae	PASSERIFORMES	Thrushes
Turdus torquatus	Turdidae	PASSERIFORMES	Thrushes
Turdus viscivorus	Turdidae	PASSERIFORMES	Thrushes

Species	Family	Order	Collision risk value source
Vanellus vanellus	Charadriidae	CHARADRIIFORMES	Shorebirds
			Matched to individual species Loss et al. 2014: Appendix D
Anas platyrhynchos	Anatidae	ANSERIFORMES	*Anas platyrhynchos*
Apus apus	Apodidae	CAPRIMULGIFORMES	*Chaetura pelagica*
Bombycilla garrulus	Bombycillidae	PASSERIFORMES	*Bombycilla garrulus*
Sturnus vulgaris	Sturnidae	PASSERIFORMES	*Sturnus vulgaris*
			Assigned mean value within dataset
Anthus campestris	Motacillidae	PASSERIFORMES	mean value for Passeriformes
Anthus pratensis	Motacillidae	PASSERIFORMES	mean value for Passeriformes
Anthus trivialis	Motacillidae	PASSERIFORMES	mean value for Passeriformes
Motacilla alba	Motacillidae	PASSERIFORMES	mean value for Passeriformes
Motacilla cinerea	Motacillidae	PASSERIFORMES	mean value for Passeriformes
Motacilla flava	Motacillidae	PASSERIFORMES	mean value for Passeriformes

Powerlines and windfarms

To weight the potential collision risks posed by powerlines and windfarms, we used a combination of morphological and behavioural traits considered indicative of collision vulnerability (e.g. wingloading proxy (mass/wingspan), binocular vision, foraging and flight characteristics), extended from the powerline collision susceptibility weightings developed by D'Amico et al. (2019) to cover all species within our study. Traits included in the calculation of the windfarm weightings were the same as those included for the powerline susceptibility weightings, but excluded the powerline use behavioural trait. Morphological and behavioural data were extracted from Cramp et al. (1994). For both windfarms and powerlines, the vulnerability values for the largest species, the mute swan (*Cygnus olor*, approximately twice the mass of the next heaviest species Common Crane, *Grus grus*), consistently heavily skewed the relative values across the dataset, so this was assigned the value of the next highest-risk species (mallard, *Anas platyrhynchos*), prior to the weightings being logged. Taxonomic orders revealed by this method to be most at-risk to windfarm collisions broadly aligned with those found elsewhere (Desholm, 2009; Thaxter et al., 2017).

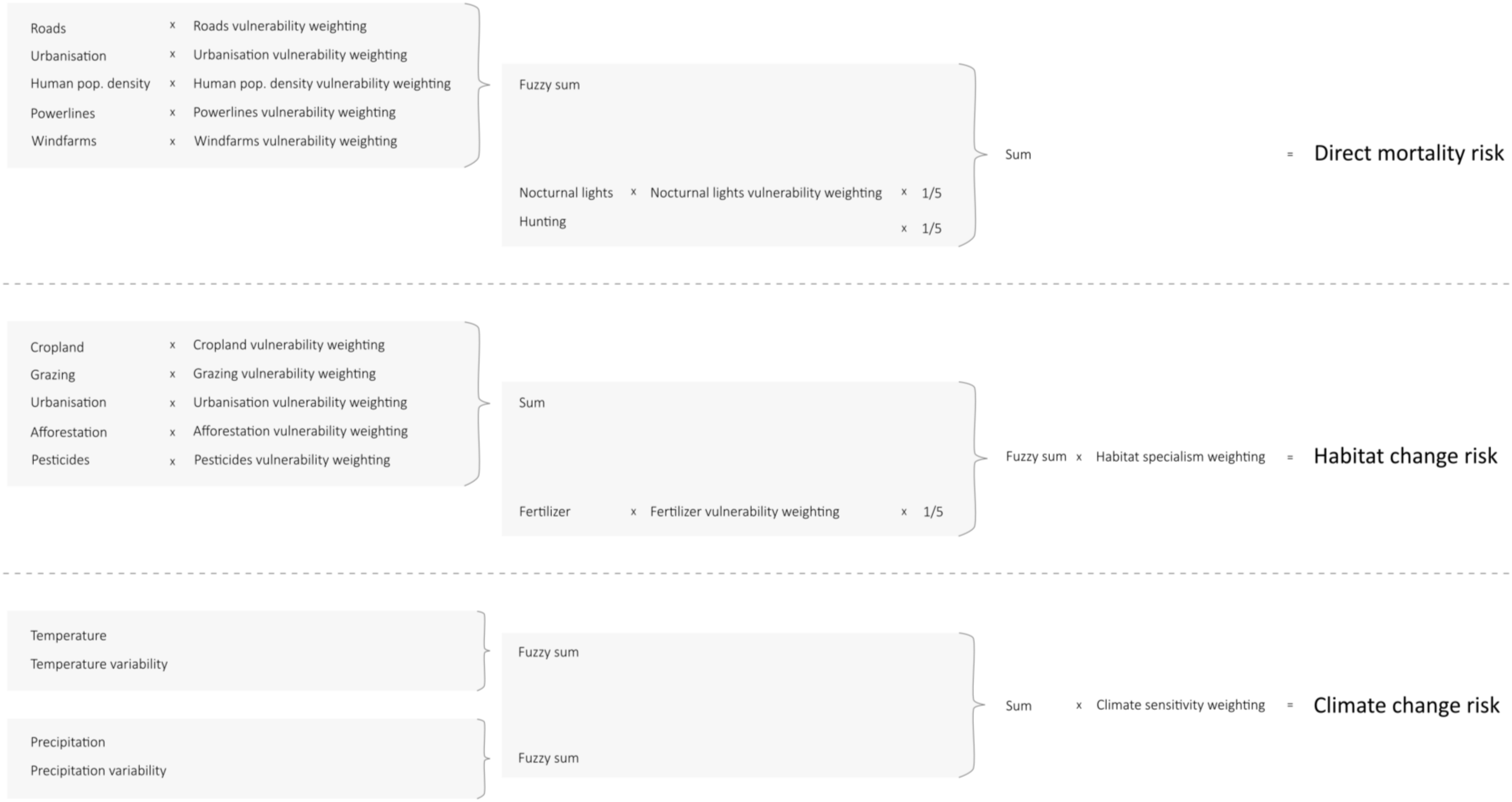


Figure S4.2 – Schematic illustrating the structure of independent and non-independent groupings of threat layers within each risk type, showing how risks were combined within the respective algorithms.

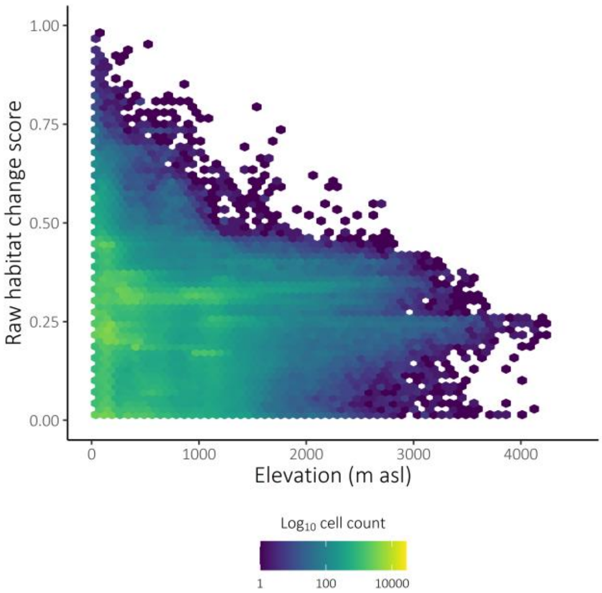


Figure S4.3 – Density of cells within the Afro-Palaearctic region (total n cells: 718,918) according to elevation and raw habitat change risk score. Elevation data obtained from the USGS Global Multi-Resolution Terrain Elevation Data 2010 30-second mean topobathy (Danielson & Gesch, 2010). At an elevation above 2000 m, 99.9% of cells had a habitat risk score below 0.49, compared to 0.71 for cells at elevations below 2000 m.

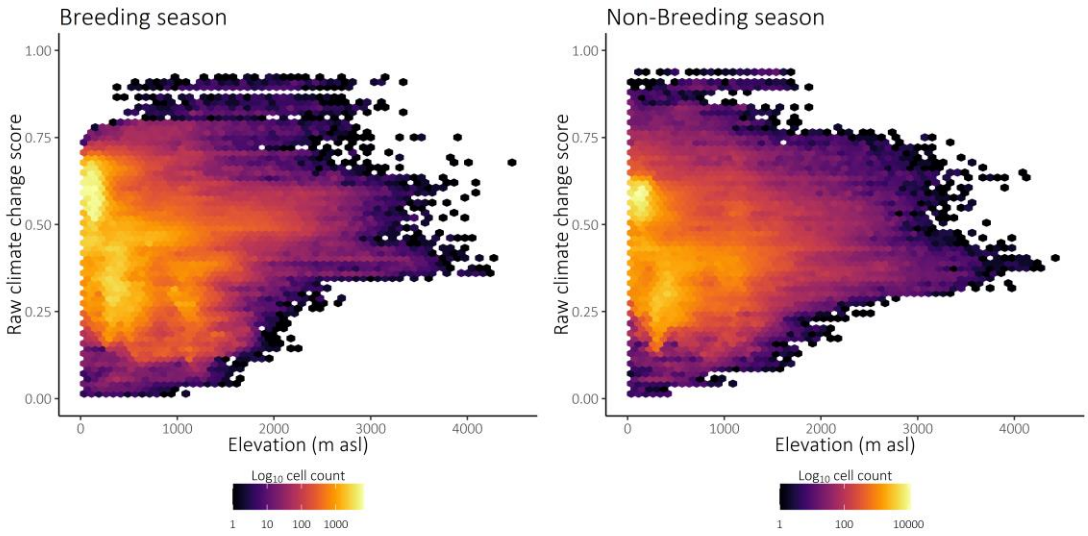


Figure S4.4 – Density of cells within the Afro-Palaearctic region (total n cells: 718,918) according to elevation and raw climate change risk scores calculated in the breeding (L) and non-breeding (R) months. Elevation data obtained from the USGS Global Multi-Resolution Terrain Elevation Data 2010 30-second mean topobathy (Danielson & Gesch, 2010). At an elevation above 2000 m, 99.9% of cells had a habitat risk score below 0. 92, compared to 0.79 for cells at elevations below 2000 m.

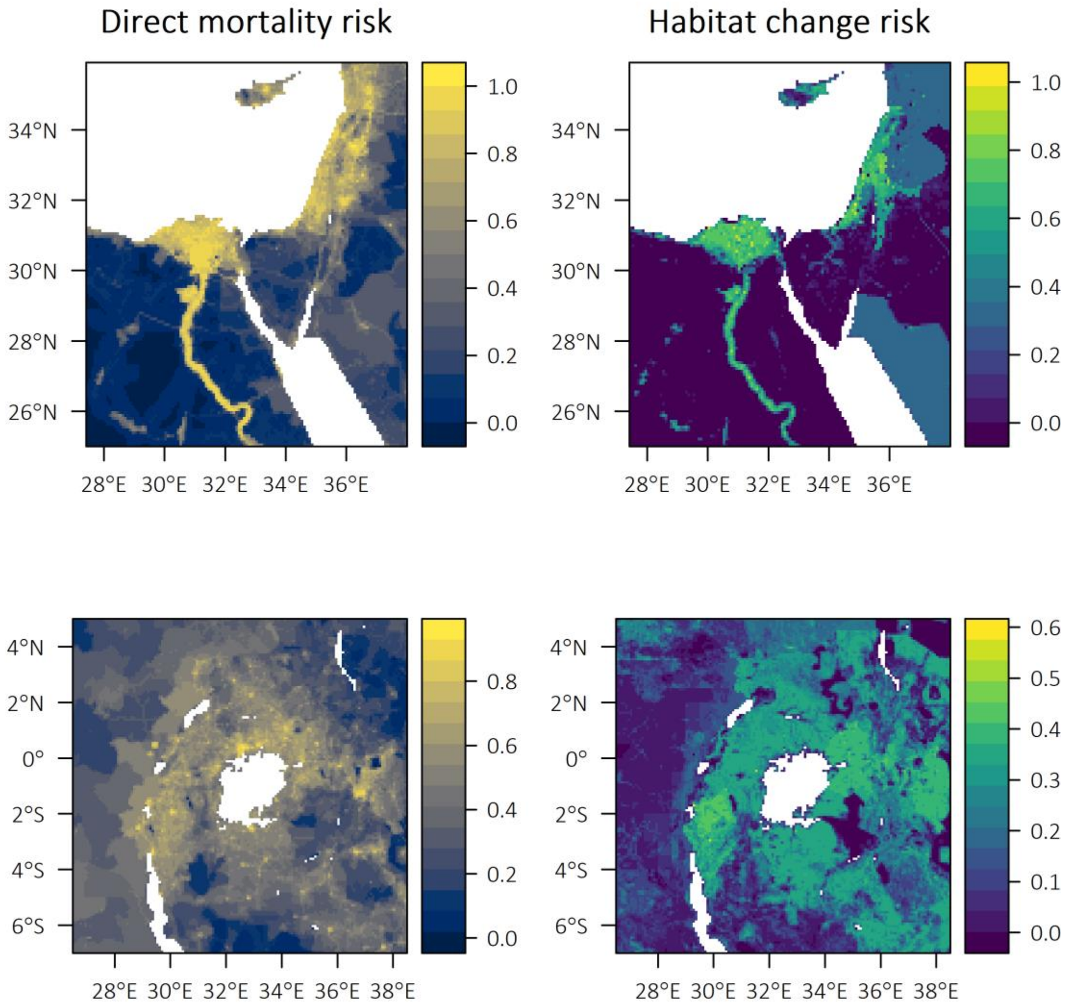


Figure S4.5 – Unweighted direct mortality and habitat change risk surfaces for the Nile delta and Levant (top) and Lake Victoria basin (bottom).

Table S4.8 – Structure and associated coefficient estimates for a subset of reduced models from global model: Population trend ~ climate NBR * migratory distance + body mass + mortality BR + habitat BR + mortality NBR*, ranked by Akaike's Information Criterion adjusted for small sample size (AICc), showing models within six AICc units of the highest ranked model. Greyed-out cells indicate parameters absent from the relevant model. Model in bold face indicates the best performing model reported in the manuscript ("Model1"). BR: breeding season range exposure, NBR: non-breeding season range exposure.*

Intercept	climate change NBR	direct mortality BR	direct mortality NBR	habitat change BR	mass	migratory distance	climate change NBR : migratory distance	df	logLik	AICc	Δ AICc	weight
0.06	-0.05		-0.32	-0.16	0.27	-0.28	0.21	8	-120.78	259.1	0.00	0.33
0.08	**-0.06**		**-0.34**		**0.24**	**-0.27**	**0.18**	**7**	**-122.50**	**260.2**	**1.10**	**0.19**
0.07	-0.03	0.11	-0.39	-0.21	0.26	-0.29	0.22	9	-120.41	260.8	1.66	0.14
0.00			-0.33		0.27	-0.20		5	-125.92	262.5	3.38	0.06
0.08	-0.06	-0.03	-0.31		0.24	-0.27	0.18	8	-122.47	262.5	3.38	0.06
-0.02			-0.32	-0.11	0.29	-0.20		6	-125.15	263.2	4.09	0.04
0.00	-0.07		-0.34		0.26	-0.24		6	-125.53	263.9	4.84	0.03
0.00		-0.03	-0.31		0.28	-0.20		6	-125.89	264.7	5.57	0.02
-0.02	-0.06		-0.33	-0.10	0.28	-0.23		7	-124.86	264.9	5.80	0.02

Table S4.9 – Structure and associated coefficient estimates for a subset of reduced models from global model: Population trend ~ climate NBR + migratory distance + body mass + mortality BR * habitat BR + mortality NBR*, ranked by Akaike's Information Criterion adjusted for small sample size (AICc), showing models within six AICc units of the highest ranked model. Greyed-out cells indicate parameters absent from the relevant model. Model in bold face indicates the best performing model reported in the manuscript ("Model2"). BR: breeding season range exposure, NBR: non-breeding season range exposure.*

Intercept	climate change NBR	direct mortality BR	direct mortality NBR	habitat change BR	mass	migratory distance	direct mortality BR : habitat change BR	df	logLik	AICc	Δ AICc	weight
0.10		**-0.03**	**-0.31**	**-0.03**	**0.28**	**-0.22**	**-0.24**	**8**	**-121.39**	**260.3**	**0.00**	**0.33**
0.10	-0.04	-0.04	-0.30	-0.03	0.27	-0.24	-0.24	9	-121.26	262.5	2.15	0.11
0.00			-0.33		0.27	-0.20		5	-125.92	262.5	2.16	0.11
-0.02			-0.32	-0.11	0.29	-0.20		6	-125.15	263.2	2.87	0.08
0.11		-0.26		0.04	0.22	-0.15	-0.27	7	-124.25	263.7	3.38	0.06
0.00	-0.07		-0.34		0.26	-0.24		6	-125.53	263.9	3.62	0.05
0.00		-0.03	-0.31		0.28	-0.20		6	-125.89	264.7	4.35	0.04
-0.02	-0.06		-0.33	-0.10	0.28	-0.23		7	-124.86	264.9	4.58	0.03
-0.02		0.05	-0.36	-0.13	0.29	-0.21		7	-125.07	265.3	5.01	0.03
0.11	-0.05	-0.27		0.05	0.21	-0.18	-0.27	8	-124.04	265.6	5.29	0.02
0.00	-0.07	-0.04	-0.31		0.26	-0.23		7	-125.46	266.1	5.79	0.02

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Quantifying spatiotemporal exposure to anthropogenic change reveals season-specific threat intensity for a long-distance migrant

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AUTHOR CONTRIBUTIONS

CB, JG and AF designed the study. CB processed the data, conducted the statistical analysis and wrote the manuscript. CH and PA provided data and advice on approaches to data processing. AF, JG and IC critically revised the manuscript and contributed to interpreting the results.

ABSTRACT

Identifying when and where organisms are exposed to anthropogenic risks is crucial to identify the drivers of biodiversity declines and implement effective conservation measures. Accurately measuring exposure to anthropogenic risks across the annual cycle requires an approach that is both spatially and temporally explicit – now increasingly achievable with recent parallel advances in remote-sensing and individual tracking technologies. We combined over nine years of tracking data for a long-distance migrant, (common cuckoo, *Cuculus canorus*), with multi-dimensional remote-sensed risk surfaces encompassing thirteen relevant anthropogenic threats (including infrastructure, hunting, habitat change and climate change), to quantify mean hourly and total risk exposure of tracked individuals throughout the annual cycle. We explore the relative contributions to risk exposure of different seasons, and quantify differences in risk exposure between migratory routes. Although mean hourly exposure to anthropogenic risk was greatest in breeding areas, total exposure to direct mortality and climate change risks was greatest during the winter, largely driven by the relative length of the wintering stage. Exposure to risks on migration varied considerably both within and between migratory flyways, and more easterly autumn migratory routes were associated with lower exposure to all risk types in the subsequent winter. At the local population scale, total risk exposure was not significantly associated with recent population trends, likely because cuckoos from shared breeding areas can follow very different migration routes and therefore encounter very different risk levels. Our approach demonstrates the value of directly combining tracking data with remote-sensed spatial information to uncover detailed insights into anthropogenic risk exposure.

5.1 INTRODUCTION

Threats associated with land-use change and intensification, human settlements and infrastructure, and climate change are all linked to biodiversity declines (Bairlein, 2016; Kirby et al., 2008; Loss et al., 2015; Maxwell et al., 2016), but their relative severity varies widely in space. Reversing biodiversity declines requires understanding where organisms are most exposed to population-limiting effects, and when in their life cycle these effects are greatest. Long-distance migratory species are experiencing particularly severe population declines (Laaksonen & Lehikoinen, 2013; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014; Yong et al., 2015), potentially because their reliance on spatially and temporally disparate resources puts them at greater exposure to anthropogenic threats throughout the annual cycle (Newton, 2008; Robinson et al., 2009). Large distances between seasonal ranges may also increase their greater vulnerability to trophic asynchrony (Both et al., 2010; Møller et al., 2008). Quantifying spatiotemporal variation in the extent of and exposure to anthropogenic risks throughout the annual cycle is therefore necessary to identify and mitigate drivers of population declines, particularly among migratory species.

The steeper declines seen in long-distance migrant populations (Vickery et al., 2014) suggests they may be particularly sensitive to factors occurring in the non-breeding seasons, and/or that declines are driven by a limited capacity to adapt to changing conditions at the breeding grounds (Møller et al., 2008). Recent research highlights the complexity of seasonal threat accumulation, with different studies finding strong effects of wintering conditions (Adams et al., 2014; Kramer et al., 2018; Ockendon et al., 2012, 2014), breeding conditions (Morrison et al., 2013; Ockendon et al., 2013), and migratory conditions (Hewson et al., 2016; Lisovski et al., 2020; Studds et al., 2017). Determining the relative importance of – and interactions between – season-specific threats requires holistic full-cycle approaches (Calvert et al., 2009; Marra et al., 2015; Martin et al., 2007; Runge et al., 2014, 2015; Sanderson et al., 2016; Small-Lorenz et al., 2013).

Many studies have sought to determine variation in threat exposure across the annual cycle from coarse knowledge of species' seasonal ranges (Buchan et al., *in review*; Kramer et al., 2018; Murray et al., 2018; Taylor & Stutchbury, 2016). Though informative, these cannot account for within-season and between-individual temporal variability in space-use, reducing their capacity to accurately measure the relative contributions of different seasons. A temporally explicit approach to quantifying threat exposure can yield greater insights, but this requires individual-scale data on when and for how long an individual is present in a given location, as well as their relative exposure to risks while at that location. The last few decades have seen swift advances in two parallel technological developments: bio-logging/tracking and fine-scale environmental remote sensing (Allan et al., 2018; Turner, 2014; Wassmer et al., 2020). Remote-sensed data has revolutionised our capacity to undertake large-scale mapping of anthropogenic change, in particular by facilitating the assessment and combination of multiple threats (Buchan et al., *in review*; Halpern et al., 2008; Kennedy et al., 2019; Venter et al., 2016). At the same time, high-resolution tracking data has transformed individual-level spatiotemporal data collection, yielding novel insights on, for instance, e.g. migratory routes (Hewson et al., 2016; van Bemmelen et al., 2019), non-migratory movements (Shamoun-Baranes et al., 2017), and survival (Buechley et al., 2021; Klaassen et al., 2014). To our knowledge, however, no studies have combined these two advances to measure year-round individual exposure to remote-sensed spatial risk variables.

Here, we combine over nine years of tracking data for a declining long-distance Afro-Palaearctic migrant bird, the common cuckoo (*Cuculus canorus, '*cuckoo' hereafter), with pan-continental spatially-explicit remote sensing to measure individual-level exposure to anthropogenic risks relating to direct mortality, habitat change and climate change across the annual cycle. We explore the relative contribution of each season to risk exposure, in terms of both mean hourly risk exposure and total risk exposure accrued over the season. Variability in autumn migratory routes (Figure 5.1) in the cuckoo has previously been linked to differences in survival on migration and population trends (Hewson et al., 2016), with birds following eastern flyways facing lower mortality rates and being more likely to breed at sites with healthier population trends. We therefore also used seasonal total risk exposure scores to investigate the extent to which the autumn flyway influences exposure to anthropogenic risk on migration and in the subsequent winter, and tested the relationship between non-breeding season risk exposure and breeding site population trends.

5.2 METHODS

Tracking data

We used over nine years of cuckoo tracking data collected by the British Trust for Ornithology (May 2011 to February 2021), involving eighty-four male cuckoos tagged from thirteen different regions within the UK with Microwave Telemetry PTT-100 tags (<5 g) following protocols outlined in (Hewson et al., 2016). Tagging was carried out under approval from the Special Methods Technical Panel of the British Trust for Ornithology, in accordance with the ethical guidelines of the UK Government Home Office.

We separated individual cuckoo tracks into four stages of the annual cycle – autumn migration, winter, spring migration and breeding season – using both geographic and behavioural criteria (Soriano-Redondo et al., 2020) and following the methods of Hewson et al. (2016). As birds were tagged during the breeding season, we started the annual cycle of each bird-year at the start of autumn migration, which we defined as the first movement of more than 50 km from the breeding location; these were individually checked and corrected to remove pre-migratory movements. The end of autumn migration was defined as the first stopover south of 15° N, where a stopover is defined as three consecutive days during which the individual has a daily displacement of less than 50 km (Hewson et al., 2016). The wintering period ran from the end of the autumn migration to the start of the northward spring migration, in turn determined as the end of the last stopover south of 15° N. We defined the end of the northward migration to be the first fix within 50 km of the final breeding location; all fixes following this were assigned to the breeding season, which ended with the start of the following bird-year autumn migration. Individuals which did not complete a season (i.e. the individual and/or tag died before reaching the season delimiting threshold) were excluded from that season (but retained in those preceding). Any bird-season with a between-fix gap of more than ten days and greater than 2000 km (e.g. due to low device battery) was flagged for exclusion from subsequent sensitivity analyses. To capture the variability in autumn migratory route (Figure 5.1), for each bird-year we extracted the longitude at which the bird crossed latitude 35° N during the southward autumn migration – the point by which the main migratory flyways across the Mediterranean have been determined.

Risk surfaces

We used the spatial threat layers assembled in (Buchan et al., *in review*), in which threats are categorised as relevant to direct mortality (roads, nocturnal lights, human population density, relative hunting threat (of small-bodied species), powerlines, windfarms, urbanisation), habitat change (fertilizer use, pesticide use, urbanisation), and climate change (temperature anomaly, temperature variability anomaly, precipitation anomaly and precipitation variability anomaly). All threat layers used were at a resolution of five arcminutes, with the exception of climate layers, which were at 30 arcminutes.

Estimating spatiotemporal risk exposure

To determine temporal exposure to spatially varying risks, it was necessary to estimate the time spent by each individual within the areas through which it passed. We used the maximum range speed (V_{mr}) of 10.4 m/s (39.96 km/h) calculated by (Bruderer & Boldt, 2001) using the formula developed by Pennycuick (1989) to estimate how long an individual cuckoo might reasonably take to cover the distance between fixes. For each between-fix track, we estimated the time spent flying (assuming a single hop) and assigned the remaining time (i.e. the between-fix time difference minus the calculated flying time) as presence at the initial fix location. As cuckoos may fly at speeds greater than 39.96 km/h, particularly during migration (Bán et al., 2018), if the time and distance between fixes indicated the bird must have travelled at a speed greater than 39.96 km/h, we used the speed given by the between-fix distance divided by time difference for that flight.

We divided the straight-line track between fix locations into segments by intersecting the tracks with a grid matching the cell resolution of the risk surfaces, and calculated the length in metres of each segment. We used segment length as a proportion of the total between-fix distance to allocate the calculated between-fix flying time, to yield an estimate for the time spent by the bird within a segment (and therefore cell). The leftover time was added to the time spent in the first segment of the between-fix track, on the assumption that cuckoos move by large hops, with only small (i.e. within-cell) movements occurring between hops.

For each temporal track segment, we extracted the corresponding cell values for each of the risk surfaces, and used a combination of linear and fuzzy summation to combine these into three risk scores per segment: direct mortality risk, habitat change risk, and climate change risk (Buchan et al. *in review*). As the climate change anomaly layers are provided for each month, we extracted the cell value for the layer corresponding to the month in which the bird passed through the cell. We multiplied these per-cell risk values by the time allocated to each track segment to calculate temporal exposure for each individual track segment. Finally, for each bird-season (n=239), we took the mean of these track segment exposure values to yield mean hourly risk exposure, and the sum of the track segment exposure values to yield total risk exposure.

Population trends

To measure population change at breeding sites in the UK, following Hewson et al. (2016), we used the standardized arithmetic difference between the BTO Bird Atlas Frequency Indices for 1988–1991 and for 2007–2011, calculated at a 10 x 10 km grid resolution (Balmer et al., 2013). Individual cuckoos were tagged at thirteen different breeding sites. To delimit these sites in space, we created a 25-km radius buffer around the capture location of each individual, and – as individuals from the same site could not be considered independent replicates – merged these buffer zones to create a polygon for each site (Figure S5.1). We then extracted the abundance change for each 10 x 10 km grid square within each site region, and calculated a mean abundance change for each site, with values weighed by area within the buffer zone, such that 10 x 10 km squares furthest from any capture location were relatively downweighted.

Analysis

We used linear mixed-effects models to explore the variation in mean hourly risk exposure and total risk exposure per bird-season (n=239) between stages of the annual cycle. For each risk type (direct mortality, habitat change and climate change) we modelled log mean hourly risk exposure and log total risk exposure as a function of season – autumn migration, winter, spring migration or breeding season – with individual bird ID (n=53) as a random effect. We used likelihood ratio tests to assess the significance of season as a predictor, and post-hoc multiple comparison tests to assess significance of between-season differences.

To assess the influence of autumn flyway on migration risk exposure and subsequent winter risk exposure, we modelled autumn total risk exposure and winter total risk exposure for each of the three risk types as a function of track longitude at 35° N. We used linear models and generalised additive models (thin plate regression splines) with default selection of smoothing parameters to explore whether there was statistical support for non-linear relationships; we used r^2 values and AIC values to compare the fit of the linear and generalised additive models. We also examined how winter total risk exposure varied with flyway destination across the winter range, using the longitude of the first winter fix (rather than at 35° N) to capture variability in flyway destination.

To explore the extent to which non-breeding season risk exposure may influence breeding site population trends, we calculated the mean total risk exposure for each non-breeding season (autumn migration, winter and spring migration) experienced by individuals from each breeding site (n=13), and used univariate linear models to assess the influence of mean per-season exposure on mean site abundance change.

We repeated all analyses on a subset of the dataset with seventeen bird-seasons removed (see Methods: Tracking data) to ensure any results we obtained were not sensitive to a small number of relatively data-poor tracks. We conducted all spatial and statistical analyses in R version 4.0.3 (R Core Team, 2020), using packages {raster} (Hijmans, 2020) and {sf} (Pebesma, 2018) for manipulation of spatial data, {mgcv} (Wood, 2011) and {lme4} (Bates et al., 2015) for creation of generalised additive models and linear mixed effects models respectively, and {multcomp} for conducting post-hoc comparisons (Hothorn et al., 2008). In all cases, we assessed significance of univariate predictors using likelihood ratio tests using the maximum likelihood estimator for standard deviation of errors, using {lmtest} (Zeileis & Hothorn, 2002) at $\alpha = 0.05$, using Bonferroni adjusted *P*-values to control for family-wise error rate in analyses with multiple tests.

5.3 RESULTS

Filtering the tracking dataset yielded 239 bird-seasons from 86 bird-years from 53 individuals (Table 5.1). Spring migration was the shortest of the four annual stages, accounting for approximately 7% of the year on average, while winter was the longest stage accounting for c. 63% of the year.

Table 5.1 – Summary statistics describing final tracking dataset filtered and categorised into seasons

	Total			Mean ±SD				
Season	Bird-years	Individuals	Fixes	Fixes bird-year^{-1}	Duration (days)	Distance (km)	Start date	End date
Autumn migration	86	53	1936	22.5	51.0	5524	21 Jun	11 Aug
				±8.6	±19	±756	±10 days	±21 days
Winter	58	37	4693	80.9	229.5	6042	12 Aug	29 Mar
				±19.6	±24	±1524	±20 days	±15 days
Spring migration	51	32	480	9.4	26.5	5629	03 Apr	30 Apr
				±3.3	±13	±815	±14 days	±8 days
Breeding	44	26	1054	24.0	42.9	127.1	01 May	13 Jun
				±8.7	±14	±91	±8 days	± 12 days

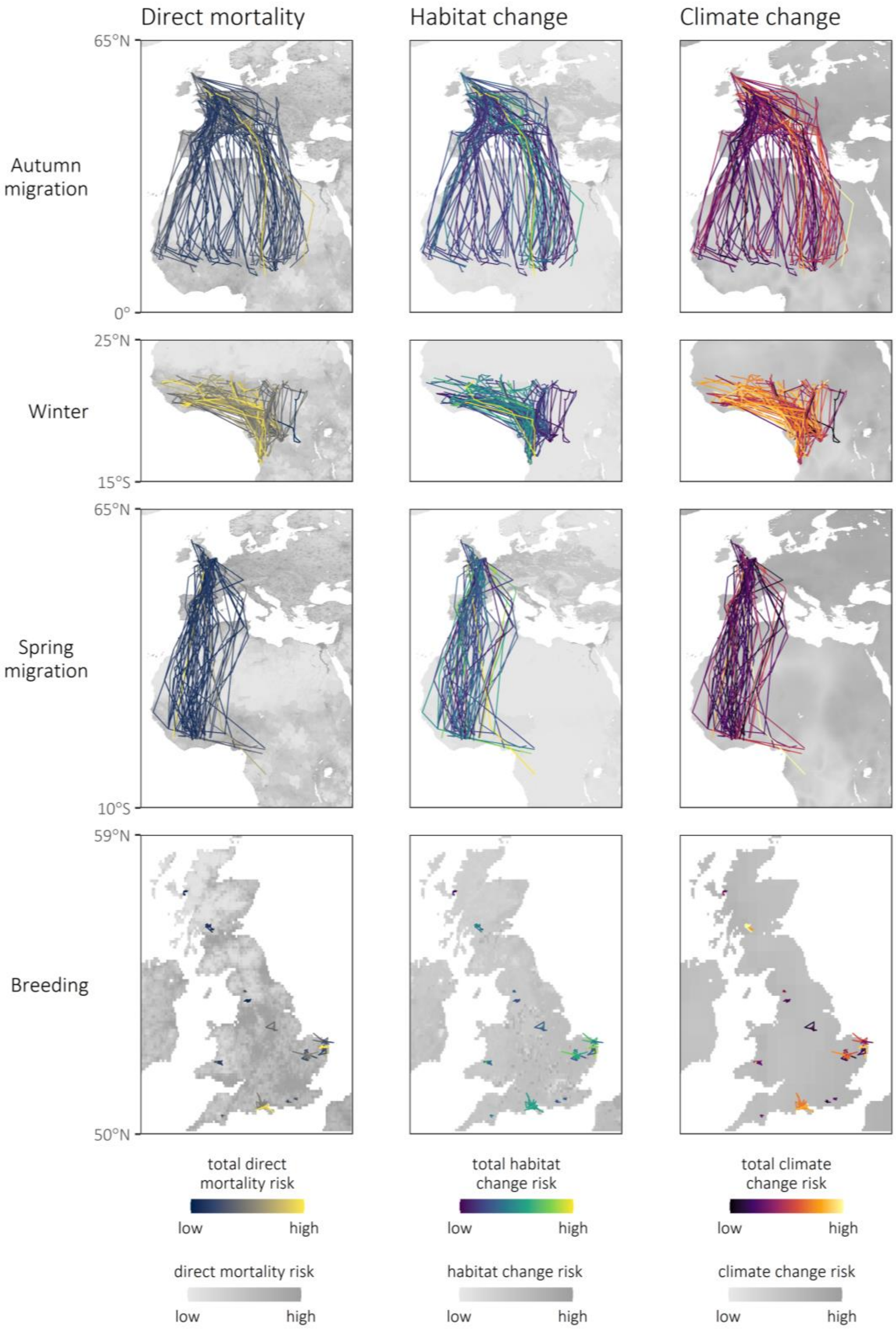

Figure 5.1 – Tracks of common cuckoos throughout the annual cycle; each line represents a bird-year – seasonal sample sizes given in Table 5.1. Lines are coloured according to total accumulated within-season exposure to the three different risk types (colours standardised within seasons). Lines are overlaid onto the risk surfaces from which exposure scores are calculated, except in the case of climate, for which the basemaps show the mean of the relevant months.

Between-season exposure

Season significantly influenced mean hourly risk exposure for all three risk types, explaining between 88% and 90% of variance in mean hourly risk exposure (Table 5.2). Post-hoc pairwise comparisons showed meaningful differences between all seasons for all risks (Table S5.1). In all cases, mean hourly risk was considerably higher in the breeding season than any other season (Figure 5.2a-c). Mean hourly direct mortality and climate change risks were greater in winter than autumn on average, and lowest in spring migration (Figure 5.2). In the case of habitat change, mean hourly risk was greater in autumn migration than spring, and lowest in the winter (Figure 5.2).

Total risk exposure again significantly varied between seasons, though less variance was explained by season (between 48 and 71%) than was for mean hourly risk exposure (Table 5.2). Post-hoc pairwise comparisons revealed significant differences between all seasons for all risks, except total habitat change exposure, which was similar between autumn migration and the breeding season (Figure 5.2g–5.2i, Table S5.1). Autumn and breeding showed the highest rates of total habitat change risk exposure, followed by spring migration, with total exposure lowest in the winter. In the case of direct mortality and climate change risks, total exposure was highest in the winter, followed by autumn migration, breeding season, and lowest on spring migration.

In the case of both mean hourly and total risk exposure, sensitivity analyses run on a subset of the dataset with seventeen data-deficient bird-seasons removed yielded similar results in all cases (Appendix S5.1, Table S5.2).

Table 5.2 – Summaries of six univariate linear mixed-effects models and associated likelihood ratio tests assessing the effect of season on mean hourly risk exposure and total risk exposure for the three risk types, with bird identity as a random effect. Post-hoc tests of pairwise comparisons are given in Table S5.1. Marginal r^2 for linear mixed-effects models calculated following (Nakagawa & Schielzeth, 2013).

Response variable			Likelihood ratio test statistics		
Metric	Risk type	Marginal r^2	χ^2	χ^2 df	*P*-value
Mean hourly exposure	direct mortality	0.89	514.87	3	<0.001
	habitat change	0.89	518.09	3	<0.001
	climate change	0.91	567.24	3	<0.001
Total exposure	direct mortality	0.70	278.37	3	<0.001
	habitat change	0.49	155.43	3	<0.001
	climate change	0.71	288.05	3	<0.001

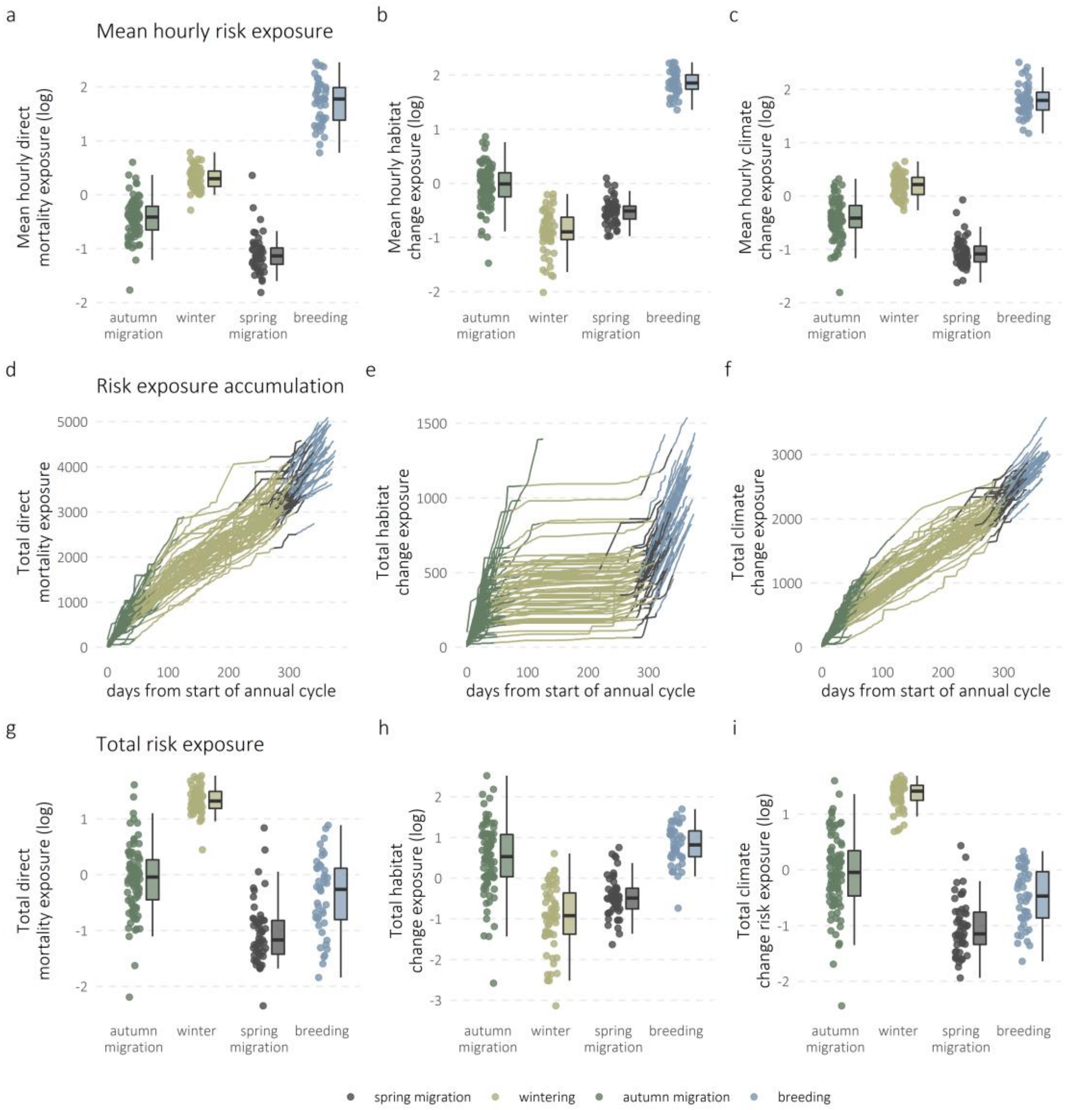

Figure 5.2 – a–c: Boxplots showing mean hourly risk exposure per season for each of the three risk types. All pairwise comparisons between seasons were statistically significant (Table S5.1). Points represent raw mean hourly risk exposure data for each bird-season; boxplots show the median value, interquartile range and Tukey-style whiskers. d–f: Line plots showing the accumulation of risk exposure throughout the annual cycle for each of the three risk types. Each line represents a bird-year as it progresses throughout the annual cycle: the x-axis represents time elapsed since the start of autumn migration, while the y-axis values represent cumulative time-weighted risk exposure measured for each risk surface cell through which the individual passed (see Methods). g–i: Boxplots showing total risk exposure for each of the three risk types. All pairwise comparisons between seasons were statistically significant, except for total habitat change exposure in the autumn migration and breeding season, which was similar (h) (Table S5.1). Points represent raw total risk exposure data for each bird-season; boxplots show the median value, interquartile range and Tukey-style whiskers.

Migratory route

We found significant variation in total risk exposure across the east-west axis of migratory flyways for direct mortality and climate change in the autumn, and for all risk types in the winter (Table 5.3), but this variation was generally non-linear (Table 5.3, Figure 5.3). The magnitude of variation in autumn total risk exposure with longitude was fairly small, with evidence for lower direct mortality risk in routes away from longitudinal extremes, and slightly higher climate change exposure along the more easterly routes (Figure 5.3). For total risk exposure in the subsequent wintering period, exposure to all three risk types decreased among individuals that took more easterly routes during the autumn (Figure 5.3d–5.3f). Generalised additive models fit the data better than linear models in all cases except for winter climate change exposure (Table 5.3), for which the linear model fit better (Table 5.3).

Sensitivity analyses excluding data-deficient bird-seasons yielded similar results (Appendix S5.1, Table S5.3), as did analyses using initial winter longitude as a measure of flyway route (Appendix S5.2).

Table 5.3 – Summary of linear and generalized additive models and associated likelihood ratio tests assessing the influence of autumn flyway longitude on autumn and winter total risk exposure scores. Models in bold are presented in Figure 5.3. Estimated degrees of freedom (edf) are presented for generalized additive models.

Response variable							Likelihood ratio test statistics		
Season	Risk type	Model type	AIC	r^2 (adj.)	Sample size	edf	χ^2	χ^2 df	*P*-value
Autumn migration	direct mortality	**GAM**	**241.18**	**0.09**	**86**	**2.58**	**11.04**	**2.58**	**0.012**
		linear	245.02	0.03	86	-	4.03	1.00	0.045
	habitat change	gam	245.53	0.05	86	3.15	7.81	3.15	0.050
		linear	248.94	-0.01	86	-	0.11	1.00	0.739
	climate change	**GAM**	**234.07**	**0.16**	**86**	**1.60**	**16.18**	**1.60**	**< 0.001**
		linear	234.76	0.14	86	-	14.29	1.00	< 0.001
Winter	direct mortality	**GAM**	**160.04**	**0.15**	**58**	**1.59**	**10.72**	**1.59**	**0.005**
		linear	160.45	0.13	58	-	9.14	1.00	0.003
	habitat changes	**GAM**	**143.04**	**0.37**	**58**	**2.05**	**28.65**	**2.05**	**< 0.001**
		linear	144.79	0.34	58	-	24.80	1.00	<0.001
	climate change	GAM	162.40	0.10	58	1.00	7.19	1.00	0.007
		linear	**162.40**	**0.10**	**58**	**-**	**7.19**	**1.00**	**0.007**

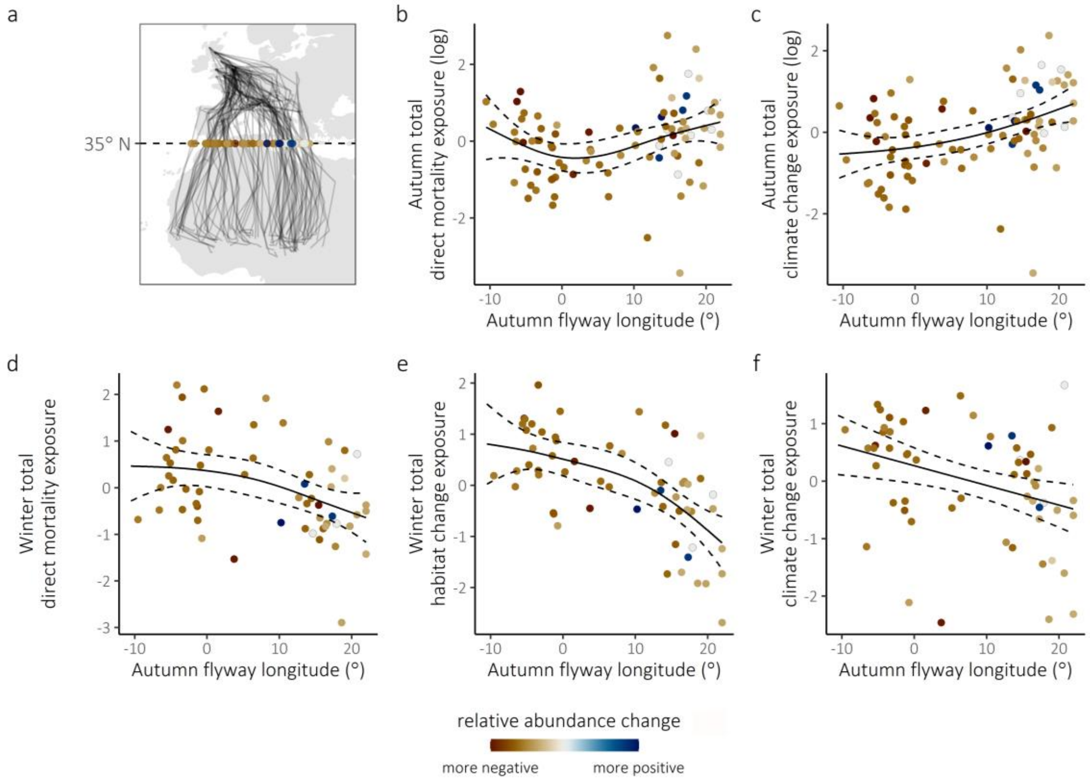

Figure 5.3 – a: Autumn migratory routes of common cuckoos, with points indicating the longitude of autumn migration (point of crossing 35° latitude). b – f: Lineplots showing the relationship between autumn flyway longitude and metrics of autumn (b, c) and winter (d – f) total risk exposure, as predicted by the most parsimonious models (bold in Table 5.3). Points show raw data, with each point representing a bird-season. Solid and dashed lines indicate model-predicted means and 95% confidence intervals respectively. Points are coloured according to the relative population abundance change at the breeding site of each individual (see Methods).

Population trends

We found no significant relationships between local population abundance trends and mean seasonal total risk exposure scores (Table 5.4). This result persisted in the sensitivity analyses (Appendix S5.1, Table S5.4). Examination of the migratory tracks in this dataset indicates relatively weak migratory connectivity in UK-breeding common cuckoos (Figure S5.2), such that our sample for each breeding site contains individuals performing very different migrations and thus being exposed to different risk levels. It is therefore unsurprising to find limited correlation between mean site-level risk exposure and breeding site population trends, as site-level means mask considerable within-site variation in migratory risks (see Discussion).

Table 5.4 – Model summaries of nine univariate models and associated likelihood ratio tests assessing the effect of mean seasonal total risk exposure for birds from each of the thirteen sites on the mean abundance change per site.

Predictor variable						Likelihood ratio test statistics			
Season	Risk type	Intercept	β	r^2	Sample size	χ^2	χ^2 df	*P*-value	Bonferroni-corrected *P*-value
Autumn migration	direct mortality	-0.20	0.06	0.06	13	0.77	1	0.381	1.000
	habitat change	-0.20	0.05	0.05	13	0.63	1	0.428	1.000
	climate change	-0.20	0.08	0.12	13	1.65	1	0.199	1.000
Winter	direct mortality	-0.20	-0.06	0.08	13	1.02	1	0.312	1.000
	habitat change	-0.20	-0.11	0.23	13	3.36	1	0.067	0.891
	climate change	-0.20	0.02	0.01	13	0.08	1	0.782	1.000
Spring migration	direct mortality	-0.20	-0.03	0.01	13	0.16	1	0.692	1.000
	habitat change	-0.20	-0.00	0.00	13	0.00	1	0.974	1.000
	climate change	-0.20	-0.04	0.03	13	0.43	1	0.514	1.000

5.4 DISCUSSION

Here, we show that combining remote-sensed risk surfaces with GPS tracking data can generate new insights into the spatiotemporal drivers of biodiversity declines, particularly among long-distance migrants where risk exposure may vary hugely across the annual cycle. Despite the more intense anthropogenic transformation of the environment in the breeding grounds of our study species (Figure 5.2a–5.2c), cumulative risk was greatest during other seasonal stages, particularly in winter (the longest stage in this species' migratory phenology). We find that easterly autumn migration routes around the Mediterranean – previously linked to higher survival and breeding site abundance in this species (Hewson et al., 2016) – are associated with lower total exposure to all three risks in the subsequent winter period. Despite our observed between-flyway variability in risks, mean site-level migratory risk exposure does not translate to local population trend effects for the common cuckoo, suggesting these effects are dampened by weak migratory connectivity in this species.

Between-season differences in risk exposure

Across all three risk types – direct mortality, habitat change and climate change – mean hourly risk exposure was highest in the breeding season. This is unsurprising given the high levels and intensity of anthropogenic transformation seen in Western Europe (Venter et al., 2016), and the typically greater impacts of climate change on temperature seen at higher latitudes (IPCC, 2013). However, accounting for the longer duration of the wintering phase in our study species (Table 5.1, Figure 5.2d–f) reveals that despite the high mean hourly risk levels on the breeding grounds, winter contributes the most to total accumulated exposure to direct mortality risk and climate change risk. This supports the results of Klaassen et al. (2014), who reported daily mortality rates of long-distance raptors to be six times greater on migration than at other points of the year, but – given the relatively short duration of migratory seasons – this amounted to similar total mortality between seasons.

As brood parasites, cuckoos have particularly short breeding seasons (Table 5.1), likely exacerbating the discrepancy between mean hourly and total breeding season threat exposure we report here (Figure 5.2). Species-specific ecological drivers of phenology (e.g. reproductive and moult strategies) (Thorup et al., 2007), in addition to responses to changes in climatic cues (Lehikoinen et al., 2004), may therefore also be important in determining how species vary in their relative accumulated threat exposure between seasons.

Levels of exposure to habitat change on the wintering grounds were low, with total habitat exposure being instead highest in the autumn migration and breeding seasons (Figure 5.2e, Table S5.1). This pattern reflects that urbanisation and agrochemical use (see Methods) are in general markedly lower in the central African wintering grounds than elsewhere in the species' annual range (Figure 5.2b). In other species, levels of exposure to habitat change risks are likely to vary significantly in relation to habitat specialism – for instance, species unable to exploit agricultural land-use types (unlike cuckoos) may be particularly exposed to habitat change risks in sub-Saharan areas where agricultural expansion has been rapid. Indeed, cuckoos have complex habitat requirements driven by host availability in the breeding season, as well as microhabitats for foraging and roosting, with evidence that cuckoos prefer mosaic semi-open habitats in the non-breeding season (Williams et al., 2016), complicating the relationship between land cover changes and cuckoo risk exposure.

Across all three risk types, both mean hourly and total risk exposure were higher on autumn migration than spring migration (Figure 5.1). The more easterly migratory routes used in the autumn tend to have greater hourly risk levels than the westerly routes (Figure S5.4), possibly because a greater proportion of these routes lie within Europe (Figure 5.2). All birds return during spring via the more westerly flyway (Figure 5.1), which may drive the lower risk exposure levels on spring migration. The greater discrepancy in total risk exposure seen between spring and autumn is also likely to be in part driven by the longer duration of autumn migration (Table 5.1).

Our finding of higher total risk exposure in the winter than during the two migratory phases does not align with observed high migration mortality rates reported for other species (Klaassen et al., 2014; Oppel et al., 2015; Sergio et al., 2019; Sillett & Holmes, 2002). It is likely the tracking data used in our analyses suffers from some degree of survivorship bias, as we excluded incomplete bird-seasons that may have arisen due to mortality. Bias could occur if, in the cases where tag death represents true bird death, the censored tracks moved through particularly high risk exposure areas. Additionally, measurements of cumulative risk exposure do not capture capacity for fine-scale behavioural adaptation to risks, such as micro-avoidance (Everaert, 2014; Plonczkier & Simms, 2012), nor the extent to which individuals are risk-naïve or -omniscient (Klaassen et al., 2006). Indeed, risk perception and avoidance may be context-dependent (Sol et al., 2018), and may itself have negative fitness consequences (Doherty et al., 2021). Incorporating risk avoidance into exposure quantification may be particularly relevant for direct mortality threats, as the capacity to adopt risk-avoidant behaviours may vary between seasonal stages (particularly between active migration and more static phases).

In future, our approach could be extended to account for avoidance behaviours if these can be detected through pattern analysis of high-resolution tracking data (including accelerometer data) and more finely-resolved risk surfaces.

Between-flyway differences in risk exposure

Hewson et al. (2016) previously established a link between migratory route and breeding site population trends in cuckoos, as the site-level proportion of tagged individuals taking more easterly autumn migration routes is positively correlated with site-level breeding population trends. We found that between-flyway differences in anthropogenic risk exposure during autumn were spatially complex, with non-linear relationships between flyway longitude and exposure to direct mortality risks, a slight trend towards increased climate change exposure for more easterly migratory routes, and no difference in exposure to habitat change across route longitudes (Figure 5.3b–5.3c). However, across all three risk types, total risk exposure in the subsequent winter was lower for individuals whose autumn migratory flyway was further east (Figure 5.3d–5.3f). This connection between lower total winter risk exposure for individuals from populations with more positive population trends points towards the importance of wintering experience, although it is not possible here to disentangle to extent to which local population trends may also be driven by breeding site effects (Buchan et al., 2021; Morrison et al., 2013). Between-flyway structuring of winter risk exposure therefore aligns with previously reported flyway-specific population trends (Hewson et al., 2016), although our study does not align with their results regarding flyway survival, as risk exposure levels do not appear to be higher on the western routes where mortality has been shown to be greater. This may again reflect potential survivorship bias in our dataset (see above), or alternatively that the previously reported survival differences are also driven by carryover effects of breeding season conditions (Harrison et al., 2011).

We also aimed to assess the contribution of non-breeding season total risk exposure to local breeding population trends, but found no relationship between risk scores and recent abundance changes. However, direct effects of migratory risk exposure on site-level breeding population change would only be expected in populations that exhibit strong migratory connectivity, such that the individuals inhabiting a site follow similar migrations and therefore have similar non-breeding experiences. In fact, migratory connectivity in UK-breeding common cuckoos is comparatively weak (Figure S5.2) – it is therefore unsurprising we did not find any relationship between mean site-level total risk exposure and population trends, as site-level means mask considerable variation in non-breeding experiences among cuckoos that breed at the same site. We were unable to link survival to risk exposure due to sample size limitations and difficulties in distinguishing between bird-death and tag-death; extending our approach to assess how individual risk exposure influence individual-level demographic parameters – breeding success, survival, condition – would yield greater insights into the effects of anthropogenic risk exposure on migratory birds.

5.5 CONCLUSIONS

Combining remote-sensed environmental information with tracking data represents a powerful means of assessing individual risk exposure, representing an important step towards better quantification of exactly where and when organisms are most exposed to anthropogenic risks. Our results reinforce the importance of full annual cycle approaches (Marra et al., 2015), and of exploring between-season temporal variability in anthropogenic impacts. Increasing availability of high spatial and temporal resolution tracking data will enable more accurate estimation of risk exposure in future; combining this with individual-level data on condition, survival and breeding success will shed further light on the demographic impacts of anthropogenic change for migratory birds, and help pinpoint key areas and issues for targeted conservation action.

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Chapter 5 Supplementary Materials

Table S5.1 Post-hoc tests of multiple comparisons carried out on models assessing effect of season on mean hourly and total risk exposure

Figure S5.1 Common cuckoo population abundance change maps

Figure S5.2 Autumn migration and wintering tracks of common cuckoo by breeding population

Appendix S5.1 Sensitivity analyses

> **Table S5.2** Summaries of linear models assessing the effect of season on mean hourly and total risk exposure, conducted on a reduced dataset with data-poor tracks removed
>
> **Table S5.3** Summaries of linear and generalized additive models assessing the influence of autumn flyway longitude on autumn and winter total risk exposure, conducted on a reduced dataset with data-poor tracks removed
>
> **Table S5.4** Summaries of univariate models assessing the effect of mean total risk exposure on mean population abundance change per site, conducted on a reduced dataset with data-poor tracks removed

Appendix S5.2 Winter destination

> **Table S5.5** Summaries of linear and generalized additive models assessing the influence of initial winter longitude on metrics of total winter risk exposure
>
> **Figure S5.3** Model-predicted relationships between initial winter longitude on metrics of total winter total risk exposure

Figure S5.4 Relationship between metrics of raw mean hourly risk exposure and autumn flyway longitude

Table S5.1 – Outputs of post-hoc tests of multiple comparisons carried out on models assessing the effect of season on mean hourly and total risk exposure for each of the three risk types: direct mortality, habitat change, climate change.

Model	Pairwise comparison			Estimate	Std. Error	z-value	*P*-value
Mean hourly direct mortality ~ season	Autumn migration	-	Breeding	-2.14	0.06	-35.8	<0.001
	Spring migration	-	Breeding	-2.81	0.07	-42.6	<0.001
	Winter	-	Breeding	-1.40	0.06	-21.9	<0.001
	Spring migration	-	Autumn migration	-0.66	0.06	-11.7	<0.001
	Winter	-	Autumn migration	0.74	0.05	13.5	<0.001
	Winter	-	Spring migration	1.40	0.06	22.8	<0.001
Mean hourly habitat change ~ season	Autumn migration	-	Breeding	-1.90	0.06	-31.88	<0.001
	Spring migration	-	Breeding	-2.37	0.07	-36.22	<0.001
	Winter	-	Breeding	-2.75	0.06	-43.14	<0.001
	Spring migration	-	Autumn migration	-0.47	0.06	-8.38	<0.001
	Winter	-	Autumn migration	-0.85	0.05	-15.74	<0.001
	Winter	-	Spring migration	-0.38	0.06	-6.23	<0.001

Model							
mean hourly climate change ~ season	Pairwise comparison			Estimate	Std. Error	z-value	*P*-value
	Autumn migration	-	Breeding	-2.23	0.05	-41.65	<0.001
	Spring migration	-	Breeding	-2.85	0.06	-48.35	<0.001
	Winter	-	Breeding	-1.60	0.06	-27.89	<0.001
	Spring migration	-	Autumn migration	-0.62	0.05	-12.13	<0.001
	Winter	-	Autumn migration	0.63	0.05	12.89	<0.001
	Winter	-	Spring migration	1.25	0.05	22.71	<0.001
total direct mortality ~ season	Pairwise comparison			Estimate	Std. Error	z-value	*P*-value
	Autumn migration	-	Breeding	0.30	0.10	2.99	0.015
	Spring migration	-	Breeding	-0.67	0.11	-5.90	<0.001
	Winter	-	Breeding	1.72	0.11	15.70	<0.001
	Spring migration	-	Autumn migration	-0.97	0.10	-10.00	<0.001
	Winter	-	Autumn migration	1.42	0.09	15.21	<0.001
	Winter	-	Spring migration	2.39	0.11	22.69	<0.001

Model	Pairwise comparison			Estimate	Std. Error	z-value	*P*-value
total habitat change ~ season							
	Autumn migration	-	Breeding	-0.33	0.13	-2.49	0.061
	Spring migration	-	Breeding	-1.28	0.14	-8.84	<0.001
	Winter	-	Breeding	-1.80	0.14	-12.79	<0.001
	Spring migration	-	Autumn migration	-0.95	0.12	-7.65	<0.001
	Winter	-	Autumn migration	-1.48	0.12	-12.32	<0.001
	Winter	-	Spring migration	-0.52	0.14	-3.86	<0.001
total climate change ~ season	Pairwise comparison			Estimate	Std. Error	z-value	*P*-value
	Autumn migration	-	Breeding	0.45	0.10	4.47	<0.001
	Spring migration	-	Breeding	-0.54	0.11	-4.87	<0.001
	Winter	-	Breeding	1.83	0.11	17.03	<0.001
	Spring migration	-	Autumn migration	-0.99	0.10	-10.36	<0.001
	Winter	-	Autumn migration	1.39	0.09	15.16	<0.001
	Winter	-	Spring migration	2.37	0.10	22.96	<0.001

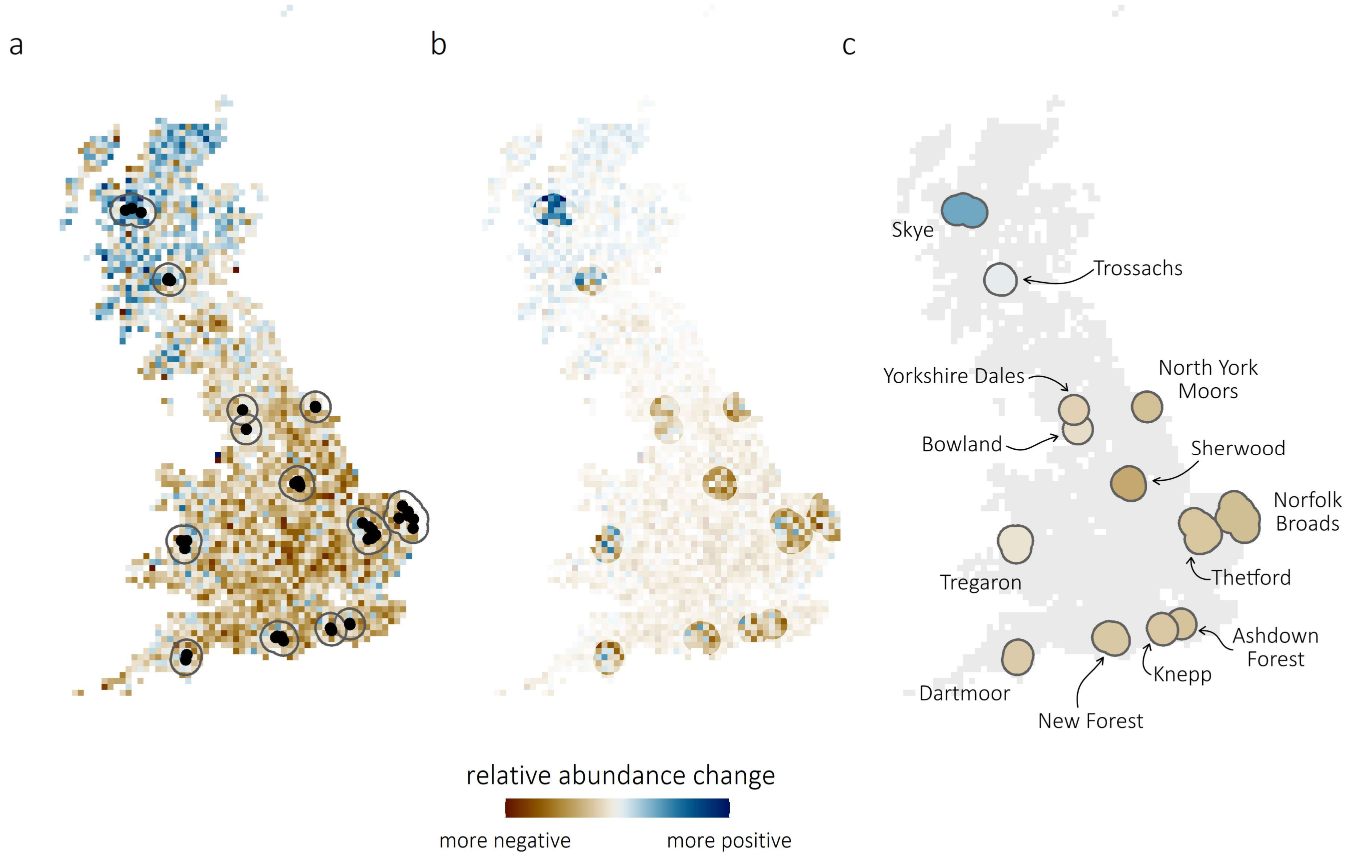
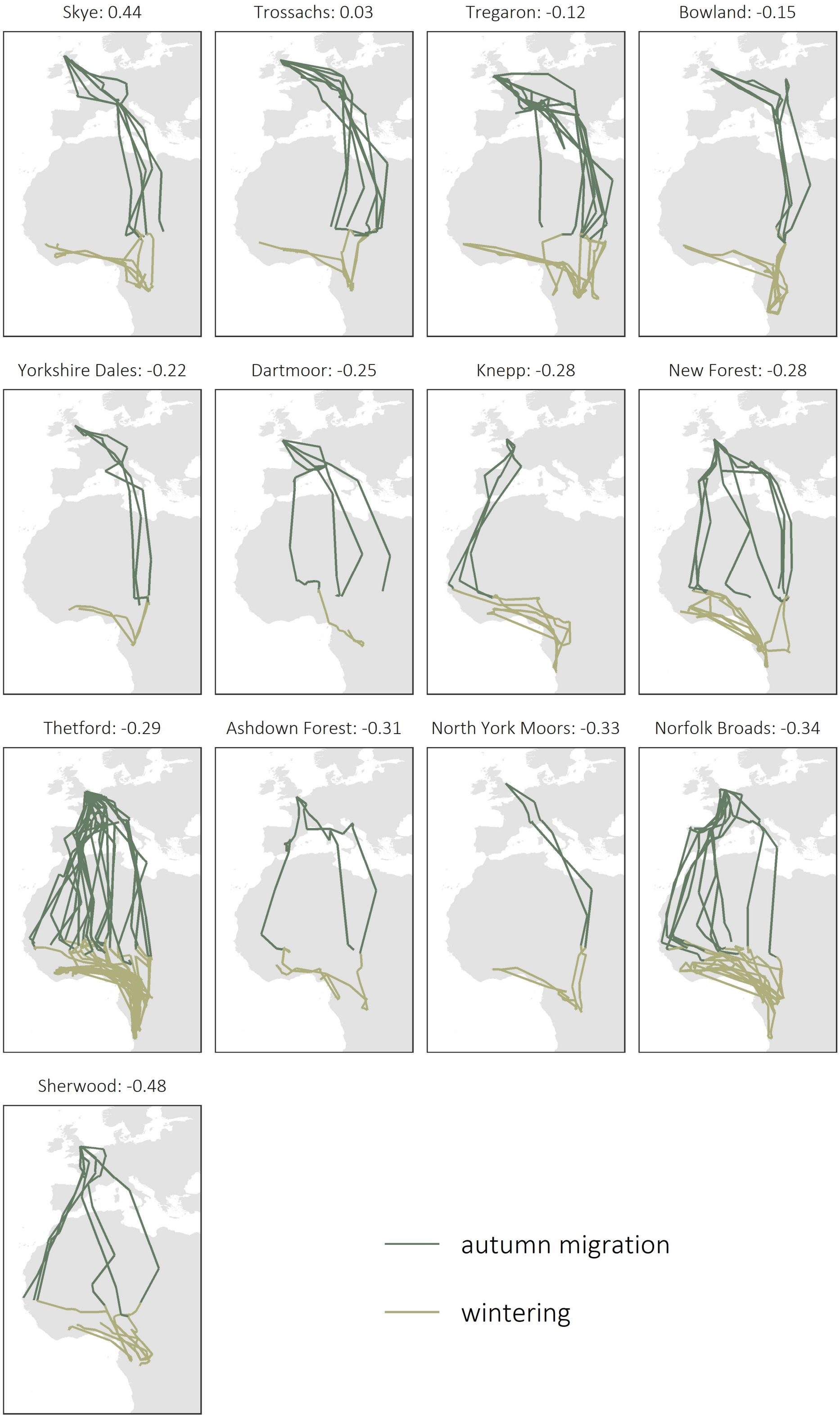


Figure S5.1 – a: Standardised population abundance change of common cuckoos between 1988–1992 and 2007–11 (Balmer et al., 2013) at a 10 km x 10km resolution. Black points indicate capture locations of each individual included within this analysis. Grey rings indicate the site region defined by a 25-km radius buffer around the capture locations. b: Standardised population abundance change included in the calculation of each site mean. c: Location of each site and relative spatial mean population abundance change.



Skye: 0.44

Trossachs: 0.03

Tregaron: -0.12

Bowland: -0.15

Yorkshire Dales: -0.22

Dartmoor: -0.25

Knepp: -0.28

New Forest: -0.28

Thetford: -0.29

Ashdown Forest: -0.31

North York Moors: -0.33

Norfolk Broads: -0.34

Sherwood: -0.48

Figure S5.2 – Autumn migration (green) and wintering tracks (yellow) of tagged common cuckoos from thirteen different breeding populations within the UK. The variability of routes taken by individuals from within a breeding site indicate weak migratory connectivity at this scale. Values at the top of each panel are the relative population abundance change (see Methods).

Appendix S5.1 Sensitivity analyses

When processing cuckoo tracking data, we flagged any bird-seasons featuring a between-fix gap longer than 10 days and greater than 2000 km, as the inferred path between these fixes is unlikely to be accurate. Seventeen of the 239 fixes (7%) fit these criteria. We re-ran all analyses reported in the main text on a subset of the full dataset, with the seventeen data-poor bird-seasons excluded.

In all cases, inference remained similar to that of the results run on the full dataset. Mean hourly risk exposure and total risk exposure both varied with stage of the annual cycle (Table S5.2), with post-hoc tests revealing the same seasonal patterns of risk exposure. The effect of migratory longitude on autumn and winter total risk exposure scores remained similar, although when conducted on the dataset without the data-poor birds there was additional statistical support for a non-linear effect of migratory longitude on autumn habitat exposure, and evidence for a linear (as opposed to non-linear) effect of longitude on winter direct mortality exposure (Table S5.3). There was again no statistical support for any effect of total risk exposure in the non-breeding seasons or annually on population abundance change (Table S5.4).

Table S5.2 – Summaries of six univariate linear mixed-effects models and associated likelihood ratio tests assessing the effect of season on mean hourly risk exposure and total risk exposure for the three risk types, with bird identity as a random effect, run on a subset of data excluding data-poor bird-seasons. Marginal r^2 for linear mixed-effects models calculated following Nakagawa & Schielzeth (2013).

Response variable			Likelihood ratio test statistics		
Metric	Risk type	Marginal r^2	χ^2	χ^2 df	*P*-value
Mean hourly exposure	direct mortality	0.90	518.35	3	< 0.001
	habitat change	0.90	514.31	3	< 0.001
	climate change	0.92	569.93	3	< 0.001
Total exposure	direct mortality	0.73	279.56	3	< 0.001
	habitat change	0.54	165.49	3	< 0.001
	climate change	0.74	293.89	3	< 0.001

Table S5.3 – Summary of linear and generalized additive models and associated likelihood ratio tests assessing the influence of autumn flyway longitude on autumn and winter total risk exposure scores, run on a subset of data excluding data-poor bird-seasons. Estimated degrees of freedom (edf) are presented for generalized additive models.

Response variable							Likelihood ratio test statistics		
Season	Risk type	Model type	AIC	r^2 (adj.)	Sample size	edf	χ^2	χ^2 df	*P*-value
Autumn migration	direct mortality	**GAM**	**231.35**	**0.14**	**84**	**2.91**	**15.84**	**2.91**	**0.001**
		linear	237.43	0.06	84	NA	5.95	1.00	0.015
	habitat change	**GAM**	**236.04**	**0.10**	**84**	**3.59**	**12.52**	**3.59**	**0.014**
		linear	242.66	0.00	84	NA	0.72	1.00	0.397
	climate change	**GAM**	**223.15**	**0.21**	**84**	**1.68**	**21.60**	**1.68**	**< 0.001**
		linear	224.11	0.20	84	NA	19.26	1.00	< 0.001
Winter	direct mortality	GAM	145.11	0.12	52	1.00	7.45	1.00	0.006
		linear	**145.11**	**0.12**	**52**	**NA**	**7.45**	1.00	**0.006**
	habitat change	**GAM**	**130.44**	**0.35**	**52**	**2.28**	**24.67**	**2.28**	**< 0.001**
		linear	132.82	0.30	52	NA	19.74	1.00	< 0.001
	climate change	GAM	148.19	0.06	52	1.00	4.37	1.00	0.036
		linear	**148.19**	**0.06**	**52**	**NA**	**4.37**	1.00	**0.036**

Table S5.4 – Model summaries of nine univariate models and associated likelihood ratio tests assessing the effect of the mean total risk exposure for birds from each of the thirteen sites on the mean abundance change per site, run on a subset of data excluding data-deficient bird-seasons.

Predictor variable						Likelihood ratio test statistics			
Season	Risk type	Intercept	β	r^2	Sample size	χ^2	χ^2 df	*P*-value	Bonferroni-corrected *P*-value
Autumn migration	direct mortality	-0.20	0.06	0.07	13	0.89	1	0.345	1.000
	habitat change	-0.20	0.05	0.05	13	0.73	1	0.394	1.000
	climate change	-0.20	0.08	0.13	13	1.84	1	0.175	1.000
Winter	direct mortality	-0.20	-0.07	0.09	13	1.18	1	0.278	1.000
	habitat change	-0.20	-0.12	0.26	13	3.90	1	0.048	0.684
	climate change	-0.20	0.01	0.00	13	0.02	1	0.885	1.000
Spring migration	direct mortality	-0.20	0.07	0.10	12	1.23	1	0.268	1.000
	habitat change	-0.20	0.08	0.11	12	1.38	1	0.241	1.000
	climate change	-0.20	0.04	0.03	12	0.32	1	0.569	1.000

Appendix S5.2 Winter destination

To explore the extent to which flyway destination affects cumulative winter risk exposure, we modelled total winter risk exposure as a function of initial winter fix longitude. We used linear models and generalised additive models (thin plate regression splines) with default selection of smoothing parameters to explore whether there was statistical support for non-linear relationships; we used r^2 values and AIC values to compare the fit of the linear and generalised additive models.

Results were very similar to those relating total winter exposure to mid-flyway longitude (Main text). Winter destination longitude predicted total winter exposure to all three risk types, with a non-linear relationship between winter destination and total direct mortality and habitat change exposure, and a negative linear relationship between winter destination and total climate change exposure (Table S5.5, Figure S5.3).

Table S5.5 – Summary of linear and generalized additive models and associated likelihood ratio tests assessing the influence of initial winter longitude on autumn and winter total risk exposure scores. Models in bold are presented in Figure S5.3. Estimated degrees of freedom (edf) are presented for generalized additive models.

Response variable							Likelihood ratio test statistics		
	risk type	model type	AIC	r^2 (adj.)	sample size	edf	χ^2	χ^2 df	*P*-value
winter	mortality	**GAM**	**152.58**	**0.27**	**58**	**3.40**	**21.81**	**3.398**	**< 0.001**
		linear	157.65	0.17	58	-	11.94	1	< 0.001
	habitat	**GAM**	**141.76**	**0.38**	**58**	**2.28**	**30.38**	**2.275**	**< 0.001**
		linear	147.07	0.31	58	-	22.52	1	< 0.001
	climate	GAM	163.72	0.08	58	1	5.87	1	0.015
		linear	**163.72**	**0.08**	**58**	**-**	**5.87**	**1**	**0.015**

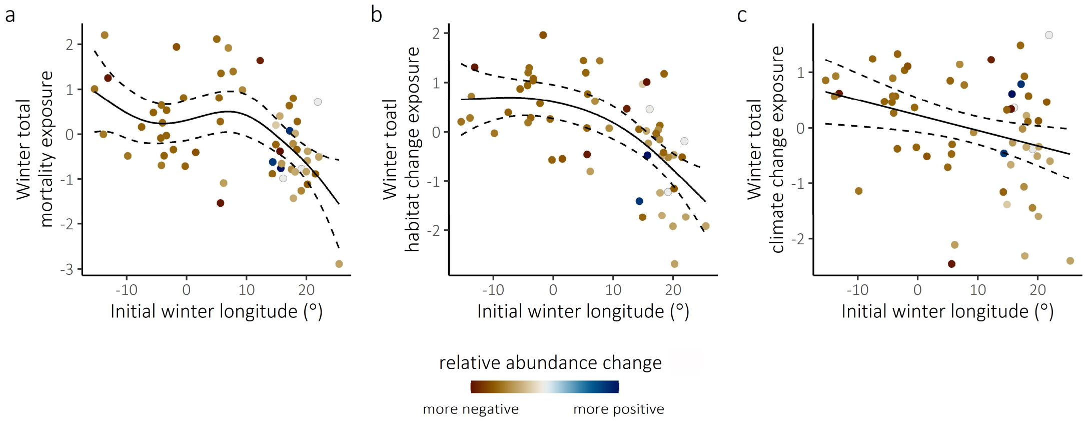


Figure S5.3 – Lineplots showing the relationship between initial winter longitude on metrics of winter total risk exposure, as predicted by models in bold in Table S5.5. Points indicate raw data, with each point representing a bird-season. Solid and dashed lines indicate model-predicted means and 95% confidence intervals respectively. Points are coloured according to relative breeding site population abundance change (see Methods).

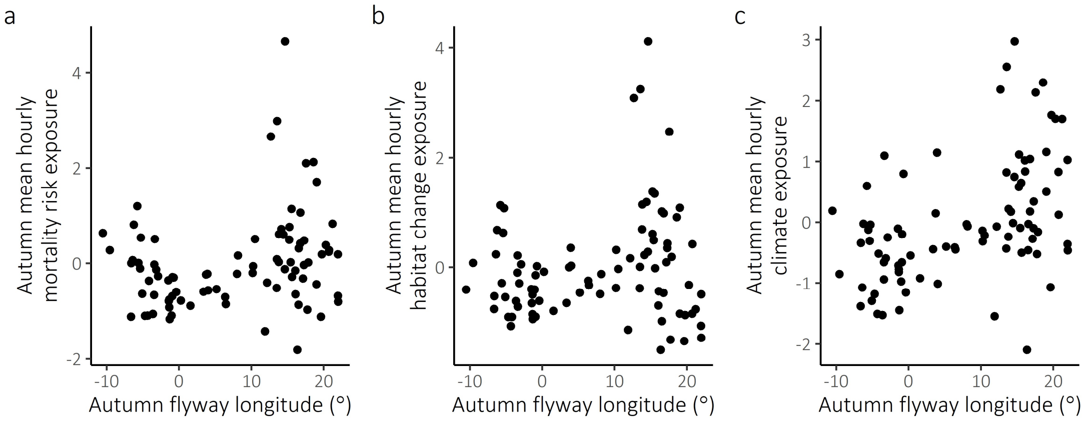


Figure S5.4 – Scatterplots showing the relationship between mean hourly direct mortality (a), habitat change (b) and climate change (c) risk exposure in the autumn migration and autumn migratory route longitudes. Points are raw data, with each point representing a bird-season.

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General Conclusions

6.1 Summary of thesis findings

Within recent studies of partially migratory systems suitable for meta-analysis, we found evidence that, **in birds, residency is associated with greater fitness outcomes than migration** (Chapter 2). Across all taxa, although fitness was approximately balanced between residents and migrants, **in cases where residency conferred a benefit, it was more likely to be associated with survival than with reproductive success**. These results both hint towards a destabilisation of the hypothesised survival benefit of migration, possibly as a result of migrants' greater susceptibility to anthropogenic change, and is reinforced by the result that the effect was stronger in longer-running studies. The evidence for a survival benefit to residency could be interpreted conversely – that where migration conferred a fitness benefit, it was more likely to be associated with reproductive success than with survival – however, given that for birds (the majority of the overall dataset) residency yielded an overall fitness benefit compared to migration, we considered this result as tentatively indicative of a survival benefit to residency.

In long-distance partially migratory lesser kestrels, we found limited evidence for carryover effects of migration to the following breeding season, with **fitness metrics instead better predicted by breeding site location** (Chapter 3). At the breeding location with lower primary productivity throughout the year, we found evidence for a short-lived negative carryover effect of migration on adult body condition, indicating that breeding site conditions may buffer individuals to any deleterious effects of long-distance migration – although the effect did not persist beyond the incubation period.

In Chapter 4, we collated and created maps of anthropogenic risk across the Afro-Palaearctic region, including surveying expert opinion to create the first map of relative bird hunting pressure to cover the whole region (Figure 4.2), and present a framework for quantifying species-specific range-level risk exposure by combining remote-sensed data with species' traits-based vulnerability weightings. In Afro-Palaearctic migratory birds, we find a relationship between range-scale non-breeding season exposure to direct mortality risks (encompassing metrics of human settlement, energy infrastructure, and hunting), such that **migrants whose non-breeding ranges are characterised by higher levels of direct mortality risk have more negative long-term population trends**. We also find evidence for a negative effect of non-breeding range climate change exposure mediated by migratory distance, and for a negative effect of breeding range direct mortality mediated by extent of breeding range habitat change (Figure 4.5). These results emphasise the potential for complex between-threat and between-season interactions, and demonstrate the utility of spatially explicit approaches to assessing drivers of population declines.

By combining remote-sensed risk surfaces assembled in Chapter 4 with GPS tracking data, we measure spatiotemporal risk exposure faced by UK-breeding common cuckoos across the annual cycle (Chapter 5). We find that, despite the high levels of human modification on the breeding grounds, accounting for temporal variation between the seasons reveals that **risk exposure is generally greatest in the winter**, with the exception of habitat change risk. As the variable autumn migratory routes in this species have been linked to variation in demographic success (Hewson et al., 2016), we explore how autumn route relates to risk exposure, finding that risk exposure varies less between routes during autumn migration than it does during the subsequent winter period (Figure 5.3). The approaches to quantifying spatiotemporal risk exposure described in this chapter are generalizable to other migratory species, providing individual species habitat requirements, risk vulnerabilities, and life history traits are considered.

Overall, in this thesis, we provide further evidence that migratory species are particularly vulnerable to ongoing anthropogenic change, and that exposure to environmental change may be disrupting the benefits of migration originally driving its evolution and maintenance as a viable life-history strategy. Our results reinforce the importance of full annual cycle approaches for the effective conservation of migratory species (Marra et al., 2015).

6.2 Broader context

Drivers of migratory behaviour

Migration is hypothesised to have evolved as a means of enhancing fitness in species inhabiting seasonal environments (Dingle & Drake, 2007; Griswold et al., 2010), particularly survival (Kokko, 2011; Lundberg, 1987; Zúñiga et al., 2017). The risks inherent in undertaking migration (Wilcove & Wikelski, 2008) – particularly long-distance migration – indicates strong selective pressure on migration, i.e. that migration must, on balance, confer a significant survival advantage relative to not migrating (Kokko, 2011; Lundberg, 1987). The evidence we present here indicates that, in birds, the hypothesised relative survival benefit yielded by migration may have diminished due to widespread anthropogenic change (Chapter 2), and that levels of anthropogenic direct mortality risks on the non-breeding ranges of Afro-Palaearctic avian migrants are particularly associated with negative population trends (Chapter 4). These results align with predictions that increasing levels of anthropogenic modification of the environment may have disproportionately negative effects for migratory species (Gilroy et al., 2016; Robinson et al., 2009), and ultimately shift the balance of relative fitness drivers towards residency (Berthold, 2001; Pulido & Berthold, 2010) or towards migratory plasticity (Lennox et al., 2016; Reid et al., 2020).

Ongoing environmental change

When assessing the influence of anthropogenic threats classified as relating to direct mortality, habitat change and climate change, we found that the degree of exposure to direct mortality risks (infrastructure collision risks, hunting, etc.) consistently emerged as a predictor of population trends (Figure 4.5), although this may to some extent reflect the comparative ease of accurately mapping these threats (Chapter 4). All of the constituent direct mortality threat layers are, to a greater or lesser extent, associated with human population density and related infrastructure. In the context of population growth (United Nations, 2019), ongoing rural-urban migration (Angel et al., 2011), and growing investment in green energy (IEA, 2020), these threats are likely to increase in intensity and in spatial coverage. Our results emphasise the importance of minimising threats associated with structural climate change mitigation measures, and more generally emphasise the threats symptomatic of current models of economic development. Nevertheless, the spatially discrete threats posed by direct mortality risks may be easier to directly mitigate than the broader scale, more chronic threats posed by habitat loss and climate change (Doherty et al., 2021).

Broader applicability

Although our assessment of anthropogenic risks focused on the regions within the Afro-Palaearctic migratory flyway (covering most of Europe, Central and Western Asia and Africa), the approaches are broadly generalizable to other migratory systems. Much attention has been paid to measuring direct anthropogenic causes of mortality in North America (Loss et al., 2012, 2013, 2015; Loss, Will, & Marra, 2014b, 2014a; Loss, Will, Loss, et al., 2014; Van Doren et al., 2021), but this has not been done in a spatially explicit or composite holistic manner. Our methods allow large-scale spatial quantification of these threats, which could yield new insights into demographic responses of Nearctic–Neotropical migratory species to anthropogenic modification of the environment – particularly if used in conjunction with the dynamic distribution and abundance mapping recently developed using eBird records (https://ebird.org/science/status-and-trends/; (Fink et al., 2020)). Our approaches would be similarly applicable to regions in the East Asian–Australasian flyway, where rapid industrialisation degrading critical habitats, agricultural intensification and hunting pressure have all been linked to population declines of migratory species (Edenius et al., 2017; Kamp et al., 2015; Murray et al., 2018; Studds et al., 2017; Yong et al., 2015).

Although this thesis is predominately focused on avian migrants, the approaches and results outlined may be broadly generalizable to other migratory systems – particularly volant species with similar evolutionary drivers of migratory behaviour and facing similar anthropogenic threats (e.g. bats, invertebrates) (Frick et al., 2020; Malcolm, 2018).

6.3 Future directions and conservation implications

Literature bias

Biases in the studies we included for meta-analysis in Chapter 2 reflect common biases in ecological literature more generally, with birds especially well represented, despite partial migration being prominent in many other orders (Chapman et al., 2011). A number of studies were excluded on the grounds of insufficient reporting of data, particularly older studies – indicating increasing rigour in reporting and in data availability. There was a particularly strong geographic skew towards Europe and North America. Again, this is partly symptomatic of existing biases in ecology (Amano & Sutherland, 2013), and possibly exacerbated by the northern hemisphere having greater seasonality of and hence migratory systems (Somveille et al., 2013). However, it is also likely to be driven in part by our having undertaken the literature searches in English alone, and there is a growing movement towards acknowledging the limitations of Anglophone-centric research in ecology and related disciplines (Amano et al., 2016; Konno et al., 2020). Future meta-analyses capturing studies from a wider range of regions and taxa may yield new and more detailed insights into the generality of migratory fitness trade-offs.

Additional demographic parameters

The single-species systems described in Chapter 3 and Chapter 5 could yield greater insights if analyses encompassed explicit survival data – particularly in light of the evidence from Chapter 2 that residency is more likely to confer fitness benefits to survival than to breeding success. In the case of lesser kestrels (Chapter 3), without data on survival we cannot conclude there are no strong demographic effects of undertaking long-distance migration, as we may simply fail to detect any, while carryover effects on reproduction may only manifest at recruitment stage. Being able to link common cuckoo risk exposure (Chapter 5) across migratory routes to survival would similarly aid in assessing the demographic importance of exposure to the threats assessed. Measuring the recruitment of juvenile individuals into populations can likewise shed light on impacts of environmental change; juvenile recruitment may have particular importance for demographic rates (Baillie & Peach, 1992; Robinson et al., 2014) or population responses to environmental change (Gill et al., 2014).

Technological advances

Technological advances facilitating the tracking of individuals continue to provide insights into the ecology of migratory species, from more traditional monitoring approaches such as metal- and colour-ringing (Balmer et al., 2013; Gunnarsson et al., 2005, Chapter 3), established biochemical approaches such as stable isotope analysis (Hobson et al., 2010, Chapter 3), and from increasingly sophisticated animal tracking and biologging systems (Robinson et al., 2010; Wikelski et al., 2007, Chapter 5). These will continue to increase knowledge of especially non-breeding ecology, still lacking in many migratory species (Faaborg et al., 2010), and complement and contribute to ongoing population monitoring schemes (Balmer et al., 2013; Brlík et al., 2021; du Feu et al., 2016). Remote-sensing technologies are similarly continuing to improve in quality and in utility to ecology and conservation (Pettorelli et al., 2014; Tulloch et al., 2015; Turner, 2014); the large spatial coverage achievable makes remote-sensed data particularly relevant to studies of highly mobile species (Runge et al., 2014). Rising use and affordability of drones (Koh & Wich, 2012), increasingly high spatiotemporal resolution satellite imagery and sophisticated modelling approaches and a culture of open access data in this subject area (Masek et al., 2020), contribute to resources such as the recently developed global 10-m land cover map created using Sentinel-2 imagery (Karra et al., 2021), and the valuable time-series data provided by longer running initiatives such as Landsat (Huang et al., 2010; Masek et al., 2020).

Use of radar technology is also gaining momentum as a means of remotely monitoring and predicting migratory flux (Bauer et al., 2019; Dokter et al., 2018; Shamoun-Baranes et al., 2014; Van Doren & Horton, 2018). Combining an aeroecological approach with ongoing population monitoring and remote-sensing risk mapping could potentially be used to quantify threat exposure explicitly during migratory movements, marrying the spatiotemporal accuracy achievable through individual-scale tagging (Chapter 5) with the demographic scale of region- to continent-level monitoring (Chapter 4).

Quantifying hunting

In mapping the threats in Chapter 3, we created, to our knowledge, the first map of relative bird hunting pressure covering the Afro-Palaearctic region. We achieved this through soliciting expert opinion and combining the responses with remote-sensed metrics of accessibility. The resulting layer represents only an estimated snapshot of the present situation; quantifying a phenomenon inherently linked to sociocultural and economic factors is difficult to accurately achieve (and potentially contentious). Rates of bird hunting – and drivers thereof – are not static, and although it would seem straightforward to use purely quantitative means to assess hunting prevalence (e.g. bag numbers, hunting licences issued), these are not necessarily objective, and will only provide an estimate to a varying degree of accuracy (depending on levels of governance (Brochet, Jbour, et al., 2019)). Elsewhere, hunting pressure has been mapped solely using remote-sensed correlates (Bogoni et al., 2020); we did not pursue this approach as the methods employed are more appropriate in cases where hunting is driven by a single identifiable factor (e.g. bushmeat demand). Surveying expert opinions yielded often insightful responses, particularly concerning historic drivers of attitudes towards/ necessities of hunting birds – a level of nuance not possible through purely indirect quantitative means. We therefore believe this represents an imperfect but currently the best measure of relative hunting across the region. That the results broadly align with existing quantitative estimates of illegal bird hunting (Brochet et al., 2016; Brochet, Jbour, et al., 2019; Brochet, Van Den Bossche, et al., 2019) (Chapter 4 Supplementary Materials) reinforces the potential importance of this resource for informing the conservation of migratory species.

Conservation of migratory species

In this thesis, we add to the considerable evidence for population declines in long-distance migratory birds (Laaksonen & Lehikoinen, 2013; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014; Yong et al., 2015), and for the relative importance of non-breeding season conditions for population trends (Adams et al., 2014; Cresswell et al., 2007; Ockendon et al., 2014; Peach et al., 1991; Szép, 1995). Nevertheless, we also find that breeding season conditions may play a non-trivial role in driving reproductive fitness (Chapter 3) and population trends (Chapter 4) of migratory birds – as reported elsewhere (Morrison et al., 2013; Ockendon et al., 2013). Indeed, our results support the evidence for potentially complex interseasonal effects (Dhanjal-Adams et al., 2019; Finch et al., 2014; Howard et al., 2020; Vickery et al., 2014), which may be idiosyncratic (Buchanan et al., 2020; Gangoso et al., 2020; Mason et al., 2019) and/or vary with life-history stage (Sergio et al., 2019) or population density (Rushing et al., 2017).

These results therefore reinforce the importance of holistic approaches, considering all demographic processes across the full annual cycle (Marra et al., 2015; Martin et al., 2007), in order to understand population dynamics and responses to anthropogenic change. Given migratory species' reliance on a variety of disparate regions and habitats, and – in many cases – intra- and international jurisdictions (Wilcove & Wikelski, 2008), successful conservation of migratory species requires similarly joined-up and collaborative approaches, explicitly incorporating species' movements and migratory connectivity (Runge et al., 2014; Small-Lorenz et al., 2013). At a broad scale, this may be achieved via transnational policy instruments (Sanderson et al., 2016; UNEP/CMS, 1979), developing interdisciplinary frameworks incorporating human socioeconomic factors (Hulina et al., 2017), and acknowledging the effects of socio-politics and governance on effective conservation (Amano et al., 2018). At a smaller scale, informed and integrated conservation of migrants may be facilitated by improving knowledge of species' ecology, identifying crucial winter stopover sites/ migratory routes/ wintering areas, and understanding spatiotemporal distribution of population-limiting effects (Faaborg et al., 2010; Martin et al., 2007; Runge et al., 2015).

Identifying population-limiting factors may inform targeted and effective conservation actions in the cases when such factors are themselves limitable or reversible (e.g. Van Doren et al., 2017). However, in some cases, directly mitigating or addressing these may be less cost-effective than actions elsewhere which buffer populations to these effects (Runge et al., 2014), particularly in light of evidence that conditions in one season may mediate the effects of conditions experienced in previous seasons (Clausen et al., 2015; Harrison et al., 2013; Lisovski et al., 2020), Chapter 3, Chapter 4). For instance, while we find evidence for the importance of direct mortality threats in the non-breeding season for population trends (Chapter 4), realistic conservation measures on the breeding grounds may nevertheless be the most immediately practical means of bolstering populations, particularly in species for which breeding site productivity has a strong influence on population persistence (Morrison et al., 2016; Robinson et al., 2014; Sanderson et al., 2016).

Migration has been framed as a phenomenon of abundance (Wilcove & Wikelski, 2008); conservation of migration as a concept must be anticipatory, acting not only prior to extinction, but, where possible, prior to scarcity (Wilcove & Wikelski, 2008), and informed by predicted population responses to ongoing environmental disruption (Barbet-Massin et al., 2009; Doherty et al., 2021; Parmesan, 2006; Zurell et al., 2018).

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