Migratory populations in a changing world: connectivity, range shifts, and responses

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Abstract

As the natural world undergoes rapid change, there are particularly strong impacts on migratory species. Their reliance on multiple distinct ranges complicates their spatial population dynamics in ways we are yet to fully understand. In this thesis I explore aspects of spatial population dynamics unique to migrants, focussing on dispersal and its significance for connectivity, range shifts, and population growth within a changing world. I firstly explore the use of quantitative metrics (Mantel correlations) of migratory connectivity strength, highlighting their vulnerability to bias and scale-dependence. Through simulations, I provide guidelines for reducing biases when applying such metrics. I then demonstrate that migratory connectivity is an emergent pattern driven by full-cycle dispersal dynamics, leading to a novel theoretical framework for dispersal in migrants including 'non-reproductive dispersal' – movements between consecutively-occupied non-breeding sites. This previously-undefined form of dispersal is driven by changes in migratory programmes, and is likely to be vital for species shifting their seasonal ranges. I explore this empirically by examining the role of cultural inheritance of migratory programmes in explaining between-species variation in range shift rates of North-American migratory birds. I find that species that migrate in mixed-age flocks (and thus have a high capacity for cultural inheritance) showed faster rates of non-breeding range shift than solo migrants, after controlling for phylogeny and other species traits. This supports the hypothesis that mechanisms of migratory inheritance play a key role in determining spatial dynamics of migratory populations. Finally, I assessed how climatic conditions experienced during distinct seasonal stages influence year-to-year population growth rates across North-American migrants, finding that season-specific climates had relatively little power in explaining interannual changes in population size. Overall, this thesis demonstrates the importance of several aspects of spatial dynamics unique to migrants, providing promising avenues for improving our understanding of migratory ecology in a changing world.

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Author contributions

The following manuscripts have arisen from this thesis, and are presented in Chapters 2, 3, 4 and 5. These are collaborative efforts, although in each case the majority of work is my own. Below I include a full citation for each chapter, and highlight my contribution.

Chapter 2: Sensitivity of migratory connectivity estimates to spatial sampling design
Vickers, S.H., Franco, A.M.A., & Gilroy, J.J. (2021). Sensitivity of migratory connectivity estimates to spatial sampling design. Movement Ecology, 9(16). https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-021-00254-w

Design of the investigation was led by SHV with significant input from JJG and support of ADAF. SHV conducted the research (development of simulation code) and led analysis of the outcomes. Preparation of the work for publication was led by SHV with significant input from JJG and support of ADAF.

Chapter 3: Non-reproductive dispersal: an important driver of migratory range dynamics and connectivity
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Chapter 5: Limited effects of breeding and non-breeding climate anomalies on inter-annual population changes in North American birds
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General Introduction

Global environments are undergoing immense adjustment. Climate change is progressing at unprecedented rates driven by anthropogenic activity and is expected to continue to advance unless drastic change in human behaviour is undertaken (IPCC 2022). This has occurred in conjunction with, and in-part caused by, widespread and drastic land-use change (Hansen et al. 2022, Schulte to Bühne et al. 2021, Song et al. 2018). Such environmental change is leading to or exacerbating a plethora of pressures on the natural world including habitat loss and fragmentation, disease-transmission, pollution, and expansion of invasive species (Hansen et al. 2022, Hellmann et al. 2008, White and Razgour 2020). In order for us to help species adjust to pressures, it is vital we continue to gain a better understanding of the impacts of environmental change on populations and what determines these impacts.

Responding to environmental change

Environmental change will often elicit a demographic and/or distributional response from species at population scales, and much of our expectations for such responses are underpinned by niche theory (Hirzel and Lay 2008, Tingley et al. 2009). Under niche theory a species' capacity to persist in a given area is controlled by physical and biological constraints required by the species for survival and reproduction, which can be further constrained by interspecific interactions (Chase 2011). This has subsequently also been further refined to include spatial constraints including source-sink and dispersal dynamics (Holt 2009). Under general theory, a species' distribution is likely to be constrained in some way by bioclimatic conditions (either directly or indirectly) and thus influenced by global climate change (Wiens et al. 2009).

Species or even sub-populations with broader climate niches may be better able to absorb certain changes in bioclimatic conditions, either due to standing phenotypic variation across the population or individual plasticity – and such populations may therefore be less sensitive to environmental change

(Carscadden et al. 2020, Ruegg et al. 2021). For other species it has been demonstrated that responses can occur through rapid adaptation in-situ via microevolutionary processes (Pulido and Berthold 2004). This can include phenological shifts such as changes in the timing of breeding (Charmantier et al. 2008, Donnelly et al. 2011, Dunn and Winkler 2010) or genetic changes that alter the fundamental niche through adaptations to traits such as thermal tolerances (Geerts et al. 2015, although this remains a knowledge gap in birds – Ruuskanen et al. 2021).

However, for many species, the ability to adapt in-situ to rapid anthropogenic change may be limited (Radchuk et al. 2019, Schaefer et al. 2008). Rather, it is expected that many species will respond to climate change through shifting their range in order to track their bioclimatic limits. Across a wide diversity of taxa we are already observing such shifts in species ranges, with a tendency for the shifts to be poleward or towards increasing altitude (Burrows et al. 2014, Chen et al. 2011, Couet et al. 2022, Gillings et al. 2015, Lehikoinen and Virkkala 2016, Parmesan and Yohe 2003, Stephens et al. 2016). This is often believed to allow species to maintain their climatic niche as temperatures tend to be lower towards higher latitudes and altitudes (Loarie et al. 2009). There are however notable exceptions to shift direction, with many species' distributional shifts failing to track climatic change or progressing in opposing directions (Lehikoinen and Virkkala 2016, Lenoir et al. 2020, Lenoir and Svenning 2014). This highlights the highly complex nature of interacting cascade effects across species communities and the diverse and rapidly-changing pressures.

For species that fail to adapt in-situ to novel conditions and also fail to colonise new areas, there remains potential to see significant distributional change in populations resulting from regional or species-wide abundance declines (Radchuk et al. 2019). Such declines may have further knock-on impacts across the species community, impacting upon the realised niches of other species. Whilst population declines can be driven by the failure to respond effectively to climate change, they may also be driven or exacerbated by various other threats such as land-use change (Northrup et al. 2019), disease (Canavan 2019), and invasive species (Beaury et al. 2020).

Migratory species under threat

Impacts of anthropogenic pressures and rapid climate change have been described across a broad variety of taxa, with widespread population declines (McCarthy 2002) and sufficiently elevated extinction rates such that we may now be facing the sixth global mass-extinction event (Barnosky et al. 2011). Migratory species have been shown to be under elevated risk of population declines in many cases (Rosenberg et al. 2019, Sanderson et al. 2006), in part due to their dependence on multiple distinct ranges across the annual cycle (Horns & Şekercioğlu 2018). By undertaking migrations - the cyclical movements of individuals between these ranges – they may increase their likelihood of being exposed to varied and compounding threats. This requires conservation efforts that span multiple distinct ranges, and account for often-differing environmental requirements between seasons (Faaborg et al. 2010).

Fortunately, many migratory species have shown at least some propensity for in-situ adaptation. Much of the evidence for this is within phenology, in particular through shifting spring arrival dates to track advancing spring climate and resource availability (Both and Visser 2001, Cotton 2003, Møller et al 2008, Sepp et al. 2011). Evidence for other forms of microevolutionary adaptation, including genotypic changes that enable populations to expand their fundamental climatic niches, remains elusive. In part this may be because such changes are challenging to detect and demonstrate, though recent genomic studies have demonstrated the importance of both adaptive processes and standing variation in enabling populations to adapt to local climate change (Bay et al. 2018).

Shifting geographic ranges have also been documented in many migratory species, and importantly these shifts have repeatedly been demonstrated to occur independently across breeding and non-breeding ranges (Auer & King 2014, Curley et al. 2020, La Sorte & Thompson 2007, Potvin et al. 2016, Rushing et al. 2020). Robustly quantifying differences in shift rates between breeding and non-breeding ranges is particularly difficult as these ranges are typically monitored using differing methodologies. Recent comparative studies that have been undertaken in Europe (Potvin et al. 2016) and North-America (Curley et al. 2020) have indicated that rates vary greatly between species, and that shifts in breeding and non-breeding ranges are typically uncoupled (i.e. they are occurring at different rates or directions). Such seasonally-uncoupled range shifts imply that populations are changing their migratory distances and potentially also directions, but the mechanisms underpinning these changes remain poorly understood. These mechanisms are a central focus of **Chapters 2, 3 and 4** in this thesis, in particular addressing an important unanswered question: what role does the migratory programme (i.e. the mechanism governing migration distance, direction, and timing) play in facilitating range-shifts, and how does the adaptive capacity of this programme influence population responses to environmental change?

Quantifying vulnerability to change

Predicting future impacts of anthropogenic pressures and environmental change for migratory species is challenging, but can assist targeted conservation action (e.g. Villero et al. 2017). Across any ecological system, interacting community effects can lead to inaccurate single-species assessments of future population response to environmental change (Araújo et al. 2012), and we are often limited by computational power or resolution/accuracy of existing environmental datasets (Lembrechts et al. 2019). Often assessments are based upon general assumptions of species' responses, with a focus upon climate niche theory and the use of species distribution modelling (SDMs; Elith and Leathwick 2009). Simple single-species SDMs have been criticised for poor predictive power for future climate effects, due in part to their inability to incorporate interspecific interactions – something that can now be achieved through joint species distribution models (Doser et al. 2021). However, effective application of either modelling approach requires a thorough understanding of the potential drivers for climate impacts, and the mechanisms that govern their demographic consequences. Much of this understanding is drawn from correlative studies of species' responses at various spatiotemoral scales, underpinned by theoretical work. Current modelling frameworks have demonstrated the importance of dispersal to range-shift responses (Shipley et al. 2021), but there remains relatively limited understanding about full-cycle effects and in particular whether the mechanisms enabling and limiting range shifts are season-dependent for migratory species (Zurell 2017).

Recent research on migrants has seen a particular focus on the role of migratory connectivity in determining vulnerability to change and effective conservation strategies. Migratory connectivity is an emergent feature of migratory populations, and describes the extent to which spatial distributions of individuals are maintained between two phases of the migratory cycle (Marra et al. 2019). 'Stronger' migratory connectivity describes a system whereby individuals in close proximity in one season are subsequently close together again in another, whilst 'weak' connectivity indicates cross-seasonal mixing of individuals from different areas. The strength of migratory connectivity has been identified as a useful predictor for risks associated with changing environments (Cohen et al. 2018, DeSaix et al. 2019, Korner-Nievergelt et al. 2017, Marra et al. 2019). Modelling studies have demonstrated greater sensitivity to habitat loss in species with stronger connectivity (Dolman and Sutherland 1994, Taylor 2019, Taylor and Norris 2010, Taylor and Stutchbury 2016), but these predictions have not been empirically tested. Moreover, several recently-developed methods for quantifying migratory connectivity are now becoming widely-used, but questions remain about their capacity to genuinely capture conservation-relevant population characteristics, as well as their potential for bias. In **Chapter 2**, I evaluate the most commonly used metric for measuring migratory connectivity in order to assess the potential for bias resulting from different sampling methodologies and advise practitioners in best-use. Another open question concerns the potential for migratory connectivity metrics to be informative about the capacity of species to respond to environmental change by shifting their ranges. I evaluate this potential avenue for quantifying change in **Chapter 3**, whilst also exploring the underlying mechanisms that determine connectivity and range-shift capacity from a theoretical perspective.

Without an improved understanding of drivers and mechanisms of species responses, our ability to quantify risks for migrants under a changing environment will remain limited, particularly in the case of non-breeding ranges and how processes during non-breeding periods influence overall population dynamics.

Drivers and mechanisms of range shifts in migrants

Adaptive range-shifting under climate change fundamentally requires colonisation of new areas. New areas may become available for colonisation due to changes in bioclimatic or ecological conditions, resource-availability, or the removal of dispersal barriers, leading to new opportunities for survival in, or access to, areas previously uninhabited (Donahue and Lee 2008). Successful colonisation of opportunities arising from these drivers requires successful dispersal (defined as movements of individuals between successive reproductive events; Runge et al. 2006), making this a key fundamental process underpinning spatial population ecology (Clobart et al 2012). Dispersal is fundamental not only for colonisation but also for metapopulation dynamics and determining gene flow across a population (Camacho et al. 2013, Hanski 1998).

Dispersal by definition involves movements between successive reproductive events (i.e. movements that result in gene flow; Runge et al. 2006), and the dispersal literature has therefore focussed exclusively on processes determining the spatial dynamics of breeding ranges. For migratory species, however, the spatial dynamics of the non-breeding range are also important. Surprisingly, the equivalent dispersal-like processes that govern these dynamics have been largely neglected by ecologists, both empirically and theoretically. These processes are intrinsically linked to the mechanisms underpinning migratory movements, in part because the act of migration itself has the potential to facilitate dispersal movements, given that migrants are prone to stochastic forces such as wind-drift, as well as navigational errors, that can take them into new areas at any stage of the annual cycle. In **Chapter 3**, I build and explore a theoretical framework for these non-breeding spatial dynamic processes. We refer to the movements involved as 'non-reproductive dispersal' which describes movements between non-reproductive sites occupied in consecutive years, or between generations. We propose that non-reproductive dispersal is a key process underlying non-breeding range shifts, just as 'reproductive dispersal' is to breeding range shifts, but involves a fundamentally different set of mechanisms that have thus far been largely overlooked.

In particular, we hypothesise that reproductive- and non-reproductive dispersal differ fundamentally in the extent to which the spatial outcomes of movement are heritable. Whilst outcomes of reproductive dispersal movements are *de facto* heritable due to the subsequent generation being born within the newly-occupied location, non-reproductive dispersal can often give rise to non-heritable colonisation events. This dynamic centres around the role of migratory programmes within non-reproductive dispersal. In **Chapter 3**, I demonstrate how non-reproductive dispersal movements arise from changes in realised migratory programmes between years or generations, which can be caused by non-heritable factors (e.g. wind drift), as well as heritable (genetic or cultural) adaptations of the migratory programme. I use simulations to explore the implications of this hypothesis for species responses to climate change scenarios.

Inheritance and adaptation of migratory programmes

The mass, co-ordinated, annual migrations of animals are one the most remarkable feats of the natural world. An indication of the complexity of these behaviours is that even defining migration itself can be challenging (Dingle and Drake 2007; N.B. in **Appendix 1** I outline several assessment criteria that can be applied to these journeys in order to formally characterise the range of spatial patterns of movement observed across taxa). For such complex spatial patterns of movement to arise, and more importantly be maintained with precision across generations, requires a capacity for migratory programmes (at least governing distance, timing, and direction) to be passed between generations (Mouritsen 2018). This transfer can take place through both genetic and cultural inheritance mechanisms, but the relative importance of each mechanism remains unclear.

Genetics basis of migratory programmes

Genetic inheritance involves the passing of genes from one generation to the next, with subsequent gene expression producing observed traits. In the context of migratory programmes, research into genetic inheritance has focussed largely on ex-situ based experiments. Migratory programmes are highly complex behaviours requiring control of timing, direction, distance, and physiology (Pulido 2007). Genetic control of migration is therefore dependent upon gene complexes, and these complexes remain poorly understood.

Within birds, one of the primary genetic-based controls of migratory programme is thought to be the physiological process of Zugunruhe, first described by Johann Andreas Naumann (1795-1817) as a state of 'migratory restlessness' (Berthold 1996). Migratory restlessness is believed to be controlled endogenously (Pedersen et al. 2018), and is likely to be a genetically heritable trait that interacts with exogenous environmental factors including photoperiodic conditions (Robart et al. 2018) and food availability (Studds and Marra 2011). The onset of migratory restlessness is believed to be one of the primary cues for initiation of migration (Eikenaar et al. 2014; Robart et al. 2018). Duration of this restlessness in captive individuals has also been found to correlate with migratory distances of wild populations, implying some control of migratory distance (Berthold 1973; but see Dingle 2006).

There is also evidence for migratory restlessness directly driving certain spatial patterns of migration such as in differential migration (Appendix 1), where population subgroups (e.g., sexes or age classes) express different migration strategies. In Eurasian Blackcap *Sylvia atricapilla* and Dark-eyed Junco *Junco hyemalis*, for example, there are significant differences in onset and length of migratory restlessness between sexes (Holberton 1993, Terill and Berthold 1989). Furthermore, in partial migrants (as defined in Appendix 1), captive-bred individuals have also displayed high heritability for the expression of migration itself. However, migratory parents do not exclusively produce migratory young in such populations (Berthold 1991) and genetic control for this decision is believed to follow a threshold model (Pulido 2007). This decision may also include environmental cues such as competition and stress (Berthold 1991, Ogonowski and Conway 2009).

There is also evidence for genetic control of migratory direction, largely drawn from experiments involving captive individuals placed in orientation cages, which have been shown to demonstrate directional preferences for migration that are broadly in-line with wild populations, in the absence of any potential for non-genetic inheritance (Helbig 1991). However, environmental cues may also play a significant role in refining direction in the wild (Nievergelt et al. 1999). Experimental cross-breeding of individuals from populations with differing migratory directionality and distance has also provided evidence of strong genetic inheritance of migratory directions, with the F1 progeny generally displaying intermediate programmes of the two parent populations (Berthold and Querner 1981, Delmore and Irwin 2014, Helbig 1991) or in some cases inheritance of a single parents programme (Toews et al. 2013, Veen et al. 2006).

The role of genetics in the development of a precise migratory programme is contested, and is likely to vary considerably between species and age-classes. Strong site fidelity - including natal philopatry – is widespread among migratory species, and many can return to a previously-used location with remarkable precision following journeys of thousands of kilometres, indicating highly accurate navigational abilities (Mouritsen 2018). Naïve migrants on the other hand, perform their first migrations without any prior knowledge of a non-breeding destination. Evidence suggests that in the absence of direct route-learning by following experienced individuals, most migratory species perform this first migration using an inherited clock and compass mechanism that governs the timing, distance, and direction of movements as a function of external cues (photoperiod and magnetic, stellar or solar information for compass orientation; Åkesson & Helm 2020, Mouritsen 1998). This basic mechanism does not allow for 'true' navigation (i.e. movement towards a specific location, rather than along a given vector), as indicated by the failure of first-time migrants to compensate for experimental displacement (Mouritsen & Larsen 1998).

More recently, examples suggestive of true navigation among inexperienced migrants have started to emerge. For example, experimental displacement of naïve juvenile Common Cuckoo *Cuculus canorus* – a species that migrates alone - indicated a capacity for some immature individuals to adjust their headings in order to correct for displacement. This suggests some species may indeed possess an inherited 'map-location' capacity (Thorup et al. 2020). Yet, migration destinations of individuals within this study showed high variability. For species that have a more limited 'clock-and-compass' control of migration, departure bearings, timings, and migratory distance are all likely to vary significantly within and between populations, inevitably generating significant spatial variation when considered over the scale of migratory journeys (Thorup et al. 2007b). This potentially random variability has previously been hypothesised to be evolutionarily advantageous, enabling selection pressure to rapidly drive migratory programme adaptation across generations, referred to as the 'serial residency' hypothesis (Cresswell 2014).

Cultural basis of migratory programmes

Cultural inheritance refers to the storage and transmission of information by imitation, teaching, and learning. Examples of cultural learning are found across many taxa, and it has been linked to transmission of avian vocalisations, feeding behaviour, and tool use (Aplin 2019). Within migratory behaviour, the role of cultural inheritance has received less attention in comparison to the role of genetics. Despite this, there is an increasing realisation of the important role cultural mechanisms may play in migration.

In birds, circumstantial evidence points towards cultural inheritance being a primary mechanism for migratory programme development across several model species (Chernetsov et al. 2004, Harrison et al. 2010, Palacín et al. 2011, Mueller et al. 2013). Cultural inheritance of migratory programme is often framed as 'follow-the-leader' type learning (Flack et al. 2016, Mueller et al. 2013), wherein naïve individuals on their first migration will follow an experienced migrant (sometimes in family groups) and subsequently adopt this route in following years (Teitelbaum et al. 2016). In species that show this strong cultural inheritance it is common to observe strong imprinting behaviour in offspring (Mueller et al. 2013). This tendency to follow other individuals can also lead to abmigration (Appendix 1) and vagrancy where individuals of another species or migratory flyway are followed.

Many examples of cultural inheritance of migratory programme display clear and obvious pathways for learning, but there may also be more subtle cultural cues that are more widespread across taxa. Even species that do not display clear 'follow-the-leader' behaviour may be using cultural cues during migration. For example, 'many wrongs' (grouped noisy estimates of navigation direction that improve accuracy by pooling individual estimates) or 'emergent sensing' (when a group can navigate collectively even when no individual has the ability to assess the correct direction of motion) may allow for greatly improved migratory programme accuracy through collective animal navigation even without prior experience of routes (Berdahl et al. 2018). Many migratory species may use cues from conspecifics during migration when moving in flocks, potentially explaining the prevalence of flight calling particularly in nocturnal migrants (Farnsworth 2005). Auditory cues may also be important in determining the final destination of migration via the phenomenon of conspecific attraction in home range selection, which has been demonstrated circumstantially through the use of call playback which has been used to expand ranges of some migrants (Anich and Ward 2017).

The importance of cultural inheritance for migratory programme adaptation over time has not been widely explored. There is evidence that flocking behaviour on migration may be a mechanism enabling site fidelity (and hence high migratory programme consistency; Harrison et al. 2010), but it is also possible that cultural inheritance (via social links during migration) may allow for more rapid population-wide shifts in migratory behaviour. This is because cultural learning can also transmit through a population horizontally (i.e. within a generation) and is not restricted to vertical transmission (across generations) like genetic pathways tend to be (Aplin 2019). I expand upon this hypothesis in **Chapter 4**, using long-term continental-scale datasets to explore whether cultural inheritance of migratory programme (via flocking behaviour) is a trait that can explain variation in range-shift rates across species, relative to those that must rely on genetic inheritance pathways.

Relative roles of each pathway

Genetic inheritance of migration is widely considered to be the primary mechanism of inheritance of a migratory programme, with Berthold (1990) arguing that it is involved in the control of all the important aspects of avian migration. However, for many species it is likely that a combination of genetic and cultural pathways determine the establishment of an individual’s migratory programme, with learning becoming increasingly important during repeat migratory journeys (Mettke-Hofmann and Gwinner 2003, Thorup et al. 2007a). From the limited species-specific case-studies we have, it appears that there can be stark differences in the relative role of each inheritance pathway between species, with some species (e.g. cranes) depending strongly on cultural inheritance and others (e.g. Common Cuckoo) depending solely on genetic mechanisms. Understandably, studies have tended to focus on species towards the extreme ends of this gradient scale, as well as species that undergo predictable changes in migratory programme as they age, which may result from cultural and/or genetic mechanisms (Helberg et al. 2009). How these age-related migratory programme changes impact the propensity of individuals to disperse and colonise new areas is not known.

Season-specific drivers of population trends in migrants

Regardless of whether species are responding to climate change by colonising new areas, their population trends will be largely driven by the impacts of environmental conditions within the areas occupied by the majority of the existing population. Uniquely, migratory species are exposed to spatially-variable rates and forms of environmental change across their annual cycles, and are thus likely to be vulnerable to season-specific pressures. Drivers of population declines in migrants may therefore operate within discrete seasonal stages (McCarty 2002), and conversely season-specific environmental changes may also relieve environmental pressures elsewhere and facilitate population growth (Somero 2010). Gaining a better understanding of season-specific sensitivity to environmental change is an important step in enabling conservation practitioners to target limited resources and efforts to protect migratory species across the annual cycle. This is especially important considering mitigation may require season-specific approaches and international efforts in migrants (Runge et al. 2014).

Climatic conditions experienced within discrete seasonal ranges have been shown to directly impact survival rates and productivity (Nott et al. 2002, Robinson et al. 2007), and indirectly through carryover effects between seasons (Finch et al. 2014, Jenouvrier 2013, Rockwell et al. 2012, Sæther et al. 2004, Sorensen et al. 2009). Many studies have examined the impacts of climatic change on long-term population trends, with strong associations found within species and across guilds (Betts et al. 2019, Eglington and Pearce-Higgins 2012, Howard et al. 2020, Mason et al. 2019, Pearce-Higgins et al. 2015, Stephens et al. 2016). However, short-term fluctuations in climate (i.e. weather) may also impact upon inter-annual population growth rates (Reed et al. 2013), particularly in migrants, and these have received less attention. Identifying population sensitives to short-term climate variability across the annual cycle may help us understand the climate impacts that underpin long-term changes in migratory species. Long-term population trends in European migratory birds have previously been demonstrated to be more closely associated with long-term climate change on the breeding grounds than non-breeding areas (Howard et al. 2020), but research across wider regions is lacking. Furthermore, there is conflicting evidence concerning the impacts of season-specific short-term climate conditions, with some evidence that these may be stronger during the non-breeding period in some species (Salewski et al. 2013). In **Chapter 5**, I address this knowledge gap by exploring the population-scale impacts of short-term season-specific climate fluctuations for a wide pool of North-American migratory birds, again using long-term continent-wide datasets.

Thesis outline

The aim of this thesis is to explore how migratory birds are responding to the challenges imposed by environmental change, from theory to measured examples. I give particular focus to the processes underlying migratory programmes and how they interact with range-shifts, migratory connectivity, and environmental change.

There is increasing interest in the emergent spatial patterns of migration across populations, with particular focus on migratory connectivity and its implications for species response to environmental change. In **Chapter 2** I use simulations to demonstrate how the most commonly used method for measuring migratory connectivity (Mantel correlations) may be prone to spatial sampling biases, and how these biases can be reduced by careful design of sampling regimes. Migratory connectivity metrics are often framed as being important predictors of species response to a changing world, and it is therefore important that we aim to improve the robustness of these metrics.

My development of simulation models underpinning Chapter 2 revealed the central role of dispersal-like processes within non-breeding ranges as determinants of emergent patterns of migratory connectivity. In **Chapter 3**, I develop a formal theoretical basis for these ‘non-reproductive’ dispersal processes, and how these depend on mechanisms allowing migratory programme consistency both across a population and between years. I develop models demonstrating the implications of these previously overlooked dispersal-like movements for the spatial dynamics of non-breeding ranges, and link this back to the information that can be gained from metrics of migratory connectivity explored in Chapter 2. Using simulations, I demonstrate the potential for non-heritable components of dispersal to determine migratory connectivity, suggesting that connectivity metrics are likely to be poor predictors of species ability to range-shift.

The models I develop in Chapter 3 suggest the importance of heritable forms of change in migratory programmes between generations in order to facilitate distributional change in migratory species. In **Chapter 4**, I further explore this concept, empirically testing the hypothesis that observed seasonal range-shift rates will be influenced by migratory behaviours that enhance the potential for heritable non-reproductive dispersal. Specifically, I hypothesise that species migrating in flocks – especially those containing experienced individuals and thus opportunities for cultural inheritance - will be have greater capacity for change in migratory programmes and thus colonise new seasonal ranges at faster rates, relative to solitary migrants that must rely on genetic change for the emergence of novel heritable migration routes. To do this, I explore centre of abundance shifts for a suite of North American migratory birds using 50 years of North American Breeding Bird Survey and Christmas Bird Count data, and relate this to a database I collated characterising migratory flocking behaviour across species from a range of sources.

Whilst range shifts have been recorded across many migratory species, the climate change impacts driving population growth rates primarily play out within species' existing core distributions. In **Chapter 5**, I explore the direct impacts of climate variability on population growth rates of migratory species, extending research that has so far focussed largely upon long-term trends to consider population sensitivity to shorter-term interannual effects. I assess the relative impact of climate variability between seasonal stages for migrants, as existing literature indicates conflicting evidence regarding which seasons are primary drivers for population growth rates.

Finally, in the **general discussion**, I discuss the findings of Chapters 2-5 and their combined implications for our understanding of migratory populations under environmental change, and suggest possible directions for future research.

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Sensitivity of migratory connectivity estimates to spatial sampling design

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Abstract

Background

The use of statistical methods to quantify the strength of migratory connectivity is commonplace. However, little attention has been given to their sensitivity to spatial sampling designs and scales of inference.

Methods

We examine sources of bias and imprecision in the most widely used methodology, Mantel correlations, under a range of plausible sampling regimes using simulated migratory populations.

Results

As Mantel correlations depend fundamentally on the spatial scale and configuration of sampling, unbiased inferences about population-scale connectivity can only be made under certain sampling regimes. Within a contiguous population, samples drawn from smaller spatial subsets of the range generate lower connectivity metrics than samples drawn from the range as a whole, even when the underlying migratory ecology of the population is constant across the population. Random sampling of individuals from contiguous subsets of species ranges can therefore underestimate population-scale connectivity. Where multiple discrete sampling sites are used, by contrast, overestimation of connectivity can arise due to samples being biased towards larger between-individual pairwise distances in the seasonal range where sampling occurs (typically breeding). Severity of all biases was greater for populations with lower levels of true connectivity. When plausible sampling regimes were applied to realistic simulated populations, accuracy of connectivity measures was maximised by increasing the number of discrete sampling sites and ensuring an even spread of sites across the full range.

Conclusions

These results suggest strong potential for bias and imprecision when making quantitative inferences about migratory connectivity using Mantel statistics. Researchers wishing to apply these methods should limit inference to the spatial extent of their sampling, maximise their number of sampling sites, and avoid drawing strong conclusions based on small sample sizes.

Keywords

Mantel test, migratory connectivity, migration, migratory spread, sampling bias

Introduction

Understanding animal migration – the cyclical movements of individuals between areas used across the annual cycle – is challenging, yet is often a prerequisite for effective conservation of mobile species. Our capacity to measure migratory movements has improved greatly in recent years through direct methods such as mark-recapture (Anderson & Green 2009) and remote-tracking technology (Fiedler 2009), as well as indirect methods such as genetic (Ruegg et al. 2014) and biogeochemical approaches (Hobson & Wassenaar 2018). With an improved understanding of individual migratory movements, researchers are increasingly focussing on quantifying resultant population-level spatial patterns. Understanding migratory connectivity (henceforth referred to as 'connectivity'), which describes the extent to which spatial distributions of individuals are maintained between two phases of the migratory cycle (most often between breeding and non-breeding grounds), has become a top priority (Marra et al. 2018). High levels of connectivity indicate that individuals residing close together in a particular season of the annual cycle are also close together in a subsequent season, whilst low connectivity indicates cross-seasonal mixing of individuals from different areas. The strength of connectivity can have important conservation implications, including playing a key role in a migratory species' propensity to adapt to a changing environment (Cresswell 2014, Iwamura et al. 2013).

Multiple statistical approaches to estimate migratory connectivity have been utilised in recent years (DeSaix et al. 2019, Korner-Nievergelt et al. 2017, Marra et al. 2018). To quantify the strength of connectivity (i.e. giving connectivity a numerical value) one of the most commonly used approaches is the Mantel test (Sokal & Rohlf 1995), which evaluates the correlation between two distance matrices: the pairwise distances between locations of sampled individuals in one season, and their equivalent pairwise distances in another (Ambrosini et al. 2009). Numerous studies have examined sources of bias in connectivity estimates derived using Mantel correlations, including issues of imbalanced sampling with respect to local abundance, incomplete spatial coverage, and location uncertainty (Ambrosini et al. 2009, Cohen et al. 2018). An extension to the Mantel approach (Cohen et al. 2018) utilises the transition rates of individuals between pre-defined breeding and non-breeding zones to control for these biases, but this method is only recommended in situations where spatial subpopulation structure is well understood, and relative abundances within origin regions can be estimated. Cohen et al. (2018) recommend using Mantel correlations when these conditions are not met, and the Mantel approach remains widely used in recent literature (e.g. Burgess et al. 2020, Imlay et al. 2018, Norevik et al. 2020, Sarà et al. 2019, but see Korner-Nievergelt et al. 2017, Tonra et al. 2019).

One issue that has received little attention in the migratory connectivity literature is the extent to which Mantel correlations can be used to draw inferences about connectivity patterns at the population scale, given that these correlations show scale-dependence (Finch et al. 2017, Phipps et al. 2019). A key aim of migratory connectivity research is to understand migratory patterns at large spatial scales (e.g. whole species ranges), requiring an implicit assumption that metrics quantified for sampled individuals accurately describe behaviour of wider populations. However, these broad-scale inferences have the potential to be strongly biased in some cases, as a product of fundamental sensitivity of connectivity metrics to the spatial extent and configuration of sampling. Estimates also frequently suffer from low precision due to sample size constraints, as the number of individuals tracked within a population is often limited by available funding resources, difficulty in retrieving tracking devices, fieldwork limitations related to catching individuals, site fidelity, and recapture rates (Cohen et al. 2018). These limitations reduce the proportion of the population that is actually studied, and mean relatively small sample sizes are commonplace in remote-tracking studies (Geen et al. 2019). Whilst lower precision can be partially accounted for through bootstrapped confidence intervals, the extent to which precision varies with sample size has not been explored in detail (Cohen et al. 2018).

Here, we use simulations to elucidate the direct mechanisms underpinning bias and imprecision in migratory connectivity estimates that use Mantel statistics. We examine the efficacy of multiple sampling scenarios across a range of connectivity levels, considering both homogenous and spatially-clumped populations. We test how the number of individuals sampled impacts the precision of measurements, and examine how the magnitude of bias depends on the extent to which estimates from sampled individuals are used to draw inferences about the wider populations from which they are drawn. Alongside simple generalised simulations that allow us to explore underlying mechanisms of bias, we also use more realistic simulated migratory populations to provide recommendations on study design that can maximise the accuracy of Mantel-based connectivity measures, within realistic limits of sampling.

Mechanisms of bias

To illustrate the fundamental issue arising from spatial sampling bias, we first consider two hypothetical sampling scenarios for a contiguous breeding population with low connectivity (Fig. 1): one where individuals are marked randomly within a single study region of varying size (Fig. 1 A-H) and another where individuals are marked within discrete sampling sites that are spread across the range (Fig. 1I-P). In both cases, the plausible range of observable distances between marked individuals is constrained by sampling extent in the season that marking takes place, which is the breeding range in our hypothetical scenario (see Fig. 1). Importantly, however, the maximum measurable distance between these sampled individuals in the non-breeding range is not constrained by sampling design, only by the destinations of the animals themselves. This could introduce a skew in the sample of pairwise distances on the sampled range (breeding grounds in this case), but not on the destination range (non-breeding grounds). As Mantel correlations explicitly compare these pairwise distance distributions between seasons, resulting Mantel statistics calculated for spatially-constrained samples may be very different from the ‘true’ values calculated for the whole population, despite the underlying migratory ecology being constant across the population (as in Fig. 1).

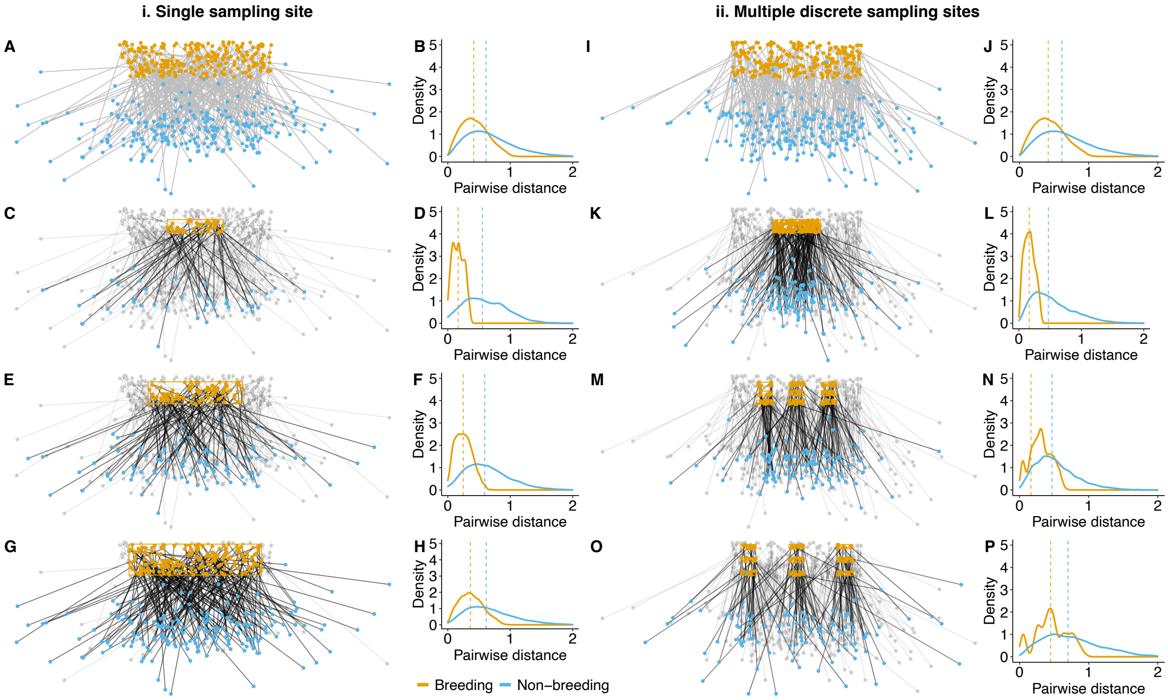

Figure 1. Hypothetical examples of spatial sampling impacts on season-specific pairwise distances between individuals, considering scenarios where sampling occurs within single regions (**A–H**) and discrete sites (**I–P**). Panels A and I show the spatial distributions of all breeding (yellow dots) and non-breeding locations (blue dots) for two simulated migratory populations, while panels B and J show the corresponding frequency distributions of pairwise distances between individuals during breeding (yellow line) and non-breeding (blue line) seasons. Panels **C–H** illustrate how sampling (yellow box) individuals across increasingly large spatial subsections the total population influences the observed distributions of breeding pairwise distances, while winter pairwise distances remain relatively unchanged. Panels **K–P** show corresponding scenarios with sampling limited to discrete sites that vary in their spread across the breeding range, with similar impacts on observed breeding pairwise distances.

Biases resulting from spatially-constrained sampling regimes could take various forms, depending on how sampling effort is distributed across the species' range. If sampling is limited to a subset of the breeding distribution (e.g. Fig. 1C), the observed distribution of breeding pairwise distances will be left-skewed relative to the true distribution across the population (Fig. 1D), leading to negative bias in Mantel correlations with respect to true statistic for the wider population. If sampling occurs in discrete areas that are widely separated across the range of a species, however, resulting pairwise distances may be right-skewed relative to the population as a whole (e.g. Fig. 1P) because site spacing introduces abrupt artificial gaps into what may be a more uniform underlying distribution of individuals across space. Given inevitable logistical constraints, migration studies do indeed typically focus on marking individuals at discrete sites within spatially-constrained study areas (Cormier et al. 2013, Cormier et al. 2016, Finch et al. 2017, Nelson et al. 2016), with considerable variation in the extent to which these are spread across full ranges. This suggests there may be constraints on the extent to which such studies can draw inferences about the connectivity of wider populations using Mantel statistics calculated from spatially-constrained samples. In the next sections, we use simulations to estimate the severity of these biases under a range of common sampling scenarios.

Simulation Methods

To examine fundamental sources of bias, we first simulated simple migratory populations that vary in their degree of migratory connectivity (Fig. SM1), and applied a range of sampling regimes to examine how Mantel statistics resulting from realistic simulated ‘studies’ compared to ‘true’ values calculated for the simulated population as a whole.

Simulating breeding and non-breeding locations

First, we created a breeding range filled with *N* individuals, placed at random by sampling x and y coordinates from a bounded uniform distribution (Becker *et al.* 1988, Fig. SM1A, *N* = 10,000), ensuring that variation in our results reflected sampling effects alone, rather than stochasticity arising from heterogeneous spacing of individuals. We simulated migratory movements by 1) shifting each individual a fixed distance due south from its breeding location (Fig. SM1A), and then 2) further shifting the individual in a random direction (sampled from a uniform distribution between 0 and 360; Fig. SM1B-C). The distance of this second shift was sampled from a lognormal distribution with SD=1, and a mean that we varied across scenarios, allowing us to simulate different strengths of connectivity (values of 3, 5 and 7 were used).

Simulating study designs

Two basic sampling designs were applied to simulated populations (Fig. 1):

Area scenarios: To test for the effect of sampling area size, a single rectangular sampling area was used, centred within the breeding area, within which 200 individuals were sampled at random for tracking. The size of this rectangular area was varied to generate three scenarios of increasing total study area with sample size held constant (sampling areas are illustrated in Fig. 1C, E, & G).

Spread scenarios: To test for effects of sampling 'spread' under a fixed study area design, 200 individuals were randomly sampled from nine rectangular sampling areas (sites) distributed in a 3x3 grid formation centred within the breeding area. Spacing between these sites was then varied to generate three scenarios of differing sampling spread, holding the size of sampled area and sample size constant in each case (sampling sites are illustrated in Fig. 1K, M, & O).

We generated 100 replicate datasets for each scenario (area and spread), and repeated this for each of the three strength levels of connectivity tested.

Estimating migratory connectivity

Using sampled individuals from each scenario, we calculated Mantel correlations using the *mantel.rtest* function within the *ade4* package in R (Dray & Dufour 2007). In each case, we assumed that all individuals sampled in the breeding range were tracked successfully to their winter locations and there was no location uncertainty. Scores were then assessed with respect to: 1) the difference between the observed Mantel score and the 'true' value calculated for the entire global population of 10,000 individuals, and 2) the difference between the observed Mantel score and an equivalent 'true' value calculated using all individuals inhabiting the strict spatial extent of sampling (henceforth 'zone').

Sample size scenarios

We tested a range of sample sizes to examine how precision varies in relation to the proportion of a population being sampled. For each level of connectivity, we randomly sampled individuals from the entire breeding range (global population *N*=10,000), applying sample sizes of 10 (0.1%), 50 (0.5%), 100 (1%), 1000 (10%), 2500 (25%), and 5000 (50%) individuals. For each sample size and connectivity scenario, 100 replicates were generated with Mantel scores calculated following the previously described method. Bias was determined as the difference between the observed score and the values for the entire simulated population of 10,000 individuals.

Patchy population scenarios

Populations in the real world seldom conform to contiguous blocks, and often show a patchy distribution. To examine how this patchiness influences the effect of spatial sampling design on Mantel statistics, we simulated populations inhabiting four equal-sized sub-populations situated at the corners of the breeding range, within which individuals were distributed at random (Fig. SM2). Migrations were then simulated using the same process described above (see Fig. SM1), but populations were then further restricted to include only individuals that reach four equal-sized regions in the non-breeding area. This was to ensure clearly delimited sub-populations during both the breeding and non-breeding period. We then applied a rectangular sampling area centred within each breeding sub-population, across which 200 individuals were sampled at random for tracking. The size of the rectangular areas was then varied to generate three scenarios of increasing total study area (with sample size held constant).

Simulating realistic species ranges

To examine how spatial sampling designs influence connectivity estimates when applied to more realistic migratory populations, we generated further simulated populations that were constrained within real-world breeding and non-breeding BirdLife range maps (BirdLife International 2019) for three bird species selected to represent diverse range structures (Henslow's Sparrow *Passerculus henslowii*, Aquatic Warbler *Acrocephalus paludicola*, and Falcated Duck *Mareca falcata*; note that subsequent simulated populations are not intended to be accurate replications of these species). To simulate realistic distributions of individuals within each range, we applied an algorithm to generate spatially-autocorrelated occurrence patterns (i.e. spatial clustering of individuals rather than a uniform distribution) using the *nlm_gaussianfield* function from the NLMR package (Sciaini et al. 2018) to generate a Gaussian random field of spatially-clustered values (scaled to vary between 0 and 1), applying an autocorrelation range of 10 and a magnitude of variation of 100 to generate spatial clustering (Fig. SM3A). We then distributed 50,000 individuals across each range in proportion to the resulting random field values (Fig. SM3B), with spatial autocorrelation ensuring that individuals were clustered in space, with areas of high and low abundance.

To generate a range of differing levels of migratory connectivity for each simulated species range, we used an algorithm that matched breeding and non-breeding locations for individuals according to their longitudinal ranks (Fig. SM3C). For each individual in the breeding range, we randomly-selected a non-breeding location from all available points within a given bandwidth of longitudinal rank, and controlled connectivity levels by varying this bandwidth. For example, with a bandwidth of 1000, an individual of longitudinal rank of 5000 on the breeding zone would be randomly assigned a point from all those between longitudinal ranks 4000—6000 on the non-breeding zone. Larger bandwidths of longitudinal ranking on the non-breeding zone therefore result in lower migratory connectivity. Bandwidth sizes of 1000, 13000, and 25000 were used to produce three levels of migratory connectivity for each species. To sample the resulting populations, we assigned discrete study areas of fixed size to the 20 highest-density cells within a coarse grid overlain across the breeding range (Fig. SM3D–E). This reflects the common logistical constraints (difficulty in catching individuals for tagging, access restrictions, and financial limitations) that may force researchers to restrict their sampling to areas where their chosen species are known to be more abundant. We then selected 200 individuals at random from these sampling sites. To explore the impact of variation in spatial sampling extent on resulting connectivity estimates, we varied the number of sampling sites from which these individuals were drawn, ranging from 3 to 20 sites selected at random from the pool of 20. We repeated this 100 times for each possible sampling scenario and level of connectivity and calculated resulting Mantel scores as well as the mean distance between centroids of sampling sites.

All simulations and statistical analysis were performed with R 4.3.0 (R Core Team 2020). Scripts for the completed analysis, including all simulations, are available as electronic supplementary material.

Results

Spatial scale fundamentally affects migratory connectivity scores

When calculated for increasingly-sized zones within a single uniformly distributed breeding population, Mantel correlation values calculated for the entire population within the zone always increase (Fig. 2). In effect, the ‘true’ migratory connectivity of a population (measured using all individuals) is dependent upon the absolute size of the area sampling occurs, even when the underlying mechanism generating connectivity for individuals is uniform across the population. This is because the Mantel method fundamentally depends on the relative spatial arrangement of individuals within each zone of interest, and hence are highly sensitive to the spatial characteristics of those zones. The more a given zone is spatially restricted by sampling, the narrower the subset of measurable pairwise distances (Fig. 1). In the case of connectivity studies where individuals are marked within one seasonal range, the censoring of pairwise distances does not take place to the same extent on the other range. This mis-match in censoring of pairwise distances results in lower Mantel scores relative to a population that is less spatially restricted (Fig. 2).

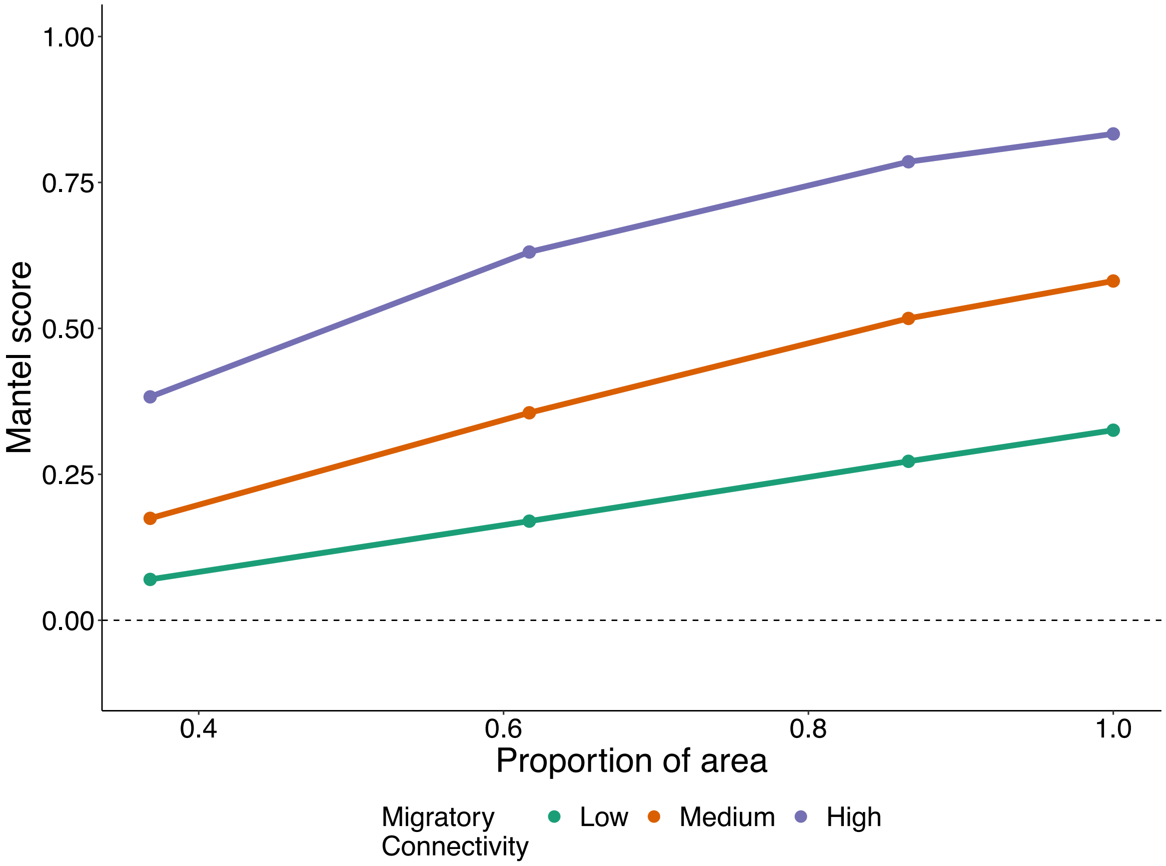

Figure 2. Migratory connectivity scores calculated by the Mantel method for all individuals (i.e. ‘true’ population-scale values) within increasingly-sized spatial zones (rectangular areas centred within the breeding population) within the whole population. Colours represent the three levels of migratory connectivity tested.

Therefore, inferences drawn from Mantel scores about the migratory connectivity of whole populations may be systematically biased if those scores come from spatially-constrained samples of individuals. When applying area-based sampling regimes (i.e. random sampling across a single zone as shown in Fig. 1i), this spatial sampling artefact resulted in consistent underestimation of connectivity scores relative to ‘true’ values for the whole population. Underestimation was more severe as the disparity between the size of the sampled area and the total area occupied by the population increases. The effect was consistent across the three strengths of connectivity tested, but was strongest for populations with weaker connectivity (Fig. SM4).

Making inferences at the spatial extent of sampling can still be biased

If inferences about the strength of connectivity are made explicitly for the individuals inhabiting the spatial extent of sampling (and not wider populations), area-based sampling scenarios produced Mantel scores without significant bias (Fig. SM5). However, the commonly-used scenario of sampling from multiple discrete study areas ('spread' scenarios, as shown in Fig. 1ii) lead to overestimation of connectivity in medium and high spread scenarios, even when inference was restricted solely to the populations within the sampled space (Fig. 3). This overestimation results from the large distances between sampling sites, which over-selects individuals of high pairwise distance during the breeding season, leading to a right-skewed sample of pairwise distances relative to the distribution for all individuals within the spatial extent of sampling (Fig. SM6).

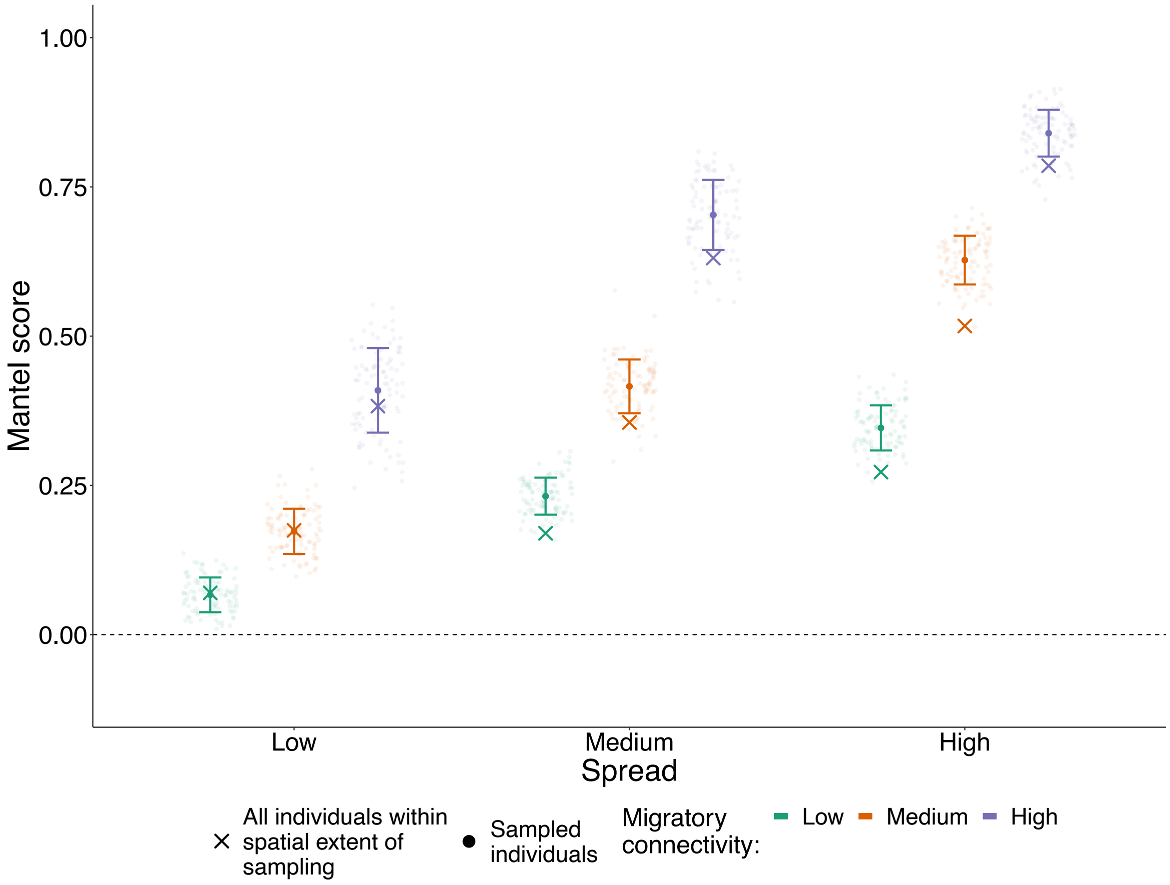

Figure 3. Mantel scores from 100 replicate simulated studies (circles) compared to that of all individuals within the spatial extent of sampling (crosses). Each replicate is calculated using 200 individuals sampled randomly across nine sampling areas which were varied in their spread. Error bars indicate standard deviation around the mean score of 100 replicates.

Large sample sizes are required to achieve precision

With random sampling across a single contiguous uniform breeding population, we found large variation in connectivity estimates across the 100 replicate simulated studies with sample sizes of 100 or less (Fig. 4). Standard deviations around the mean of connectivity estimates were largest for lower connectivity scenarios, with SD as high as 0.23 (under sample size of 10*,* ‘low’ connectivity). With sample sizes of 1,000 and above, SD around mean connectivity estimates fell to a negligible level in the context of a score on the scale of -1 to +1 (SD < 0.025 across all strengths of connectivity tested). This indicates that with sample sizes of 100 individuals or fewer, precision of resultant scores may be very low even under ideal sampling designs.

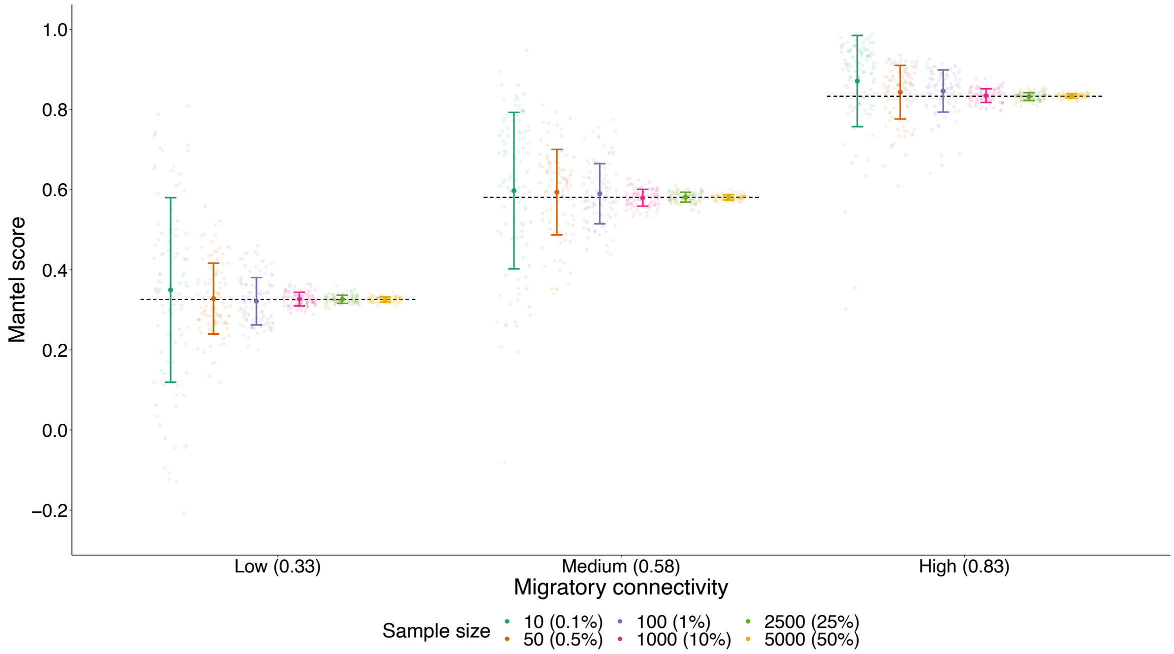

Figure 4. How number of individuals that are sampled influences precision in Mantel scores. Each point represents a replicate simulated study for a given sample size, randomly sampled from across the whole population. Error bars indicate standard deviation around the mean score of 100 replicates.

Patchy populations also show bias

In the scenario where random sampling was applied within increasingly-sized sampling zones across four distinct breeding sub-populations, inferences about the strength of connectivity for individuals inhabiting the strict zone of sampling produced metrics with limited bias (Fig. 5A). However, any attempt to extend inferences about the strength of migratory connectivity to the wider population beyond the spatial extent of sampling would lead to overestimation of migratory connectivity compared to the whole population (Fig. 5B). This bias was strongest in the scenario with smallest sampling area and weak connectivity.

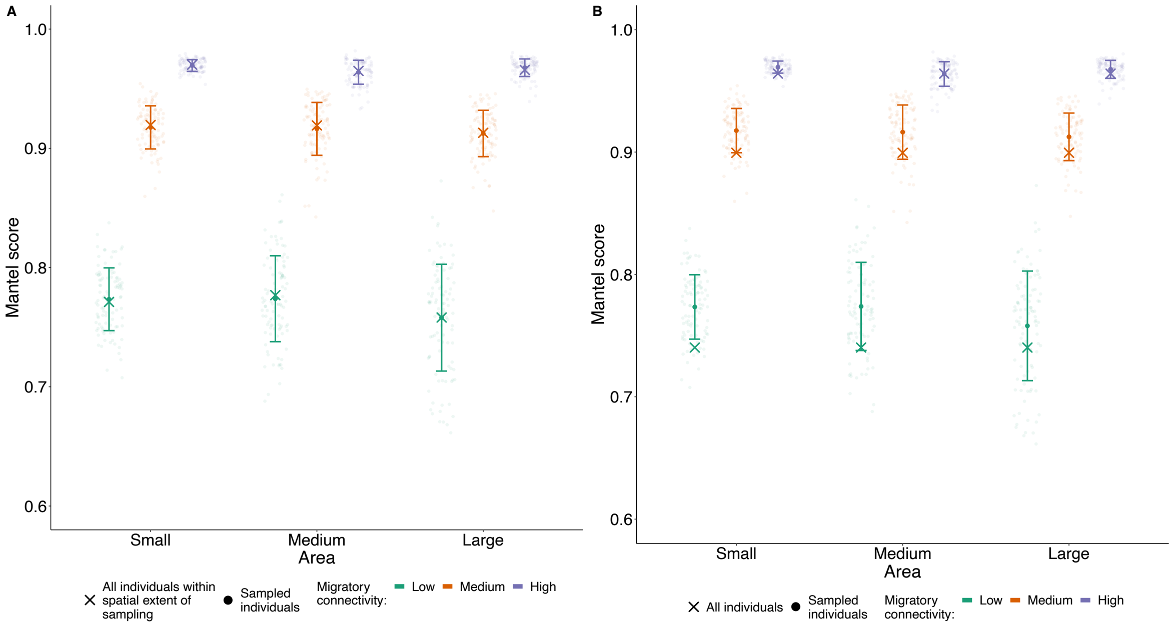

Figure 5. Mantel scores from 100 replicate simulated studies (circles) for each connectivity level, relative to 'true' values for all individuals within the zone of inference (crosses). **A)** 'True' migratory connectivity value for the populations solely within the spatial zone of sampling. **B)** 'True' migratory connectivity for a zone encompassing the entire population. Each simulated study comprised of 200 individuals sampled randomly across four equal sized sampling areas centred within sub-populations which varied in size. Error bars indicate standard deviation around the mean score of 100 replicates.

Complex patterns of bias emerge in more realistic population simulations

Applying realistic sampling regimes to real-world species range scenarios revealed how the mechanisms described above can lead to both over- and underestimation of true migratory connectivity estimates, depending on the spatial arrangement of sampled areas with respect to range geography. Across all three simulated 'species', bias was greatest when smaller numbers of discrete sampling locations were used (Fig. 6). With 5 or fewer sampling areas, replicate studies yielded hugely variable connectivity estimates within each population, with true connectivity tending to be underestimated when selected sites were relatively close together, and overestimated when they were far apart (Fig. 6).

The three simulated species showed subtly different patterns of overall bias, linked to the arrangement of potential sampled sites relative to the range as a whole. In the Henslow's Sparrow range scenario, the sampled sites were widely dispersed across a large breeding range (Fig. 6A), leading to large between-site distances and hence consistent overestimation of connectivity, even when large numbers of sites were used (Fig. 6D, G, and J). In the Falcated Duck range scenario, all sampled sites fell within a more discrete area within the range (Fig. 6C), resulting in systematic underestimation of population-scale connectivity, regardless of the number of sampling sites used (Fig. 6F, I, and L). Where the spatial extent of sampling provided consistent coverage of the entire population, as with the Aquatic warbler range scenario (Fig. 6B), there was no consistent pattern of directional bias, but estimates remained hugely variable and often yielded large over- and underestimates of true connectivity depending on the precise arrangement of sites selected from the pool available (Fig. 6E, H, and K).

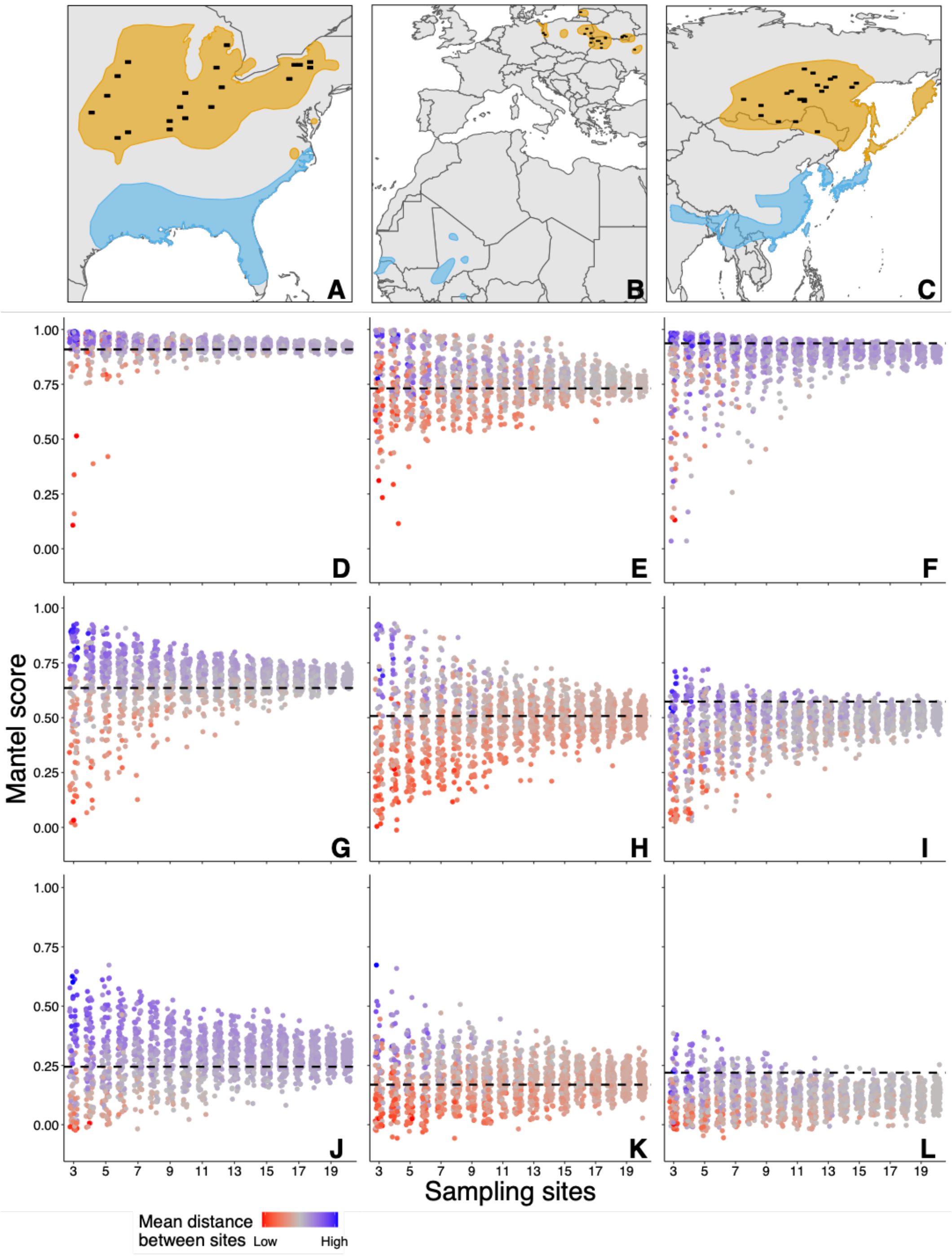

Figure 6. Breeding (orange) and non-breeding (light-blue) distributions of three simulated species (top, **A-C**), with filled black rectangles indicating the 20 potential sampling sites. Below each population are Mantel scores from replicate simulated studies applied to populations simulated within each range with three levels of connectivity; high (top, **D-F**), medium (middle, **G-I**), and low (bottom, **J-L**). Each point represents a sample of 200 individuals taken from between 3 and 20 sampling sites, with sites selected at random from the pools shown in Panels **A-C**. Point colour represents the mean distance between sampling sites in a given replicate study (blue is high, grey is medium, and red is low).

Discussion

There is an increasing demand in ecology and conservation for robust measures of the strength of migratory connectivity (Marra et al. 2018). We have shown the potential for bias and high uncertainty when broad-scale inferences about connectivity are made using Mantel statistics, driven by the fundamental dependence of these metrics on the spatial arrangement of samples. The strength of connectivity in a single population, as measured by the Mantel method, will always vary with the spatial scale of inference, with larger spatial sub-sections of a population likely to show higher connectivity scores. As a result, any attempt to infer the strength of connectivity for a contiguous species-level distribution from a spatial subset of individuals may lead to biased estimates. If inference is restricted to the strict spatial extent of sampling, random sampling across the area of inference can produce unbiased estimates of connectivity, but the use of disparate sampling sites is likely to cause overestimation. Even under ideal sampling practices (random sampling across a single area), which are in many cases unachievable, replicate estimates for a single population vary widely when sample sizes are small (100 or fewer tracked individuals). Within more complex and realistic simulated populations, these mechanisms can generate huge variation in connectivity estimates derived for a single population, depending on exactly where within the range samples are taken. These results indicate strong dependence of Mantel metrics on the design of spatial sampling regimes, and can help to inform best-practice in study design and improve accuracy.

Previous studies have suggested combining the Mantel test with cluster analysis to control for population structuring (Ambrosini et al. 2009), as well as calls for the measure to be used in conjunction with an absolute measure of population spread (the degree to which individuals from a single breeding population spread out during the non-breeding season) to better disentangle the properties of connectivity (Finch et al. 2017). These proposals do not, however, address fundamental biases that arise from constraints on observable pairwise distances under different sampling regimes, demonstrated by our simulations. Whilst recently-developed extensions to the Mantel approach using between-region transition rates could plausibly account for some of these biases (Cohen et al. 2018), the data requirements for these methods can be prohibitive, and use of Mantel statistics remains widespread (e.g. Burgess et al. 2020, Imlay et al. 2018, Norevik et al. 2020, Sarà et al. 2019, but see Korner-Nievergelt et al. 2017, Tonra et al. 2019). Our simulations suggest that biases can only be avoided by careful study design, and in particular the explicit restriction of inference to clearly delimited spatial subsets of populations.

Our results suggest that making inferences about the strength of connectivity for wider populations beyond the spatial extent of sampling can lead to significant bias (Fig. 2, Fig. 5). As metrics of connectivity are fundamentally scale dependent, 'true' connectivity values for sub-populations within a small portion of the breeding range are likely to be lower than 'true' values calculated for the entire breeding range, even if movement behaviour is universally governed by the same process. This illustrates that connectivity, as measured by these metrics, is a spatial pattern and not necessarily a fundamental species-level trait or characteristic.

Given that real-world studies may be limited to sampling individuals from small subsets of their target species' ranges, our results suggest that underestimation of population-scale migratory connectivity is likely to be commonplace. However, in species with spatial heterogeneity in migratory programme such as migratory divides (e.g. Barn Swallow *Hirundo rustica* in North America; Hobson et al. 2015), the directionality of this scale-dependent bias may be further complicated by what sub-population is sampled. Accurate estimation of connectivity at a population level may therefore only be possible where sampling is exhaustive, but even here researchers must carefully consider their sampling design. True random sampling is likely to be impossible to achieve across large areas, especially with study species that are difficult to trap, or tag retrieval is required. A multiple sampling site approach may be more feasible to implement in practice (e.g. breeding site sampling locations in Finch et al. 2017), yet the sites should be well distributed throughout the area of inference, with careful consideration of site spacing. Sites either spaced very far apart, or clumped close together, may lead to biased metrics with respect to wider populations. Our more realistic simulated scenarios suggest that more accurate estimates of connectivity will be achieved by using larger numbers of sampling sites spread across the area of inference, even if this leads to lower sample sizes of marked individuals within each site. Practitioners must therefore balance maximising the number of sampling sites used, with the practical limitations of such study designs.

Whilst our results are limited to simulations, the scenarios we have examined can be considered as simplified 'best-case' scenarios for sampling regimes. Real-world data collection will inevitably be more complex, and may include additional factors of bias such as non-representative sampling of a population and differential survival rates between cohorts that may affect tag retrieval (Weiser et al. 2016). In practice, ascertaining the connectivity of an entire large population using Mantel correlations may always be unfeasible, and in these cases, care should be taken to avoid making general population-level inferences from subsamples. Given the potential for bias, we suggest that researchers should carefully consider on a case-by-case basis whether simpler visual representations of spatial connectivity may ultimately be just as informative as quantitative connectivity metrics. In some use cases, such as temporal comparisons of Mantel statistics within a single study (Knight et al. 2021), biases may be consistent with respect to the variable of interest (time) and thus allow for robust comparisons. Comparisons of Mantel scores between studies, however, are likely to be particularly vulnerable to bias, especially where sampling regimes differ substantially.

Conclusions

Due to fundamental scale-dependence, the notion of a single 'true' connectivity value that applies to a species is unlikely to be realistic. The development of new and broadly-applicable statistical methods to control for this spatial dependence would be extremely valuable for future connectivity research. Nevertheless, our work suggests that with good sampling design and explicit clarity over the spatial extent where inference is made, deriving meaningful population-level measures of connectivity using Mantel correlations remains feasible. Where random sampling of individuals across the whole area of inference is not possible, we recommend maximising the number of discrete sampling sites and avoid cases where sampling site spacing (either too much or too little) is likely to cause overt bias. We also strongly advise against making inferences about the strength of connectivity of a population that extends well beyond the spatial extent of sampling. We hope that with these recommendations, measures of connectivity will be more robust.

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Data availability statement

The code and data used to conduct this analysis can be accessed at www.github.com/SHVickers94/Sensitivity-of-migratory-connectivity-metrics-to-spatial-sampling-design (Vickers, 2021).

Supplementary material

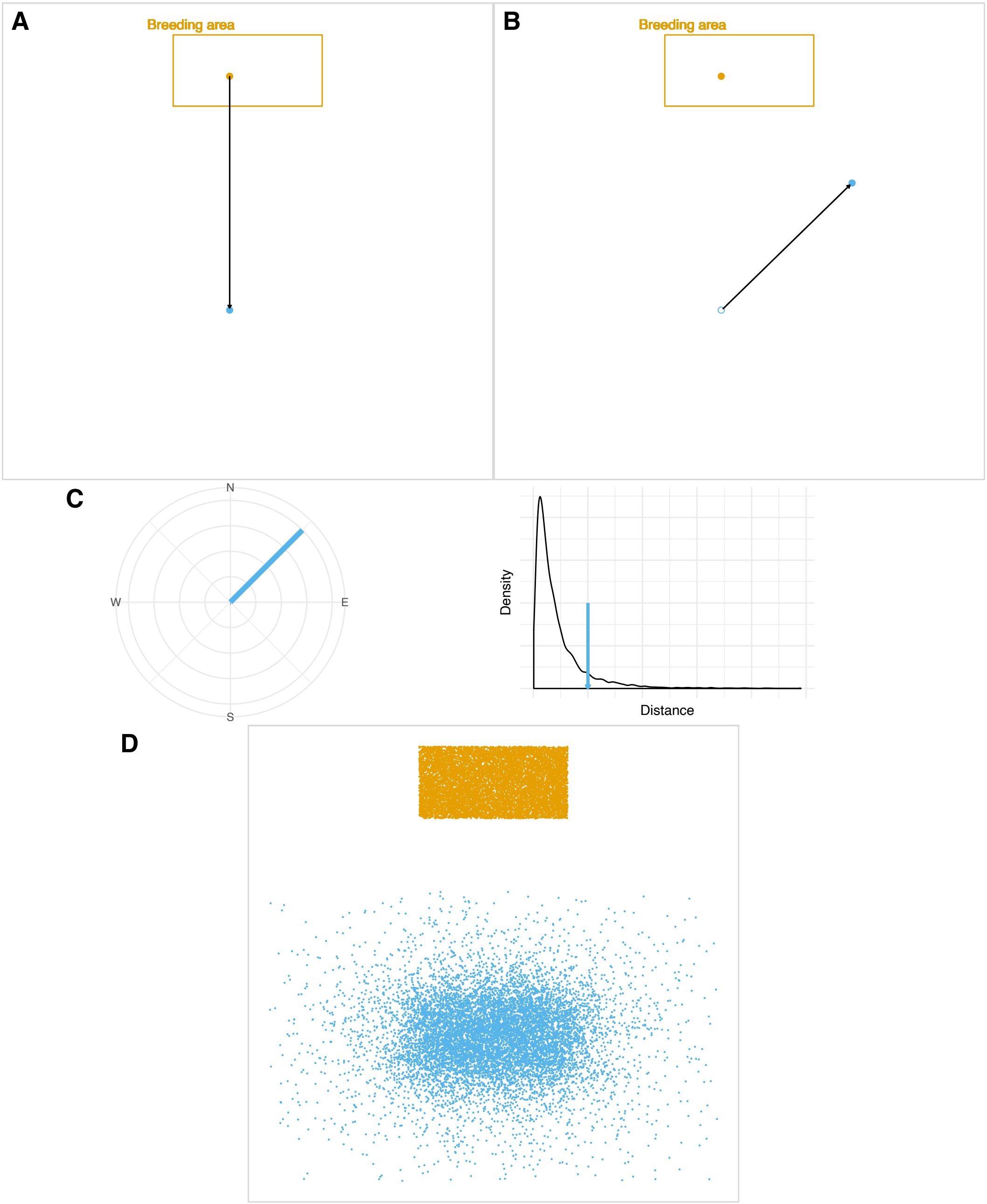


Figure SM1. Simulating the breeding and non-breeding locations of 10,000 individuals. **A.** An individual is given a breeding location by placing the individual at random within the breeding area. The individual is then moved a set distance in a southerly direction **B.** The individual is then moved to a final non-breeding location. The direction of this movement is taken at random (**C left**) and the distance is drawn from a log-normal distribution (**C right**) which we varied to change the relative strength of migratory connectivity. **D.** This process is repeated for 10,000 individuals in the simulated population.

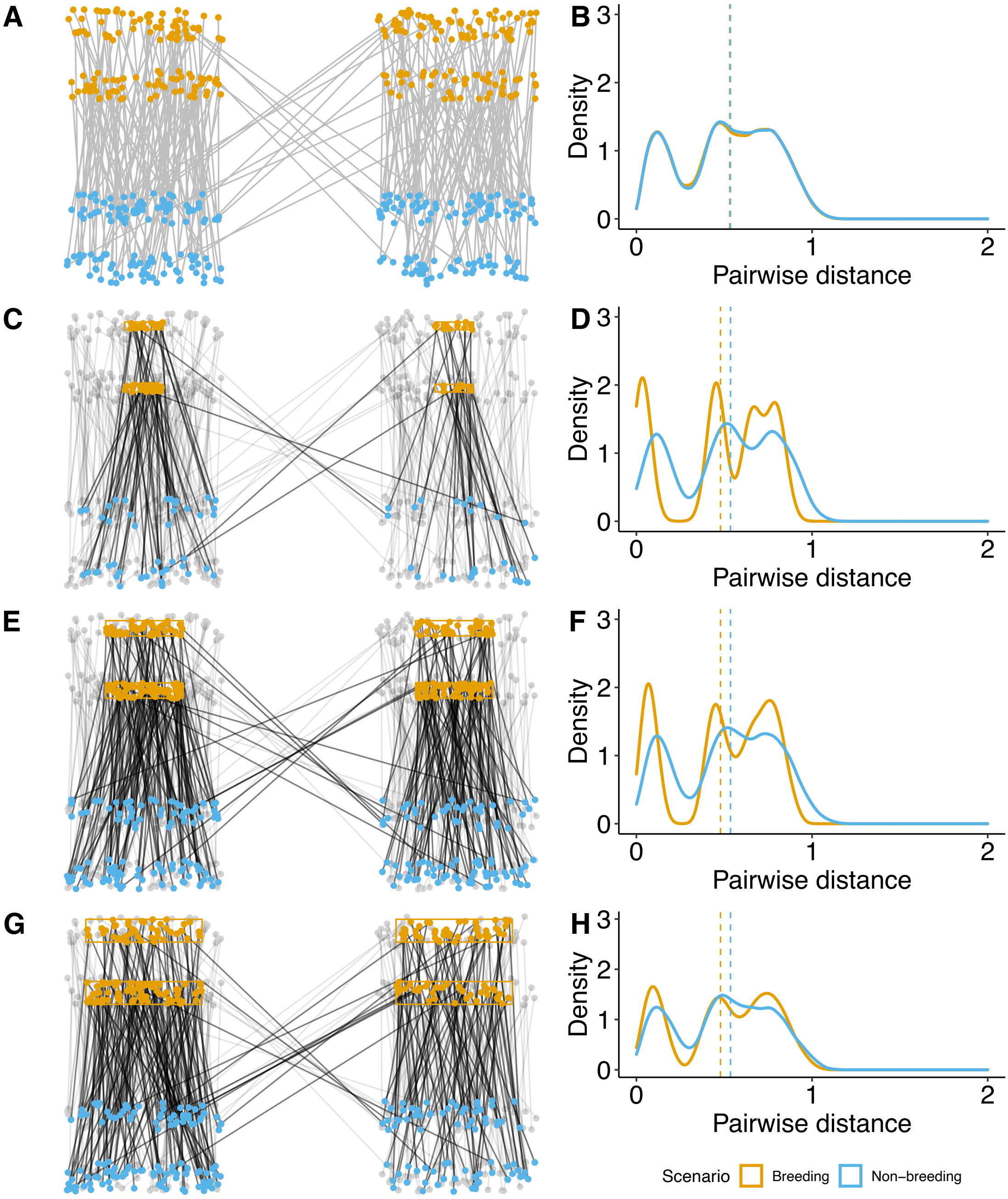


Figure SM2. Hypothetical examples showing the spatial distribution (**A**) of breeding (yellow dots) and non-breeding locations (blue dots) for a migratory patchy population and the corresponding frequency distributions (**B**) of pairwise distances between individuals during breeding (yellow line) and non-breeding (blue line). Panels **C**, **E** and **G** show increasingly large spatial subsections within each sub-population, together with the corresponding pairwise distance frequency distributions (**D**, **F** and **H**), highlighting how distance distributions vary with sampling area for breeding, but less so in non-breeding seasons. Total population is shown as translucent and individuals within a spatial subsection shown coloured in in plots **C**, **E** and **G**.

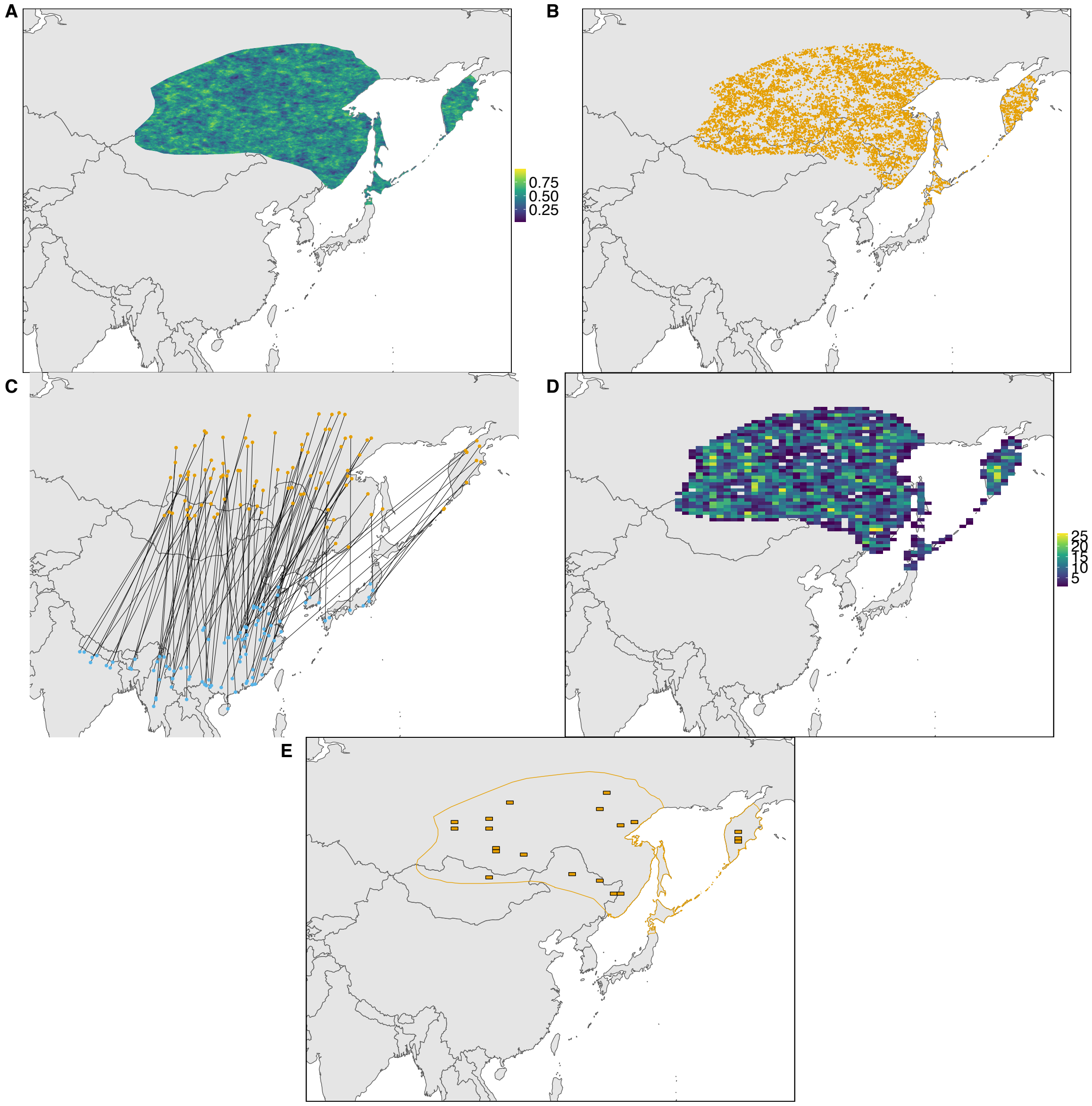


Figure SM3. Production and sampling of a simulated realistic migratory population. **A)** Generating spatially autocorrelated occurrence probability values across a real-world species range (breeding range Falcated Duck Mareca falcata shown here). **B)** 50,000 individuals are then distributed across the range with locations weighted by cell occurrence probabilities (10,000 shown here). **C)** Individuals are then linked between seasons by random selection of corresponding points, varying the level of simulated connectivity by changing the bandwidth of longitudinal rank (1,000 individuals shown here, low-medium migratory connectivity scenario). **D)** A coarse grid is overlaid on the breeding zone, across which we calculate the number of individuals in each cell. **E)** The 20 cells with the highest number of individuals are taken as sampling sites.

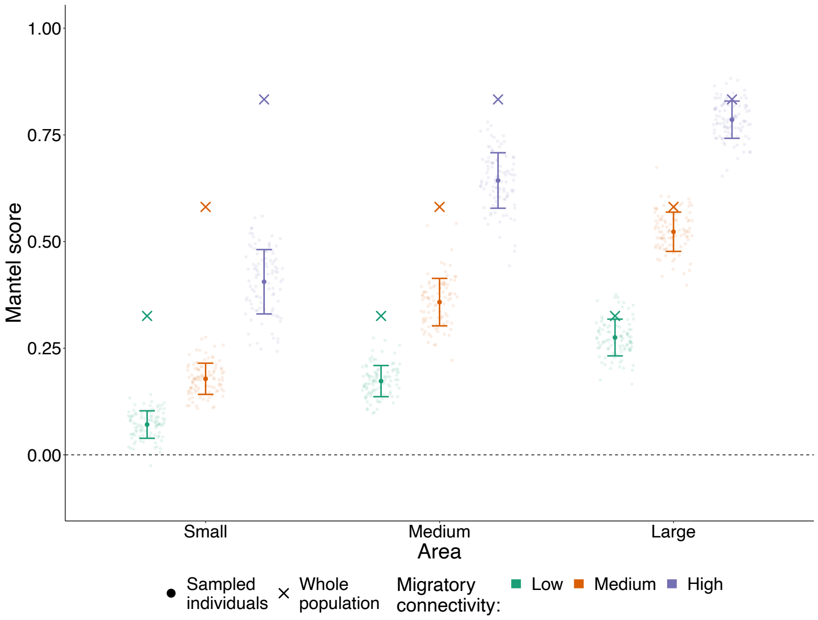


Figure SM4. Mantel scores of sampled individuals (circles) compared to 'true' values for the whole population (crosses) across three simulated connectivity levels. Each replicate is calculated using 200 individuals sampled randomly across a single area which was varied in size. Error bars indicate standard deviation around the mean score of 100 replicates.

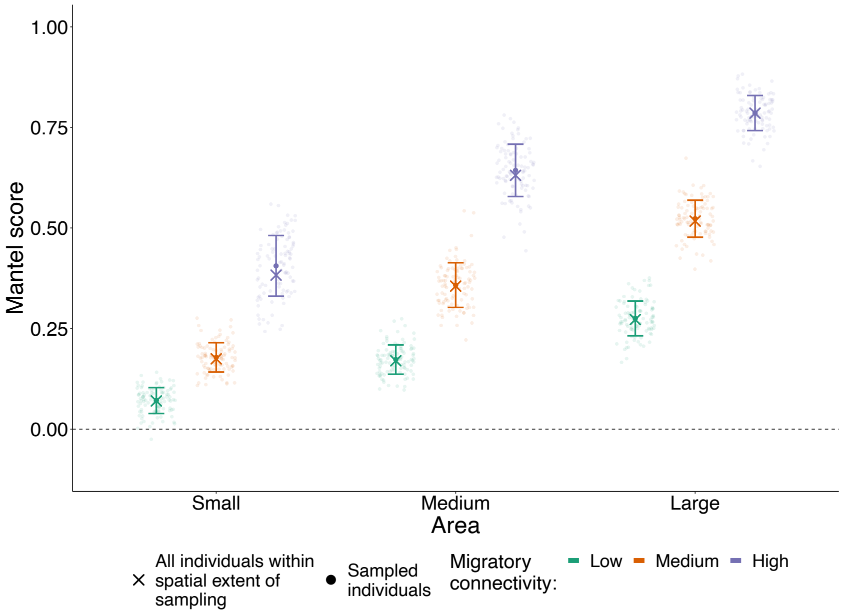


Figure SM5. Mantel scores from 100 replicate simulated studies (circles) compared to that of all individuals within the spatial extent of sampling (crosses). Samples comprised of 200 individuals sampled randomly across a single area which was changed in size. Error bars indicate standard deviation around the mean score of 100 replicates.

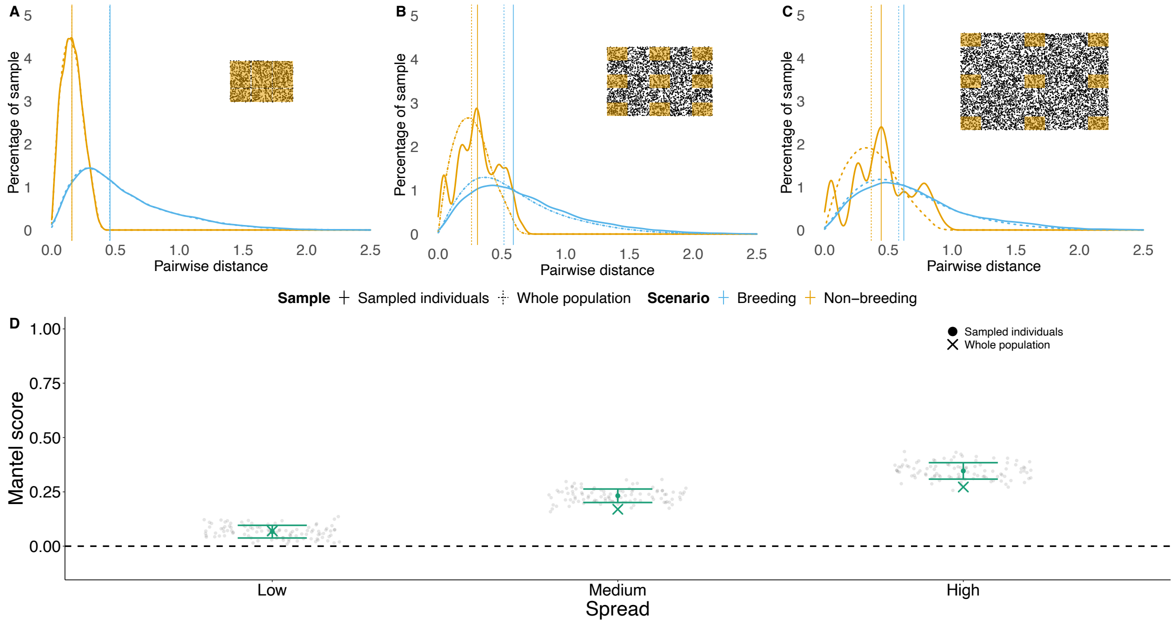


Figure SM6. A-C: Density plots of pairwise distances between individuals under spread-based scenarios, depicting how the distribution of sampled pairwise distances (solid lines) varies with the scale of sampling, relative to true distance distributions for the whole population (dotted lines). Inset schematics visualise the sampling regime on the breeding ground, with highlighted region indicating the zone of sampling. **D:** Mantel scores from 100 replicate simulated studies (circles), compared to the whole population of 10,000 individuals (crosses). Samples comprised 200 individuals chosen randomly across the nine sampling areas which varied in their spread. Error bars indicate standard deviation around the mean score of 100 replicates. These examples show the lowest level migratory connectivity simulated (Mantel MC 0.33).

3

Non-reproductive dispersal: an important driver of migratory range dynamics and connectivity

Vickers, S.H., Franco, A.M.A., & Gilroy, J.J. (In review). Non-reproductive dispersal: an important driver of migratory range dynamics and connectivity. Ecography.

Abstract

Dispersal is the primary ecological process underpinning spatial dynamics in motile species by generating flux in reproductive locations over time. In migratory species, dispersal can also occur around non-breeding ranges, but this form of dispersal currently lacks a unifying theoretical framework. We present a novel conceptual model for dispersal in migrants that builds upon traditional dispersal literature, differentiating ‘reproductive’ dispersal (i.e. changes in breeding locations) from ‘non-reproductive’ dispersal, which we define as movements resulting in inter-annual or inter-generational changes in non-breeding locations. Crucially, unlike reproductive dispersal where movement outcomes are naturally propagated between generations, the outcomes of non-reproductive dispersal can be non-heritable. We use simulations to illustrate how variation in this heritability exerts a strong influence on both migratory connectivity and range shift propensity. When exposed to spatially-uncoupled shifts in habitable ranges (i.e. seasonal climate niches shifting at different rates), long-term persistence of simulated populations required changes in migratory programmes to arise through heritable forms of non-reproductive dispersal (e.g. mutations in migratory gene complexes). By contrast, non-heritable dispersal mechanisms (e.g. navigation errors) cannot drive long-term shifts in non-breeding ranges, despite being a major component of realised dispersal and migratory connectivity patterns. Migratory connectivity metrics conflate these heritable and non-heritable drivers of non-reproductive dispersal, and therefore have limited power in predicting population responses to environmental change. Our models provide a framework for improving our understanding of spatial dynamics in migratory populations, and highlight the importance of teasing apart the mechanisms that drive migratory variability in order to evaluate and predict range plasticity in migrants.

Keywords

Dispersal, range dynamics, range shift, climate change, migration, migratory connectivity, mantel, non-breeding

Introduction

Dispersal is central to a suite of eco-evolutionary processes including the colonisation of new sites, metapopulation maintenance, source-sink dynamics, and gene flow (Johst et al. 2002, Kendrick et al. 2012, Reed 2004). Dispersal is particularly important in the context of anthropogenic change, as it influences whether populations can track shifting zones of environmental suitability (Collins et al. 2013, IPCC 2014, Peterson et al. 2003, Thuiller 2004), as well as persist in fragmented landscapes (Chaine & Clobert 2012). Whilst dispersal has been subject to intensive study, most theoretical and empirical work focusses on movements within and around breeding ranges (e.g. Bocedi et al. 2014, Le Galliard et al. 2012, Ronce 2007). However, population dynamics are also sensitive to dispersal processes occurring within and around non-breeding ranges, particularly in species that undergo seasonal migrations (Potvin et al. 2016, Zurell et al. 2018a). These dispersal processes have received far less attention from scientists, despite emerging awareness of the critical role non-breeding ranges can have on population dynamics in migrants (Marra et al. 2019, Rushing et al. 2020). Indeed, dispersal processes relating to the non-breeding range currently lack a formal theoretical foundation, or even definition, in the ecological literature.

Here we address this gap by developing a novel conceptual model for dispersal in migratory species, explicitly differentiating the movement processes that influence breeding locations – which we term 'reproductive dispersal' - from those influencing non-breeding locations – termed 'non-reproductive dispersal' (Fig. 1). We propose a key distinction between these processes with important implications for both migratory connectivity and spatial range dynamics, relating to the extent to which the spatial outcomes of dispersal are heritable. We hypothesise that the degree of heritability in non-reproductive dispersal outcomes will strongly influence range dynamics in migratory species, particularly under scenarios of environmental change. We test this hypothesis using individual-based simulations, demonstrating that our capacity to quantify and predict real-world range dynamics in migratory species, including patterns of migratory connectivity, may be enhanced by a better understanding of the processes that underpin non-reproductive dispersal.

A novel conceptual model for dispersal in migrants

Just as reproductive dispersal can occur in either mature individuals (often termed 'breeding dispersal', Fig. 1A) or immatures prior to their first breeding ('natal dispersal', Fig. 1A; Greenwood & Harvey 1982), non-reproductive dispersal can occur through a) changes in non-breeding locations occupied by mature individuals in different years (analogous to 'breeding dispersal', Fig. 1B), or b) in immatures through differences in their non-breeding localities relative to their parents (analogous to 'natal dispersal', Fig. 1B).

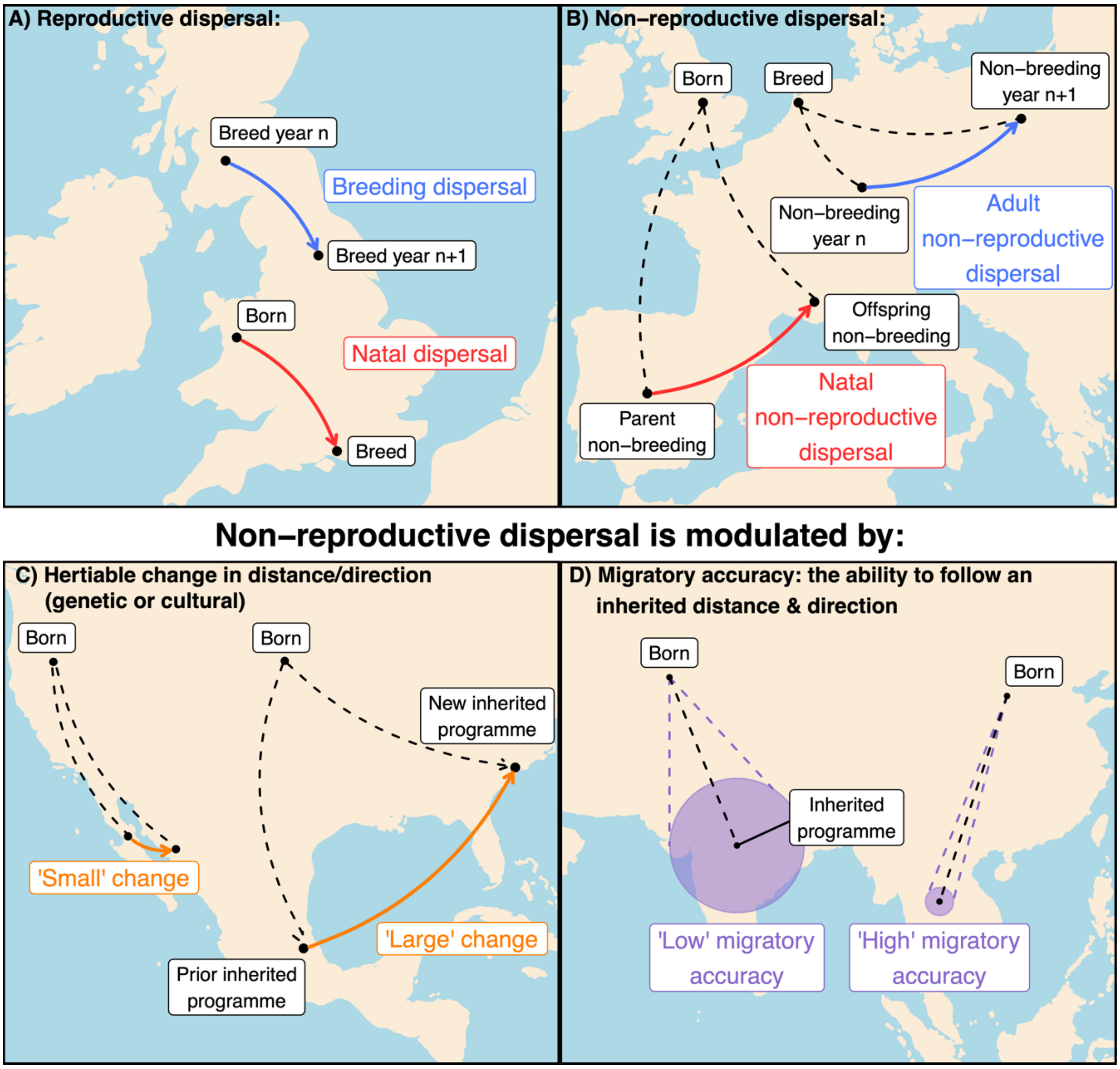


Figure 1. Conceptual dispersal framework for migratory species. Dispersal may be **A**) Reproductive dispersal or **B**) Non-reproductive dispersal. These dispersive movements can be either breeding (blue) or natal (red) describing the life stage that these movements occur. Non-breeding dispersal can be generated by **C**) heritable and/or **D**) non-heritable changes.

Non-reproductive dispersal

Both forms of dispersal can arise through similar mechanisms – for example through random exploratory movements, or through navigational errors or drift during migration that carries individuals outside their previous range (at any stage of the annual cycle). In the case of reproductive dispersal, the proximate mechanism is unlikely to exert significant influence on subsequent site occupancy, as long as offspring survive and exhibit some degree of natal philopatry (as is typical in migratory species; Greenwood & Harvey 1982). For non-reproductive dispersal, the proximate mechanism may be critical: migrants that are drifted to new sites by winds, for example, may lack a mechanism to pass this new migratory destination on to future offspring (Berthold 2003, Dufour et al. 2021). Even if they survive and return to breed, their offspring are likely to inherit their original (non-drifted) migratory programme and thus return to the original non-breeding area (Berthold 2003).

This highlights how range dynamics of migrants are fundamentally linked to mechanisms by which organisms navigate between their seasonal ranges. Migratory navigation has been subject to intensive study (e.g. Berdahl et al. 2014, Bingman & Ewry 2020, Broms et al. 2012, Riveros & Srygley 2010, Zein et al. 2021), but the interplay between navigation and dispersal in the context of spatiotemporal range-dynamics has been little explored. This is despite evidence that migratory patterns may be rapidly changing in many species under climate change (Curley et al. 2020), potentially indicating high rates of change (or plasticity) in species' evolved migratory programs.

Migratory heritability influences dispersal outcomes

The inheritance of migratory programmes can occur through genetic or cultural mechanisms (Harrison et al. 2010, Liedvogel et al. 2011), with significant variation across taxa - although our understanding of the extent of this heritability remains limited. Migration is known to have a strong genetic basis in many organisms (Berthold 2003, Gu et al. 2021, Liedvogel et al. 2011, Zhan et al. 2014), and for species that do not migrate in groups, it is often assumed that juveniles must complete their first migratory journey using only a genetically encoded mechanism (e.g. 'clock and compass') that determines the distance, direction, and timing of movements (Froy et al. 2003, Helm & Muheim 2021, Mouritsen 1998). This is likely to involve polygenic complexes spanning an organism's sensory and circadian apparatus, morphology, and neurophysiology (Gu et al. 2021, Merlin et al. 2020). Mutations in this genetic basis (or plasticity in migratory programme of adults in culturally inherited systems), have the potential to generate significant heritable changes in migration (Fig. 1C), and thus the intergenerational colonisation of new non-breeding ranges. Whilst there is evidence for rapid evolution of migratory programmes (Bearhop et al. 2005, Fiedler 2003, Sutherland 2008), it is unclear to what extent these changes are derived from standing variation within the population or novel heritable changes arising in migratory programmes (Merilä et al. 2001, Pulido 2007).

Dispersal in migrants (both reproductive and non-reproductive) also depends partly on the ability of individuals to accurately follow their inherited migratory programme. This capacity is likely to vary significantly both within populations and between species, and can be thought of as an individual-specific trait that we term ‘migratory accuracy’ (Fig. 1D). Crucially, this component of migratory variability could theoretically generate significant amounts of non-heritable dispersal in and around non-breeding ranges. In other words, new non-breeding sites colonised through low migratory accuracy are unlikely to be occupied by future generations, as any deviation from the genetically-determined migratory route arising from drift or low navigator accuracy is unlikely to be heritable.

In organisms that migrate alone, we might expect migratory accuracy to be generally low, particularly among immature individuals that are more vulnerable to weather-related drift, compass errors, or lack learned waypoints to assist in spatial navigation (Cresswell 2014, Finch et al. 2017, Vansteelant et al. 2017). We might therefore expect non-reproductive dispersal distances to be high in species that do not migrate in groups, at least regarding distances between the non-breeding locations of parents and their offspring (Fig. 1D). Importantly, however, the lack of heritability means this dispersal may not translate into a capacity for rapid change in non-breeding distributions.

Non-reproductive dispersal underpins migratory connectivity

We further hypothesise that magnitude of both reproductive and non-reproductive dispersal will exert a strong influence on the degree of migratory connectivity in a population – i.e. whether spatial aggregations of individuals are maintained between consecutive phases of the migratory cycle (Marra et al. 2019). Strong connectivity implies that individuals residing close together in one season also migrate to similar regions in subsequent seasons – this is only likely to be maintained over time if populations exhibit both high migratory accuracy and low between-individual variability in migratory programmes, at least within local contiguous populations. Weaker migratory connectivity indicates greater cross-seasonal mixing of individuals from different areas, and thus would be a natural consequence of non-reproductive dispersal occurring either through low migratory accuracy or high variability in inherited migratory programmes.

Despite being highly dependent on spatial scale (Vickers et al. 2021), migratory connectivity has been widely-proposed as a useful indicator of how migratory species will adapt to changing environments (Cohen et al. 2018, DeSaix et al. 2019, Korner-Nievergelt et al. 2017, Marra et al. 2019), with stronger connectivity often being taken to imply greater population sensitivity to perturbations like habitat loss (Dolman & Sutherland 1994, Taylor & Norris 2010, Taylor & Stutchbury 2016, Taylor 2019). However, because measurements of connectivity represent a temporal snapshot of emergent patterns, rather than capturing the underlying dispersal mechanisms that drive spatial dynamics, it is unclear how informative these metrics are for predicting spatial population responses to change. These models also lacked a mechanistic basis for migratory connectivity development and did not consider spatial range dynamics (Dolman & Sutherland 1994, Taylor & Norris 2010, Taylor & Stutchbury 2016, Taylor 2019). Given our hypothesis that low migratory accuracy (non-heritable) is likely to contribute significantly to realised migratory connectivity patterns, we predict that connectivity metrics may be relatively uninformative about species capacities for rapid spatial change.

To test these hypotheses about migratory dispersal and connectivity, we developed an individual-based simulation model to examine how non-reproductive dispersal influences both realised migratory connectivity patterns and population responses to environmental change. For the latter, we focus on realistic scenarios of shifting seasonal climate niches (i.e. the geographic regions where survival is possible), allowing us to evaluate whether climate-change vulnerability in migratory species could be predicted from metrics of migratory connectivity.

Simulation Model

Simulating dispersal within a migratory population

We created an individual-based model representing a sexually-reproducing population that performs a linear migration between two equally-sized seasonal ranges (full details in Supporting information). Simulated populations have a 50/50 sex ratio and a starting size of 10,000 individuals, with non-overlapping generations (i.e. each individual survives only one migratory cycle). Each individual is assumed to follow an inherited migratory programme analogous to a 'clock and compass' mechanism (widely used as a general model for navigation in non-social migratory species; Åkesson et al. 2017, Helm & Muheim 2021, Mouritsen 1998, Muheim et al. 2018). This programme encodes the distance and direction individuals move between their breeding and non-breeding locations, modelled as two parameters dictating the magnitude of latitudinal and longitudinal displacement made by each individual in moving between the breeding and non-breeding range. We assume the migratory programme is inherited from both parents, such that offspring inherit the mean latitudinal and longitudinal displacements of their parent's migratory programmes. Empirical studies suggest that pairings of individuals with differing migration orientations often produce intermediate orientations in offspring (e.g. Albert et al. 2006, Berthold & Helbig 1992, Helbig 1991), suggesting that this assumption is likely to be reasonable for many real-world systems (but see Delmore & Irwin 2014, Väli et al. 2018).

We incorporate density dependent reproduction by limiting the number of offspring produced by each female to a value of 2*b where b is the proportion of local carrying capacity k that is currently occupied (where k = 25 individuals per grid cell across the range), with upper and lower limits set at 1 and 10 offspring per female (see Supporting information). Mating is random within grid cells, with all females breeding once (i.e. males may breed with multiple females). To incorporate reproductive dispersal, all offspring disperse away from their natal site to a new breeding location, moving in a random direction with a distance drawn from a heavy-tailed kernel that was selected to produce a realistic spread of both long and short reproductive dispersal distances within the modelled environment (Nathan et al. 2012). For this we used a Gamma distribution with rate parameter 0.0001 and shape parameter varying across dispersal scenarios: 0.5 = 'low', 1.5 = 'medium', 3.0 = 'high' (see Supporting information for more details).

We incorporate non-reproductive dispersal via two mechanisms. Firstly, the inherited migratory movement of each individual can undergo generational change through mutations of the inherited programme. In each year, mutations occur in a proportion of new offspring (representing the rate of mutation in the migratory gene complex) and these modify the inherited non-breeding location by shifting it in a direction drawn from a uniform distribution (~U(0,359)) by a distance drawn from a Gamma distribution. We consider a range of scenarios where populations differ in the amount of heritable migratory change ('mutation size'), achieved by varying the shape parameter of the Gamma distribution (0.5 = 'low', 1.5 = 'medium', 3.0 = 'high; SM1b) with the rate parameter fixed at 0.0001. We also consider scenarios of varying mutation rate by changing the proportion of offspring carrying mutations (low = 1%, medium = 10%, and high = 50%).

The second source of non-reproductive dispersal – migratory accuracy – is incorporated by shifting the inherited (or mutated) non-breeding location of each individual in a random direction and a distance, analogous to individuals deviating from their inherited migratory programme during migration as a result of stochastic factors such as weather drift or navigational errors. The size of these displacements is again drawn from a Gamma distribution which varies between scenarios according to the shape parameter (0.5 = 'low', 1.5 = 'medium', 3.0 = 'high; rate fixed at 0.0001; SM1b).

Individuals whose final non-breeding destinations fall outside the non-breeding range are removed from the population. Density dependent survival is applied within the non-breeding range by setting a carrying capacity of 25 individuals per grid cell, with surplus individuals being selected at random from those within the cell and removed from the population. All surviving individuals then migrate to the breeding range in the subsequent year, returning to the location where they settled following reproductive dispersal after birth. The model therefore represents a system with pre-migratory natal reproductive dispersal, which has been shown in several taxa (Ciaglo et al. 2021, Pärt et al. 2011).

We run each model for a 500-year burn-in, within which stable population and range dynamics were always achieved. To ensure model variation is not influenced by starting conditions, we set the starting migratory programme of all individuals to be an identical fixed latitudinal displacement with no longitudinal displacement, such that spatial arrangement of individuals in the non-breeding range is identical to that of the breeding range (i.e. perfect connectivity; see Supporting information). Variation in migratory destinations then emerges during the burn-in period as a result of the scenario-specific mechanisms of reproductive and non-reproductive dispersal described above. All model runs achieved multi-generational stability in population size and the strength of migratory connectivity within the 500-year burn-in period (see Supporting information).

Range shift scenarios

After the initial 500-year burn-in period, we expose each simulated population to gradual shifts in the habitable zones for the breeding and non-breeding seasons. Shifts persist for a 50-year period. We simulated two sets of range shift scenarios:

Coupled range shift – both breeding and non-breeding habitable zones shift in the same direction at the same rate (equivalent to 1.5% of a zones latitudinal range per year)

Uncoupled range shift – breeding and non-breeding habitable zones shift in the same direction, but one range shifts at a faster rate than the other (in our case the breeding zone shifts 3% of the zones latitudinal range per year compared to 1.5% for the non-breeding zone).

We generated 100 replicates of each scenario across each combination of four dispersal parameters (i.e. reproductive dispersal, migratory mutation size, migratory mutation rate, and migratory accuracy), resulting in 8100 model runs per range shift scenario.

Response metrics

Population-scale outcomes of range shift scenarios were measured with two metrics: population size, and the strength of migratory connectivity (i.e. population spatial flux). Migratory connectivity was measured annually by randomly sampling 100 individuals from across the breeding range, ensuring unbiased estimates (Vickers et al. 2021). We calculated a Mantel correlation using the mantel.rtest function within the ade4 package in R (Dray & Dufour 2007). Mantel correlations measure the strength of connectivity on a scale of -1 to +1 (though correlations are seldom negative), where 1 indicates perfect maintenance of spatial structure between seasons, and 0 indicates random seasonal population mixing. We evaluated the demographic response of populations to shifts in habitable zones by calculating proportional change in population size from the year immediately preceding initiation of range shift to the end of the 50-year shift period. All statistical analyses and simulations were performed with R 4.1.0 (R Core Team 2021). Scripts for the completed analysis are available as electronic supplementary material.

Results

How do dispersal drivers affect range shift rates?

In uncoupled range shift scenarios where one seasonal habitable zone shifts at a faster rate than another, both reproductive and non-reproductive dispersal were critical for population maintenance. Importantly, most variation in population persistence across model runs was explained by differences in migratory mutation rate and size, but not migratory accuracy (Fig. 2). Despite being a major source of realised non-reproductive dispersal, variation in migratory accuracy had little impact upon population persistence as new areas colonised through this mechanism were unlikely to be utilised by future offspring (Fig. 2).

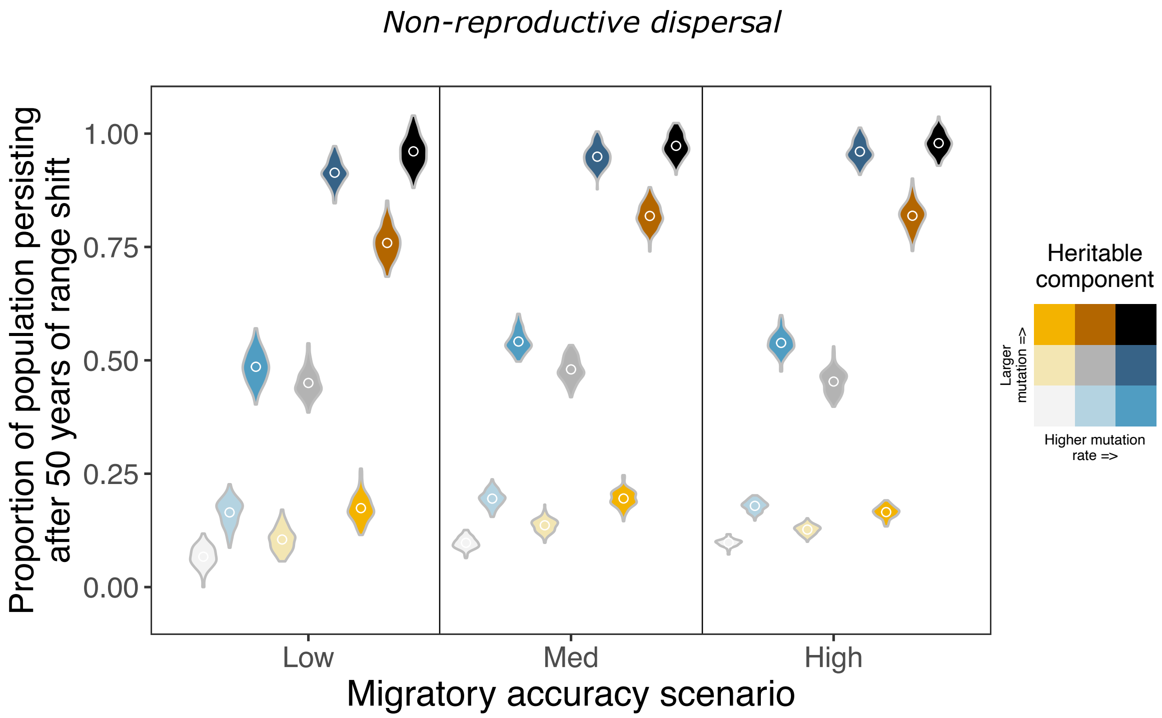


Figure 2. Persistence of simulated populations following uncoupled shifts in seasonal habitat zones, where breeding habitable zones shift more rapidly than non-breeding. Violin plots represent density distributions of individual model runs, spanning scenarios that vary in the levels of three drivers of non-reproductive dispersal (migratory accuracy, mutation size and mutation rate). White outlined points indicate mean values for each given scenario.

As the inter-range distance increases under uncoupled shift scenarios, populations with low mutation rate and small mutation size consistently failed to track the expanding northern limit of the breeding and southern limit of the non-breeding ranges respectively, and declined significantly at the contracting limits (Fig. 3F–H), even when reproductive dispersal was high (Fig. 4). This pattern aligns with some real-world patterns of change, for example in Neotropical migratory birds where many species have shown limited expansion at the northern margin of their breeding range, and contraction of their southern margin (Rushing et al. 2020). In our simulations, even where reproductive dispersal was sufficient for individuals to colonise newly-available areas in the breeding range, a lack of heritable change in the migratory programme meant these individuals maintained their inherited migration distance and thus failed to cross the increasing non-habitable gulf between seasonal ranges (Fig. 3H). Conversely, populations with high mutation rate and/or large mutation size were more readily able to keep pace with shifting habitable zones (Fig. 3B–D). This stark divide in population outcomes occurred despite the two scenarios having comparable frequency distributions of non-reproductive dispersal distance prior to the initiation of range shifts (Fig. 3A & E). This suggests that disentangling heritable and non-heritable drivers of non-reproductive dispersal is likely to be essential for better understanding the threat to migratory species posed by climate change (Zurell et al. 2018a).

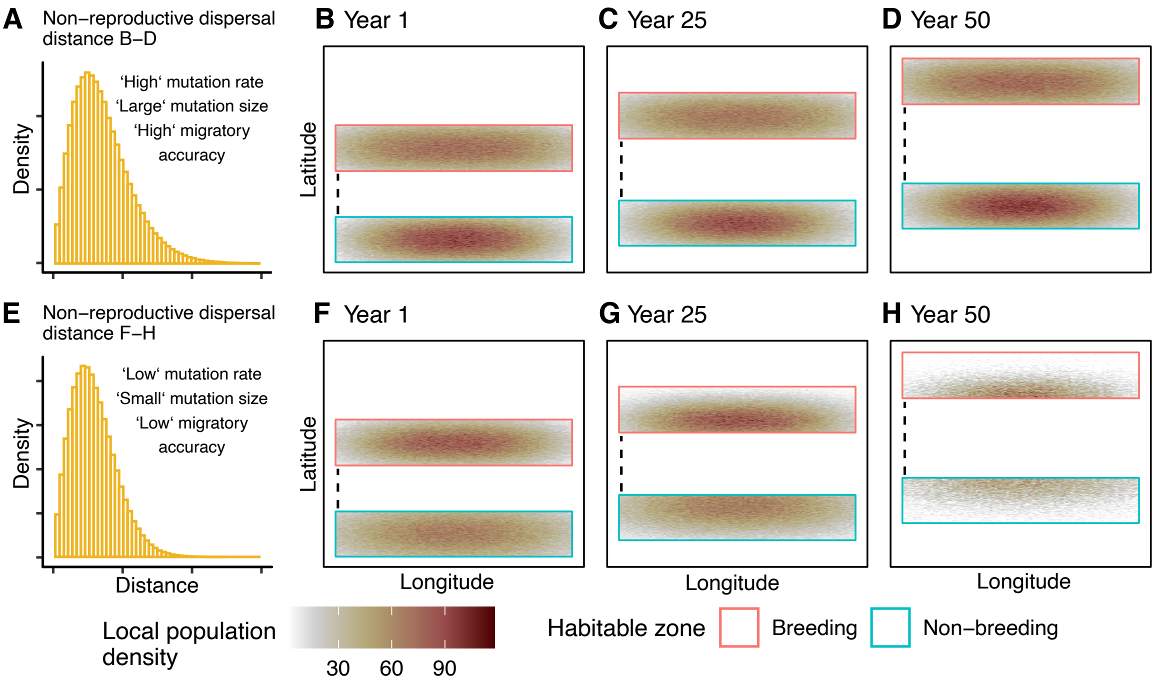


Figure 3. Realised non-reproductive dispersal distances in two example simulated populations, one with high mutation rate, large mutation size, and high migratory accuracy (**A–D**) and another with low mutation rate, small mutation size and low migratory accuracy (**E-H**). Plots **B-D** and **F-H** illustrate the composite distribution of individuals for 100 simulation replicates within breeding (red) and non-breeding (blue) habitable zones as they shift northward over a 50-year period, where the breeding habitable zone shifts at twice the rate of the non-breeding habitable zone.

In scenarios with limited natal reproductive dispersal, more complex interactive relationships emerged between reproductive and non-reproductive dispersal (Fig. 4). For scenarios with slower rates of heritable change in the migratory programme (i.e. lower mutation rates, smaller mutation sizes), population persistence was lowest when reproductive dispersal was high. This pattern is driven by a mismatch in season-specific dispersal rates, whereby populations with high reproductive dispersal rapidly colonise the expanding northern habitable zone, but this outpaces the rate at which heritable changes emerge in the migratory programme. With uncoupled seasonal shifts, such migratory changes are essential in allowing populations to adapt to the increasing distance between seasonal habitat zones. This leads to the counterintuitive result that population persistence is greater when reproductive dispersal rates are lower (but still sufficient for some breeding range expansion) as this reduces the risk that breeding range expansion outstrips the rate of heritable change in the migratory programme.

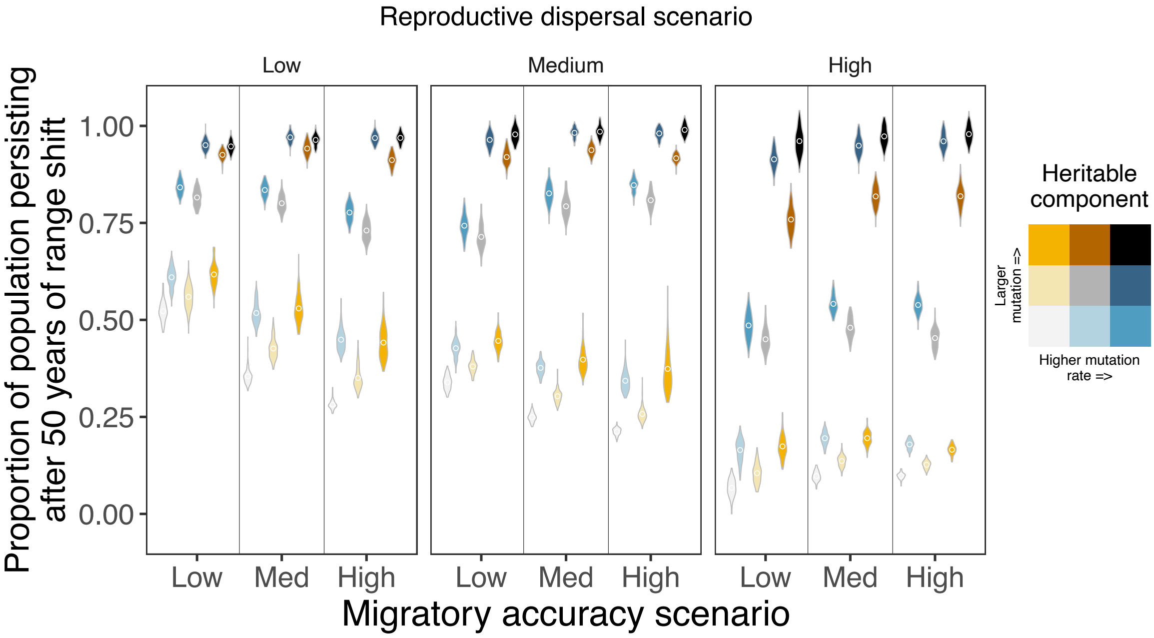


Figure 4. Interactive effects of non-reproductive and reproductive dispersal on population persistence in response to uncoupled shifts in seasonal habitable zones (breeding zone shifting more rapidly than non-breeding zone). Violin plots represent density distributions of replicate model runs for scenarios that vary in four drivers of dispersal (reproductive dispersal, migratory accuracy, migratory programme mutation rate, and mutation size). White outlined points indicate mean values for a given scenario.

When coupled range shifts occur (i.e. both seasonal habitable zones shift in the same direction at the same pace) population loss was relatively limited in all our modelled scenarios, and natal reproductive dispersal rates had the largest impact on population persistence (Fig. 5). These scenarios do not exert selection pressure for changes to the inherited migratory distance and direction, and instead failure to disperse with the expanding northern breeding range limit is the primary cause of population loss. Nevertheless, non-reproductive dispersal contributes to population persistence when reproductive dispersal is insufficient to keep pace with breeding range shifts (Fig. 5, low reproductive dispersal scenarios), as the emergence of novel shorter migrations allows the standing population to track the northward-shifting non-breeding range.

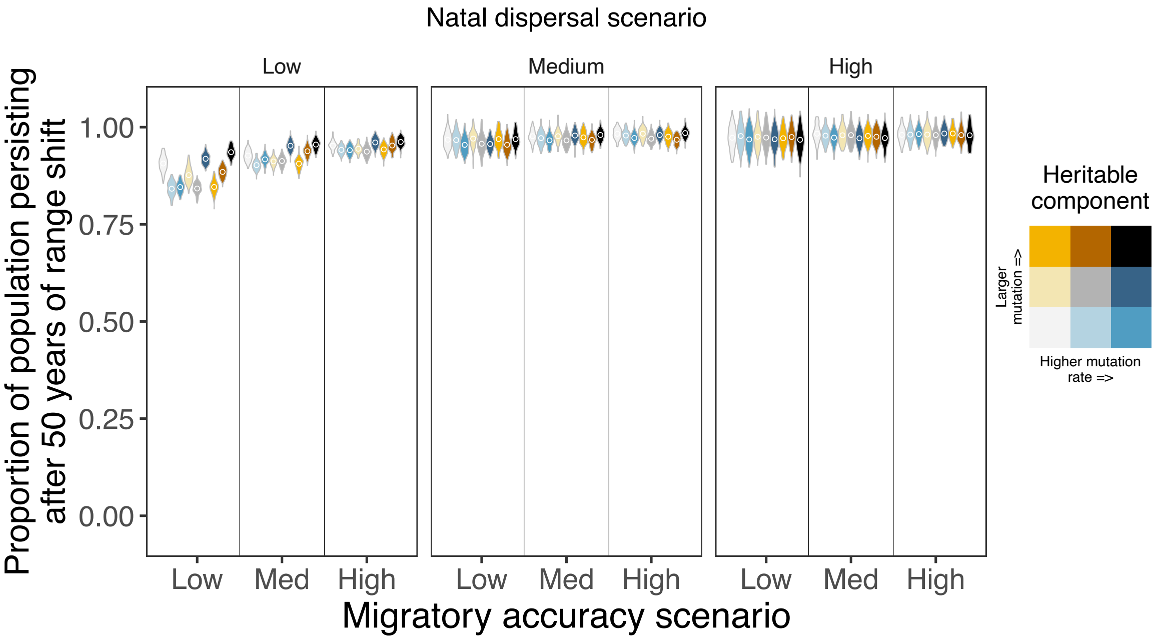


Figure 5. Population persistence under coupled range shift scenarios where breeding and non-breeding habitable zones shift northwards at the same rate. Violin plots represent density distributions of replicate model runs for scenarios that vary in four drivers of dispersal (reproductive dispersal, migratory accuracy, migratory programme mutation rate and mutation size). White outlined points indicate mean values for a given scenario.

Do Migratory Connectivity metrics predict range shift rates?

The strength of migratory connectivity, as measured in the population at equilibrium prior to environmental perturbation, proved to be a poor predictor of subsequent population persistence. Our simulations show that it is theoretically possible to achieve almost any outcome, from full population maintenance to population extinction, from starting populations with similar strengths of observed migratory connectivity (Fig. 6).

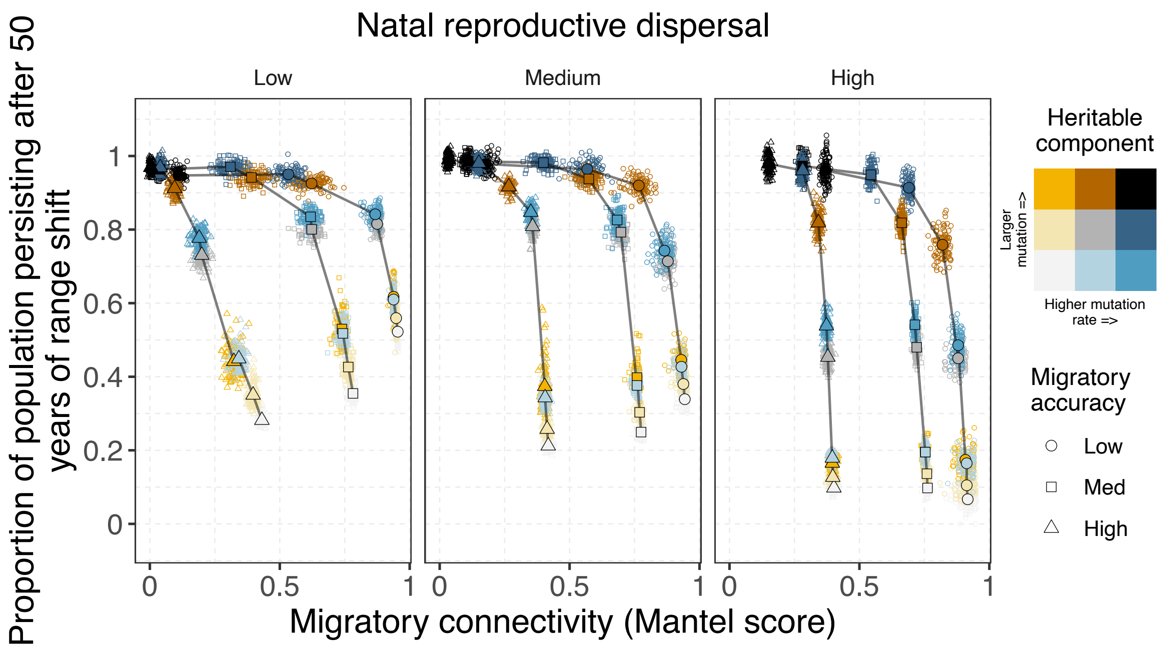


Figure 6. Relationship between realised migratory connectivity and the persistence of populations under uncoupled shifts in seasonal habitat zones. Connectivity is measured as the Mantel correlation at the end of a 500-year burn-in period, prior to range shift exposure. Points represent model runs for a given combination of the four drivers of dispersal (reproductive dispersal, migratory accuracy, migratory programme mutation and size). Black outlined points indicate mean values for a given scenario.

Migratory connectivity metrics fail to predict population responses to shifting environmental niches because both heritable and non-heritable components of non-reproductive dispersal combine to generate the observable connectivity pattern. As such, the same degree of spatial population disaggregation between seasonal ranges, and hence connectivity, can emerge from very different mechanisms. Where shifts in seasonal habitable zones are uncoupled, a population with weak migratory connectivity (and hence high rates of observable non-reproductive dispersal) may be unable to colonise new seasonal ranges if that connectivity is primarily driven by low migratory accuracy. In coupled shifts, where variation in responses was modest, connectivity metrics again showed little correlation with rates of population persistence (see Supporting information).

Discussion

Understanding the mechanisms that underpin spatial range dynamics in migratory species is vital in order to predict future responses to environmental change (Johnston et al. 2019). Whilst populations can adapt in situ to changing climates through phenological change (Socolar et al. 2017, Chmura et al. 2019) or niche expansion (Sjödin et al. 2018, Sun et al. 2014), range shifting has been vital to many species' responses (Hällfors et al. 2021, Singer 2017, Visser & Both 2005). Non- reproductive dispersal is critically important in determining range shifts in the non-breeding phase of the annual cycle, but has previously lacked a unifying theoretical framework. Our models demonstrate how the capacity for spatial change depends on the underlying processes by which dispersal between non-breeding locations occurs, and in particular the extent to which the processes generate heritable outcomes. Non-reproductive dispersal differs from reproductive dispersal in fundamental ways, and the complex balance between heritable and non-heritable drivers also means quantitative metrics like dispersal distance distributions or migratory connectivity may generate misleading inferences about species' propensity to adapt to environmental change.

If climate change causes coupled shifts in the seasonally habitable zones of migratory species, their inter-range distances will remain broadly constant over time. Therefore populations can track both seasonal ranges by maintaining an existing migratory programme (i.e. distance and direction), provided that reproductive dispersal is sufficient to colonise new breeding areas. In these circumstances, heritable non-reproductive dispersal is not a requirement to facilitate range shifts but may act as a buffer against population declines where reproductive dispersal is limiting. It is unclear how common seasonally-coupled shifts are in reality, though some lines of evidence suggest that uncoupled shifts may be more frequent (Curley et al. 2020, Howard et al. 2018, Zurell et al. 2018a). Our models suggest that species experiencing uncoupled shifts (i.e. seasonally habitable zones shifting at different speeds or in different directions) may only be able to track such shifts via heritable adaptations to their migratory programmes (either genetic or cultural).

Gradual latitudinal range shifts of the kind simulated here are widely recorded in nature (Hitch & Leberg 2007, La Sorte & Thompson 2007, Zuckerberg et al. 2009), but more complex multidirectional range shifts comprising of both latitudinal and longitudinal shift are also commonplace (Curley et al. 2020, Fei et al. 2017, Huang et al. 2017, Potvin et al. 2016) as well as rapid changes in migratory patterns (Dufour et al. 2021, Sutherland 1998). In North American birds, recent evidence suggests that non-breeding ranges have shifted closer to breeding ranges in many species (Curley et al. 2020), implying changes in the distance between seasonally habitable zones, but limited change in migratory direction. This form of adaptation could arise through short-stopping at traditional stop-over sites on a pre-existing migratory route, potentially through plastic responses to behavioural cues (Elmberg et al. 2014, Sutherland 1998, Teitelbaum et al. 2016). Migratory distance is at least partially genetically determined in some birds (Gu et al. 2021), suggesting that short-stopping may also involve heritable changes in the magnitude of migratory movements. For species whose seasonal climate zones are shifting longitudinally as well as latitudinally, or shifting further apart rather than closer together, more complex heritable changes in both the direction and distance of movement may be necessary. This may be particularly acute among trans-equatorial migrants, where season-specific range shifts towards higher latitudes would invariably lead to increasing migratory distances (Howard et al. 2018).

Heritable changes in the direction and distance of migratory programmes may be facilitated through mutations in navigator gene complexes, or alternatively through cultural change and inheritance (Gill et al. 2019). Culturally-inherited systems may differ dramatically in range shift propensity compared to the genetic inheritance system we modelled, but they are likely to similarly exhibit both heritable and non-heritable elements of non-reproductive dispersal. In systems with strong cultural inheritance, the migratory accuracy of adults could play an outsized role in determining rates of inter-generational change, as adult migratory plasticity may facilitate rapid colonisation of new sites (Teitelbaum et al. 2016). However, tracking studies suggest spatial migratory plasticity in adults is generally quite low, at least within birds (Gill et al. 2019). Species with strong cultural inheritance of migratory programmes may however incur Allee effects if population densities fall below critical sizes required for effective cultural transfer of migratory routes (Berdahl et al. 2016, Gil et al. 2018), leading to rapid declines in migratory accuracy and a breakdown in migratory connectivity.

Future challenges: Quantifying non-reproductive dispersal

Whether the mechanisms are cultural or genetic, an important barrier to improving our understanding of migratory range dynamics is the ability to quantify the magnitude of non-reproductive dispersal occurring in real populations (i.e. distances shown in Fig. 1 b), and in particular the extent to which the outcomes of this dispersal would be heritable. Better quantification of dispersal may be achieved through multi-generation tracking of migration across cohorts, allowing direct comparison of destinations between parents, offspring and siblings. If variance in migratory programmes is significantly lower between close relatives within a local population, we might infer a significant role of heritable drivers (genetic or cultural) in generating non-reproductive dispersal, relative to non-heritable drivers (low migratory accuracy). However, this may be complicated by spatio-temporal autocorrelation (e.g. individuals from the same region following similar migratory programmes due to physical barriers) and the practical limitations of being able to undertake tracking studies on the scale required (e.g. tagging costs and retrieval).

Measurements of migratory connectivity can provide an accurate proxy measurement of the amount of non-breeding dispersal within a population, although these do not allow partitioning of heritable and non-heritable components and are thus unlikely to meaningfully inform assessments of migratory range shift potential. Population-scale connectivity metrics instead capture the emergent outcome of spatial fluxes arising through the combined effects of reproductive and non-reproductive dispersal. Previous studies have assumed that weak connectivity implies substantial genetic variation in migratory programmes, with the potential to buffer against environmental change (Webster et al. 2001). Whilst this may be true for scenarios of habitat loss (Dolman & Sutherland 1994, Taylor & Norris 2010, Taylor & Stutchbury 2016, Taylor 2019), our models suggest this is unlikely to be the case with respect to shifting environmental niches. Moreover, high standing genetic variation in migratory programmes alone may be insufficient to promote colonisation of new breeding and non-breeding areas, if environmental niche shifts are spatiotemporally uncoupled. Such shifts may require the emergence of novel heritable migratory programmes rather than short-term selection on standing migratory variation, especially if seasonal habitable zones are shifting further apart. In the context of current rates of change, it is unclear whether climate velocities are outpacing rates of evolutionary change in migratory behaviour. However, some evidence suggests that migratory species are failing to keep pace (Bay et al. 2018), highlighting the pressing need to develop tools to measure the extent to which observed migratory changes occur through heritable mechanisms.

Quantifying dispersal distances has traditionally been achieved through tracking of individuals, either through mark-capture-recapture (Smith et al. 2004), remote tracking technologies (Stillman et al. 2021), or through molecular genetic parentage analysis (Woltmann et al. 2012). Accurately quantifying reproductive dispersal distances can be notoriously difficult (Studds et al. 2008), however, and quantifying non-reproductive dispersal distances brings additional challenges. For example, non-breeding home ranges are often larger and less clearly-defined relative to breeding home ranges (Tseng et al. 2017, Zurell et al. 2018b), although discrete non-breeding home ranges are still commonplace in migrants (Priotto et al. 2002, Williams et al. 2015, Zurell et al. 2018). Centroid distances between seasonal home ranges could thus be used to directly measure non-reproductive dispersal distances (Sweanor & Sandegren 1989), perhaps in combination with genetic parentage analysis. Nevertheless, measurements of non-reproductive dispersal must decompose patterns emerging from heritable and non-heritable drivers in order to be genuinely informative about population change.

Migratory life cycles also add considerable complexity to the measurement of reproductive dispersal. Because reproductive dispersive movements can occur pre- or post-migration, the migratory journey itself has the potential to facilitate both natal and breeding dispersive movements - for example, an individual that fails to orientate back to its natal location (or previous breeding location) may breed in a new area and thus perform a reproductive dispersal movement. Conditions experienced on the non-breeding grounds may also influence the distance and direction of natal dispersal (Studds et al. 2008), or have additional carry-over effects on subsequent reproductive success that may impact population dynamics (Sedinger et al. 2011). This additional source of variation in dispersive movements is likely to be important in determining range shift rates in both seasons. Further model development exploring these additional sources of dispersal, and testing of alternative dispersal kernel distributions, may lead to improved insights into migratory range dynamics.

Conclusion

Non-reproductive dispersal has not been previously recognised as an important process in ecology, despite playing a key role in the range dynamics of migratory species. Whilst reproductive dispersal sensu stricto is supported by a comprehensive theoretical literature, the existing framework does not capture the distinct set of dispersal processes that operate around non-breeding ranges. As non-reproductive dispersal movements generate both heritable and non-heritable outcomes, teasing apart the mechanisms of dispersal will be essential to improve our understanding of the plasticity of migratory systems. Whilst dramatic changes in migratory ranges are known to have occurred in many species (Ruegg & Smith 2002, Sutherland 1998), we currently lack a robust capacity to predict future changes or identify the constraints to change that leave some species imperilled. Improving our understanding of non-reproductive dispersal will be challenging but is likely to generate major advances in our understanding of migratory populations.

Supplementary Material

Full supplementary material including R code can be found by visiting the following address:
https://shvickers94.github.io/NRD_supplement/Supplementary_material.html

SM1: Supplementary Methods

Creation of starting population

Distinct breeding and non-breeding ranges were defined within co-ordinate ranges of 0 and 1 on the longitudinal axis and 0.66–1 and 0–0.33 for the latitudinal axis (breeding and non-breeding respectively).
[R code]

Non-reproductive dispersal

Within the breeding range 10,000 individuals were placed with a uniform distribution and a sex ratio of 50/50.

[R code]

Each individual was then given a southerly movement equal to the distance between breeding and non-breeding range centroids so to replicate the breeding population distribution on the non-breeding zone. This population was then used as the starting population of all burn-in replicates and has a ‘perfect’ connectivity score (Mantel correlation) of 1.0 as there is zero population mixing.

[R code]

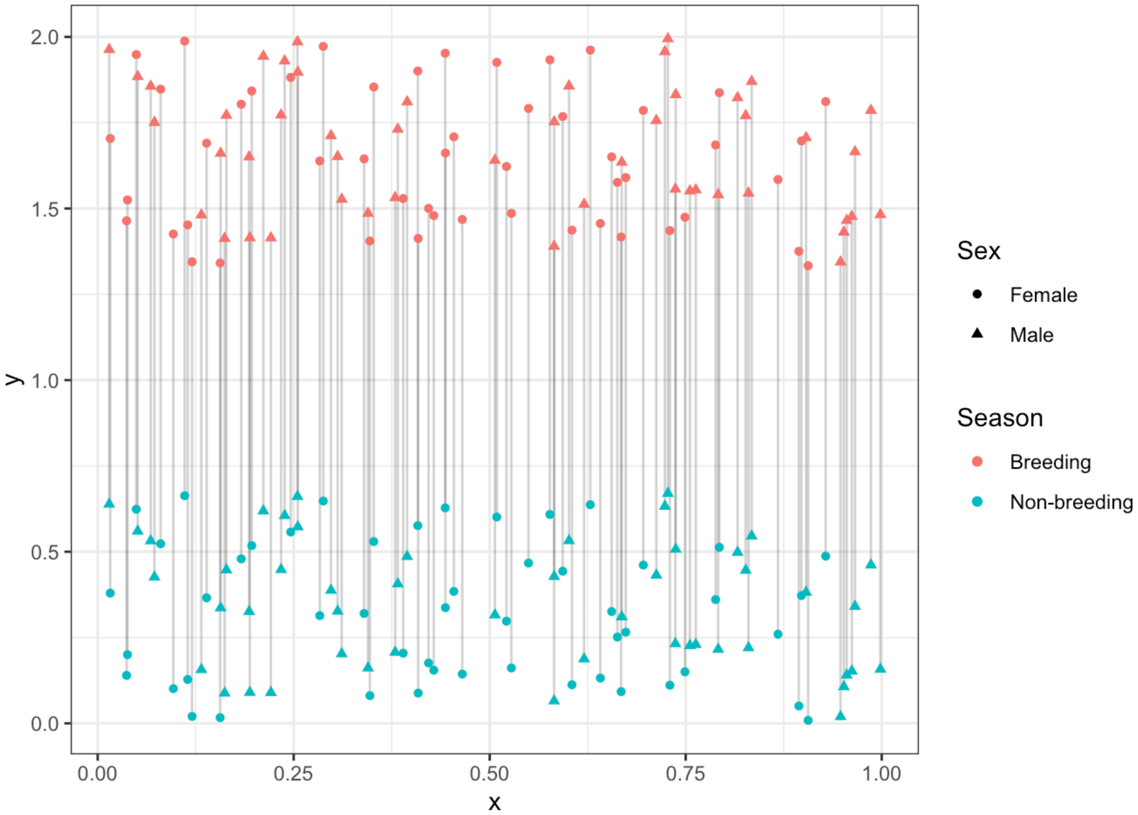


Figure SM1a. Example starting population for a subsample of 100 individuals (usually 10,000). An individual’s breeding and non-breeding location is linked by a line.

The 500-year burn-in

Within the burn-in phase there are nine customisable parameters, five of which were fixed in our simulations and four that were varied across three distinct levels:

- Simulation length (in years) – fixed at 500.
- Individuals sampled (for Mantel correlation) – fixed at 100.
- Carrying capacity – fixed at 10,000 (initial population size).
- Density dependent breeding – fixed equation, see below.
- Density dependent survival in the non-breeding ground – fixed at 25 surviving individuals per grid cell (20x20 grid, 10,000 individuals total carrying capacity).
- Mutation rate (for gene encoding migratory distance & direction, where rate is the proportion of population that mutates each generation) – 0.01, 0.1, and 0.5.
- Mutation size (modifier for rgamma distance kernel that modifies inherited distance & direction) – 0.5, 1.5, and 3.
- Natal dispersal (shape parameter for rgamma distance kernel) – 0.5, 1.5, and 3.
- Migratory accuracy (ability to follow inherited migratory programme, controlled through shape parameter for rgamma distance kernel) – 0.5, 1.5, and 3.

Non-reproductive dispersal

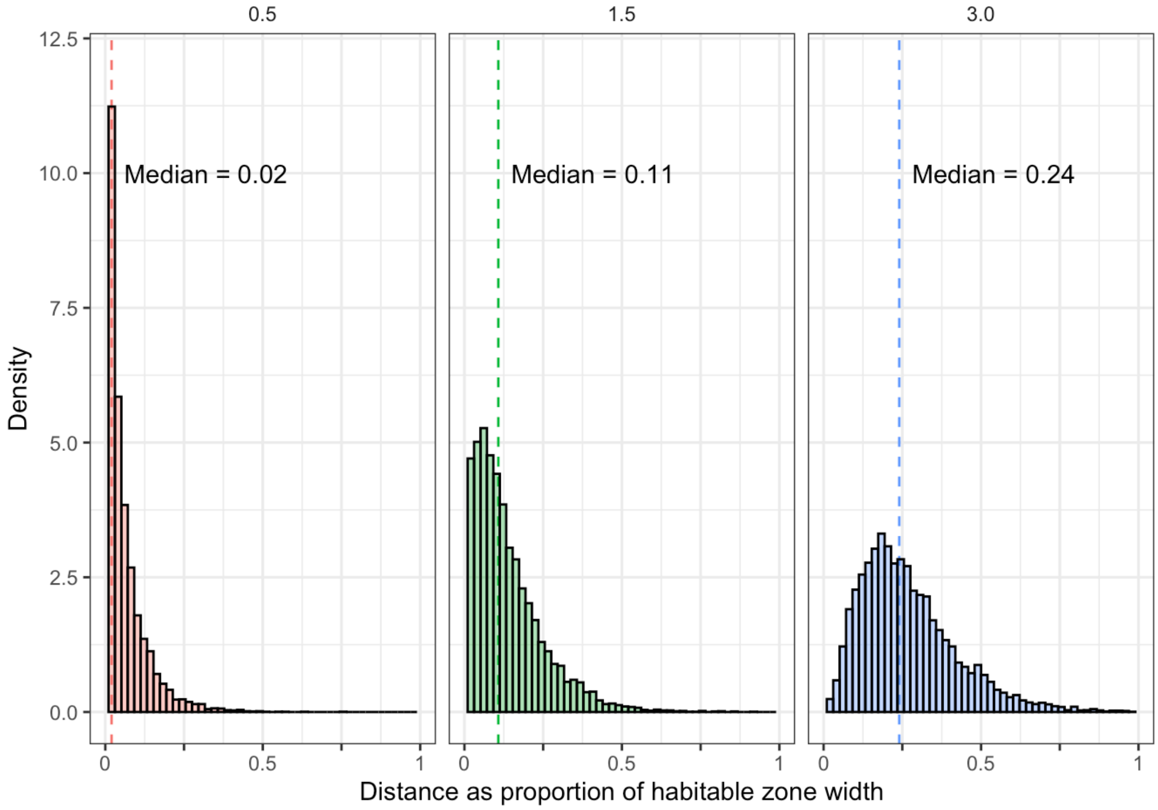


Figure SM1b. Density histograms of dispersal distances (as a proportion of the habitable zone width) produced through the function rgamma() with a sample size of 10,000, rate parameter of 0.0001, and shape parameters of either 0.5, 1.5, or 3.0 referred to as 'Low', 'Medium', and 'High' dispersal scenarios respectively in the manuscript. Distance of natal reproductive and natal non-reproductive dispersal for an individual was drawn from such distributions by random sampling. For natal reproductive dispersal, realised distances were drawn directly from a single kernel. For natal non-reproductive dispersal, realised dispersal distances were a product of sampling a kernel once for migratory accuracy related dispersal and sampling a (potentially different) kernel again if a mutation in the inherited migratory programme occurs.

Density dependent breeding

A 20x20 cell grid is drawn over the breeding range and a count of individuals within each grid cell is taken. Within each cell a breeding modifier is calculated as the cell carrying capacity (carrying capacity of the breeding range divided by the number of grid cells) divided by the abundance of individuals within the cell. The value is then capped at 5, such that each female within the population is limited to 10 offspring per generation. Each female within the grid cell is then matched with a random male in that grid cell, each female will pair once per year, but males may pair with multiple females. Number of offspring is then calculated as 'breeding modifier*2', if this value is less than 2 then the number of offspring will be fixed at either 1 or 2 based upon 'if(sample(seq(100,200),1) < round(brd_mod*2, 2)*100){offspring=2}else{offspring=1}'.

Each female thus always has at least 1 offspring if there is a male to pair with within the grid cell. This process is repeated for each female within each of the 400 grid cells. Worked example: with a carrying capacity of 10,000 individuals, each grid cell (400 in total) has a carrying capacity of 25. If a grid cell has 28 individuals, the breeding modifier will be 25/28=0.89 for a 'breeding modifier*2' of 1.78. As 'breeding modifier*2' is less than 2, probability-based selection of offspring number between 1 and 2 is enacted with a 78% chance of 2 offspring being selected.

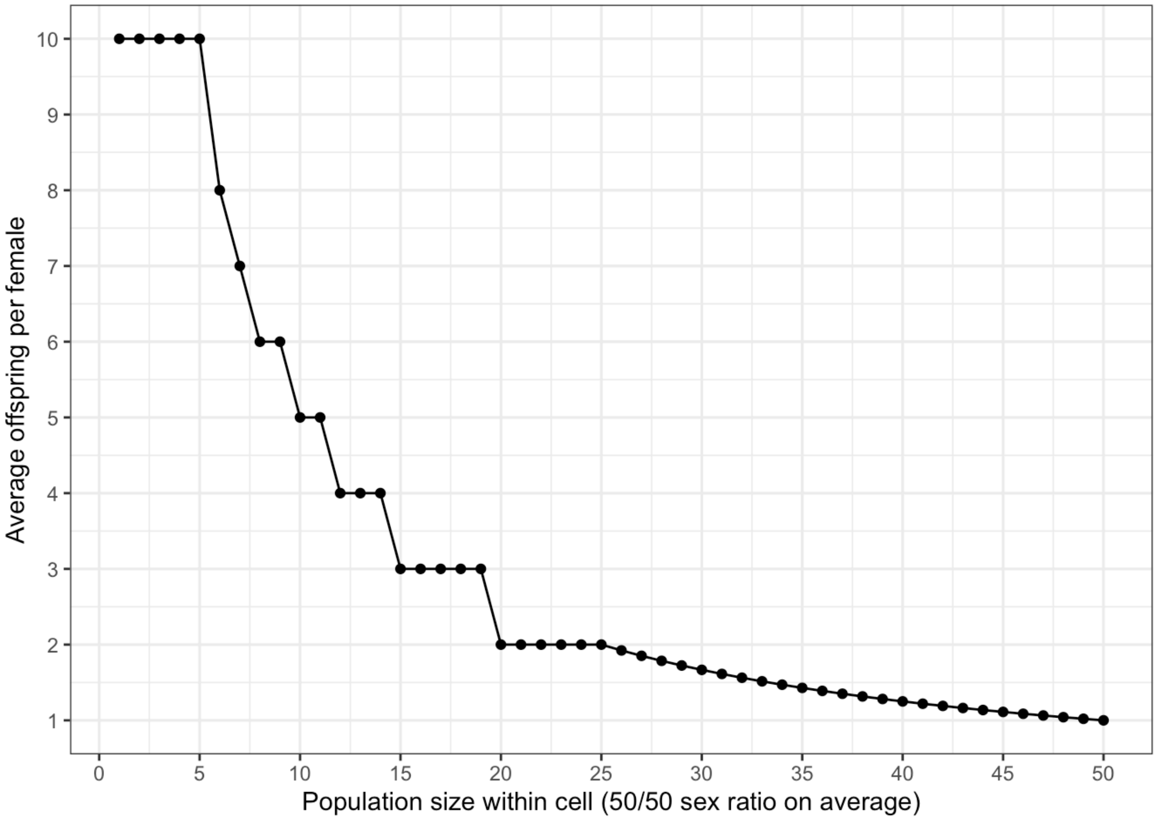


Figure SM1c. How the number of offspring produced per female differs based upon population size within a grid cell.

Non-reproductive dispersal

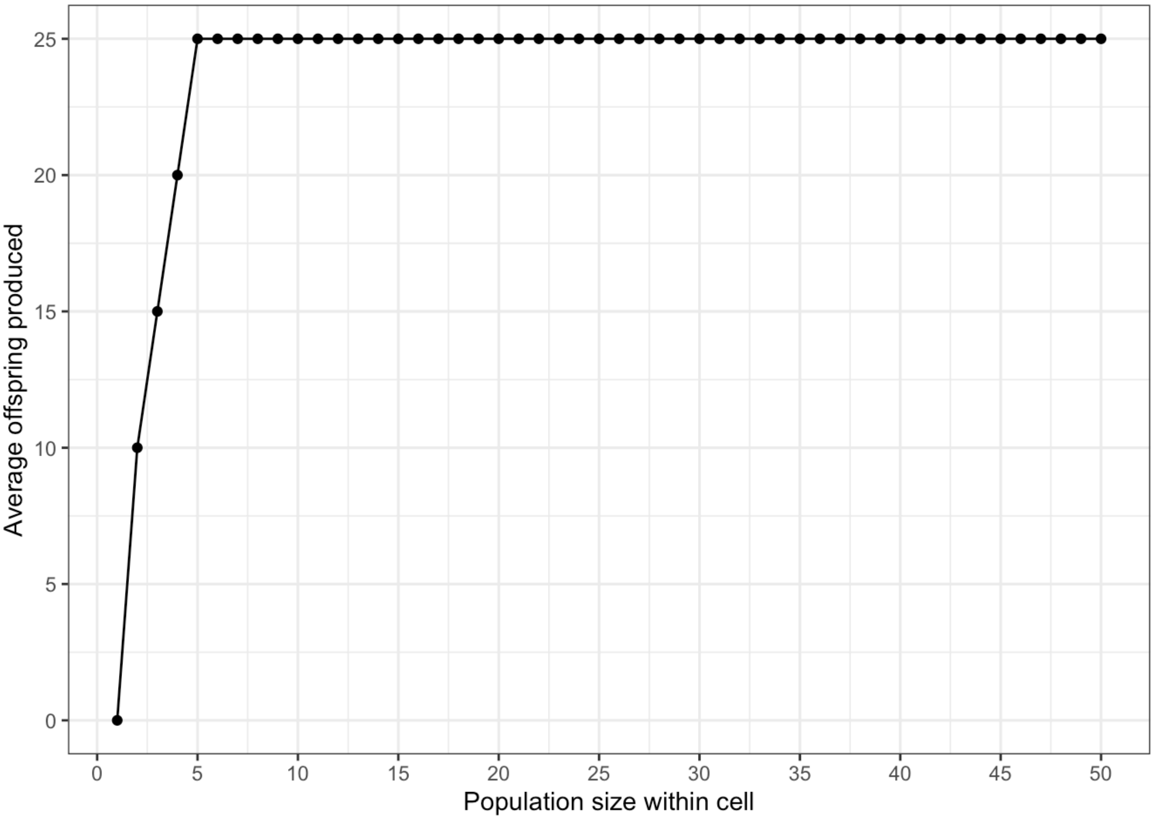


Figure SM1d. How population size within a cell relates to the number of offspring produced.

Natal dispersal

For each female that produces offspring, the offspring will have a starting location half-way between the mother and fathers breeding location. From this location the offspring then undertakes natal dispersal. The direction of this dispersal movement is chosen at random, and the distance is drawn at random from a Gamma distribution with n of 10,000, a rate parameter of 0.0001, and a shape parameter that is varied to produce varying mean breeding dispersal movement distances. This new location is then the breeding locations for these offspring, such that this can be thought of as a pre-migratory dispersal to find the future breeding ground. Any individuals that disperse outside of the breeding range are then removed from the population.

Inherited distance & direction of migration

Each offspring is given an inherited migratory distance and direction. This is achieved by taking the mean latitudinal and longitudinal distances between each of the parents breeding and non-breeding locations, to give a genetically encoded non-breeding destination that is half-way between the two parents non-breeding locations. For each individual, there is a 1 in 1/mutation rate chance of the genetically inherited programme mutating (e.g., for a mutation rate of 0.01 this is a 1 in 100 chance). When a mutation occurs the inherited non-breeding location is shifted a random direction with a distance drawn from Gamma distribution with n of 10,000, a rate parameter of 0.0001, and a shape parameter that is varied to produce varying mean mutation ‘sizes’. The result is a new genetic non-breeding destination where the distance and direction have both been altered.

Non-heritable non-breeding dispersal

For each individual, additional non-breeding dispersal is incurred due to non-heritable factors such as a species-level ability to follow the inherited distance and direction, and environmental factors such as wind drift. To emulate this, each individual is shifted in a random direction from its genetically encoded non-breeding destination with a distance drawn from a Gamma distribution with n of 10,000, a rate parameter of 0.0001, and a shape parameter that is varied to produce varying mean non-inheritable non-breeding dispersal distances. This is then the final non-breeding location for that individual. Any individual that is outside of the non-breeding zone is removed from the population.

Repeat

This process is looped on a yearly iteration for a total of 500 iterations (years). All breeding adults are removed at the end of each iteration and offspring breed in their second year. Measured migratory connectivity is therefore for the previous years’ offspring.

Measuring connectivity

At the start of each yearly iteration 100 individuals are sampled at random from the breeding range and corresponding individuals non-breeding locations are also taken. Pairwise distances are measured for both regions and the strength of migratory connectivity is measured using the function mantel.rtest(). As such the measured connectivity is for the previous year and for the first iteration of the burn-in phase this Mantel score will always be 1.

The process was repeated 100 times to produce 100 replicates. Each replicate was split into nine sections and run in parallel on the University of East Anglia High Performance Computing (HPC) cluster, which uses a SLURM job handler. The burn-in code shown below may therefore be prohibitively slow to run on a single system and the code chunk Sys.getenv('SLURM_ARRAY_TASK_ID') may not work on your system.

Full burn-in code

Full code used to implement the burn-in. To reduce computation time the following code was split into nine sub-sections based on combination of fixed value of variables g and s with each sub-section run concurrently. This had no effect on simulation results as these sub-sections are independent of one another.

[R code]

Burn-in results

The burn-in phase produced 8100 populations (100 replicates of the 81 unique combinations of variables measured) that rapidly reached long-term stable population size and Mantel scores around relatively small annual stochastic variation. Stochasticity is a result of the random sampling of the distance kernels as well as sample size related precision in Mantel scores when measuring migratory connectivity.

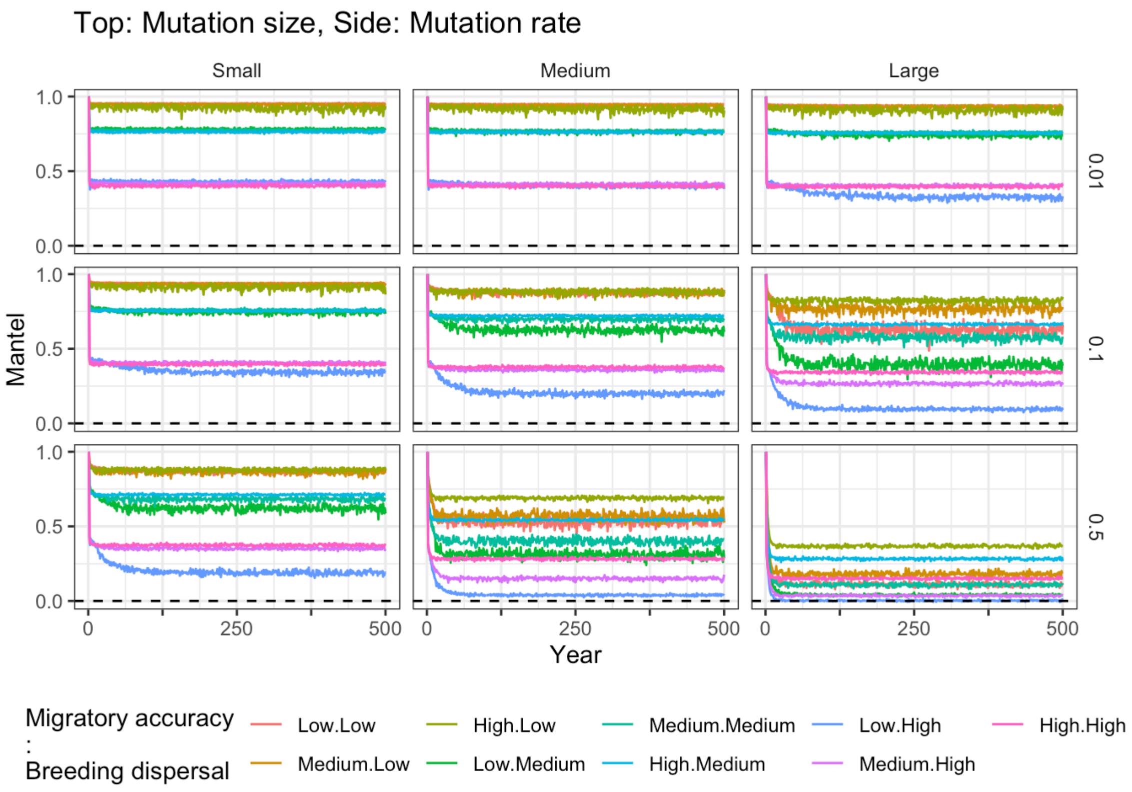


Figure SM1e. Mantel scores through the burn-in period. Lines are for averaged scores across the 100 replicates.

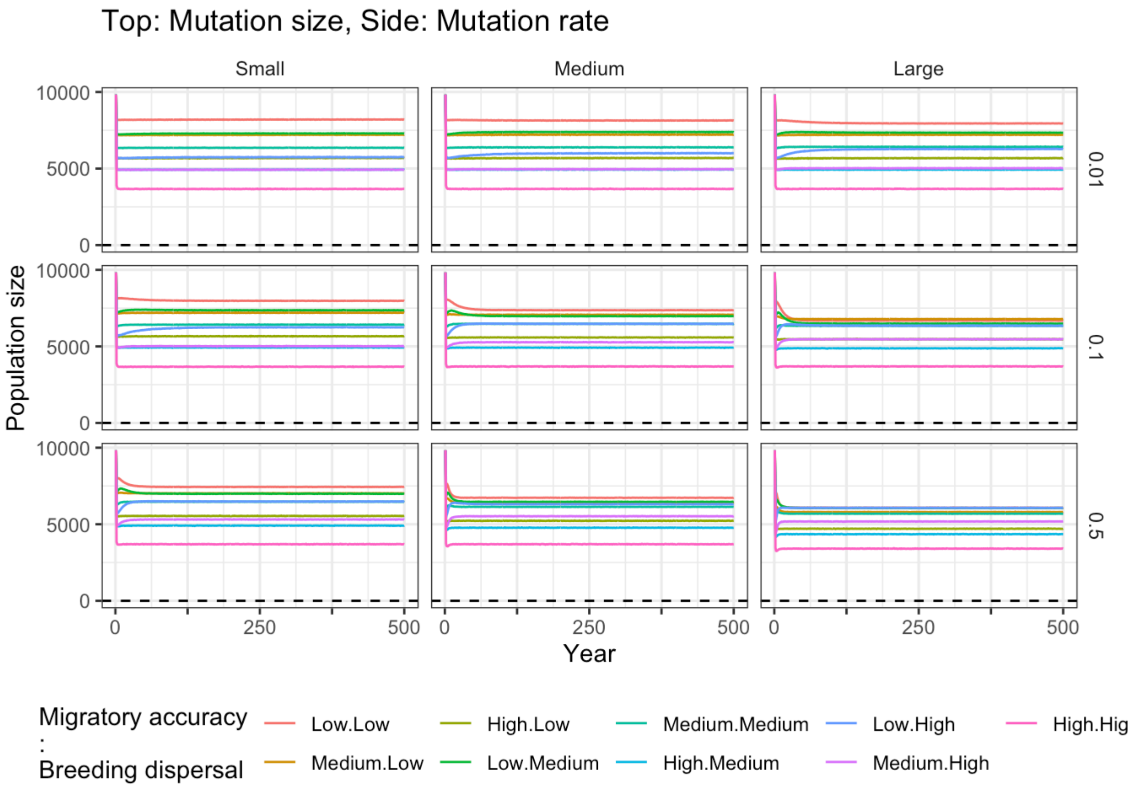


Figure SM1f. Population sizes through the burn-in period. Lines are for averaged scores across the 100 replicates.

Enacting range shift

After the 500-year burn-in period finishes, annual incremental range shifts are enacted for a 50-year period.Range shifts were undertaken with two distinct types – coupled and uncoupled.
Populations were taken from the end point of the burn-in phase, such that the first iteration of the range shift period is year 501. From here the iterative yearly process continues along the parameters and methodology set out in the burn-in phase, with the addition of shifting habitable zones.

Coupled

Both ranges shift in a northerly direction at the same rate. Rate of change was 0.02/year (coordinate units, ranges both have coordinate heights of 0.66).
Code
[R code]

Uncoupled

Both ranges shift in a northerly direction but at different rates. Rate of change for the breeding range was 0.02/year, and for the non-breeding range it was 0.01/year year (coordinate units, ranges both have coordinate heights of 0.66).
[R code]

Data handling

Burn-in

Annual measures of Mantel score and population size of the 8100 separate populations are collated. Average Mantel scores and population sizes are calculated across the final 50 years of the burn-in period for each population.
[R code]

Range shifts

Annual measures of Mantel score and population size of the 8100 separate populations are collated.
[R code]

Summarising results

Response is measured as the proportion of the population retained between the onset of range shift and its end 50 years later. Metrics of response are calculated for each of the 8100 populations, as well as averaging measures across the 100 replicates.
[R code]

Manuscript figures

Code snippets below detail the code used to create each of the manuscript figures utilising the datasets created through the previous sections. Final figures are not shown here.

Figure 1

[R code]

Bivariate legend

The bivariate legend is created separately and added to several figures below. Manuscript figures included within the manuscript received some post-production editing in Adobe Illustrator that did not alter the results shown. Therefore figures produced here are not exact replicates of manuscript figures.
[R code]

Figure 2

[R code]

Figure 3

To produce figure 3 dispersal distances need to be calculated for two of the 81 population scenarios. For the two populations scenarios (‘high natal dispersal, low mutation rate, small mutation size, and low migratory accuracy’ & ‘high natal dispersal, high mutation rate, large mutation size, high low migratory accuracy’) the following snippet of code was added to the burn-in code detailed above.
[R code]

Non-reproductive dispersal

Figure 4

[R code]

Figure 5

[R code]

Figure 6

[R code]

SM2: Figure SM2

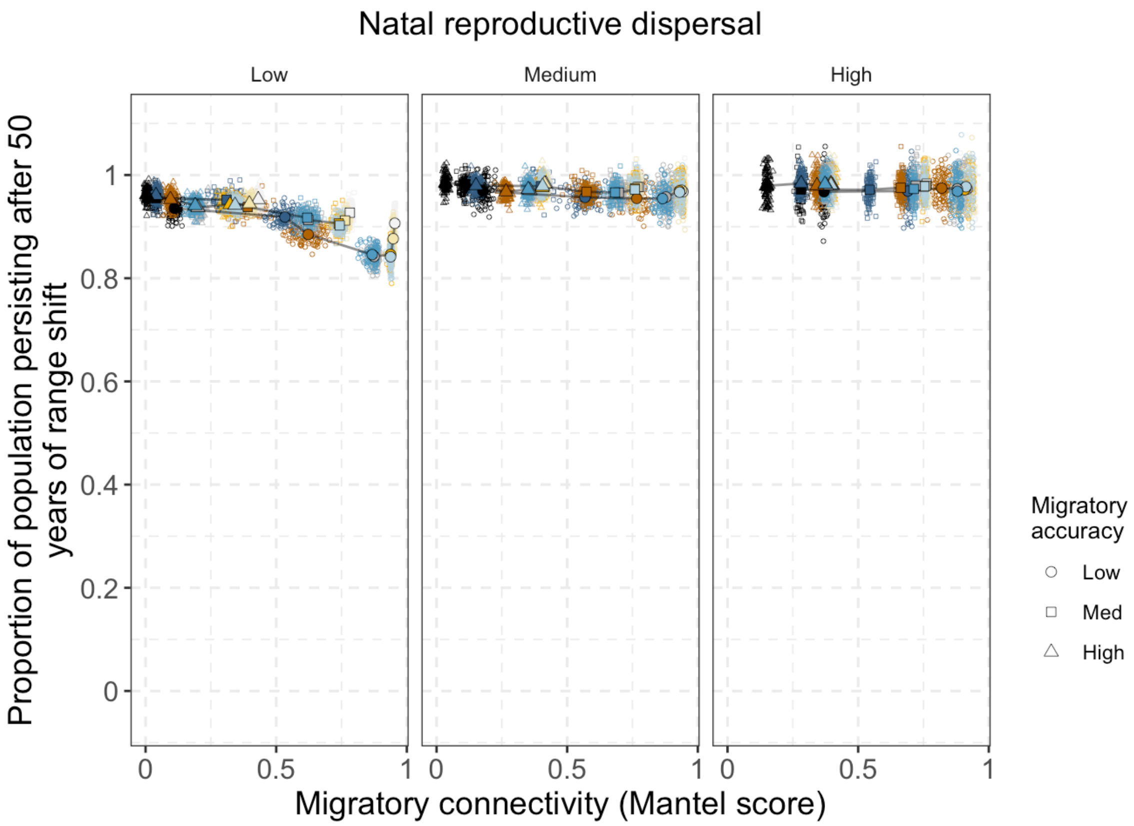


Figure SM2. Relationship between realised migratory connectivity and the persistence of populations under coupled shifts in seasonal habitat zones. Connectivity is measured as the Mantel correlation at the end of a 500-year burn-in period, prior to range shift exposure. Points represent model runs for a given combination of the four drivers of dispersal (reproductive dispersal, migratory accuracy, migratory program mutation and size). Black outlined points indicate mean values for a given scenario.

4

Migratory flocking behaviour and its role in facilitating range shifts

Vickers, S.H., Meehan, T.D., Michel, N.L., Franco, A.M.A., & Gilroy, J.J. (In prep). Migratory flocking behaviour and its role in facilitating range shifts.

Abstract

Rapid anthropogenic climate and land-use change are presenting species with unique challenges, with evidence suggesting that migratory species may be particularly negatively impacted. In response, many species are shifting their spatial distributions, but for migratory species that rely upon multiple distinct seasonal ranges this poses additional challenges. Tracking climate-driven shifts in habitable zones, for example, is likely to necessitate changes to migratory programmes if seasonal zones shift independently in space. Such changes may be limited by the mechanisms that allow novel migratory programs to be transferred to subsequent generations, which can be either genetic or social. Here we used 50 years of Breeding Bird Survey and Christmas Bird Count data to assess annual rates of change in both breeding and winter centres of abundance (COA) as an index of seasonal range-shift rates across 122 migratory bird species. We hypothesised that range-shift rates would be higher among species that migrate in flocks, reflecting the capacity for rapid cultural transmission of novel migration routes between generations, relative to species that migrate solitarily and therefore rely on changes in genetically-determined navigation. We built a novel trait database encompassing behavioural, demographic, and biological traits from a range of sources, including a suite of migratory flocking characteristics. Across our sample, phylogenetic generalised least squares analysis demonstrated that migratory flocking behaviour was a significant positive predictor of non-breeding centre of abundance shifts, with species that migrate in mixed-age flocks shifting at the fastest rates, and solo migrants shifting slowest. Flocking behaviour was more important than any other predictor in explaining non-breeding range-shift rates, suggesting that a propensity for cultural inheritance of migratory programmes may play an important role in facilitating distributional responses to climate change in migratory species. Flocking behaviour was not a significant predictor of breeding range COA shift rates, however, which were better explained by absolute population trends and migration distance. Our results highlight the need to gain a greater understanding of migratory programme inheritance, and how this may interact with species responses to a changing world.

Keywords

Migration, centre of abundance, range shift, migratory behaviour, inheritance

Introduction

Birds are experiencing widespread and drastic declines worldwide, affecting an estimated 48% of extant species (Lees et al. 2022) amounting to population losses in the billions (Burn et al. 2021, Rosenberg et al. 2019). These declines are particularly apparent in migratory species (Rosenberg et al. 2019, Sanderson et al. 2006), whose exposure to anthropogenic threats may be exacerbated by their reliance upon multiple distinct spatial ranges throughout the annual cycle (Buchan et al. 2022, Horns & Şekercioğlu 2018).

Threats to species are multi-faceted (Bairlein 2016) but are increasingly permeated and exacerbated by climate change (Jetz et al. 2007, McLaughlin et al. 2002, Mantyka-Pringle et al. 2015). Whilst some species have demonstrated rapid adaptation to novel climates in-situ (Bradshaw & Holzapfel 2006, Crick et al. 1997, Holt 1990), many others are responding through distributional shifts (Chen et al. 2011, Freeman & Freeman 2014, Rushing et al. 2020, Thomas et al. 1999). The speed at which species colonise new areas may be a limiting factor in their response to climate change, particularly where populations are also exposed to other threats due to anthropogenic activity (Cang et al. 2016, Jezkova & Wiens 2016, however see Wiens et al. 2019). For migratory species, rapid distributional changes have been demonstrated in both the breeding and non-breeding ranges (Auer & King 2014, Curley et al. 2020, La Sorte & Thompson 2007, Rushing et al. 2020), and there is evidence that these shifts may be spatially independent of one another (Curley et al. 2020, Potvin et al. 2016). A prerequisite for such seasonally-independent shifts is the capacity for population-scale changes in the distance and direction of migratory movements (Fig. 1; Curley et al. 2020), and hence underlying migratory navigation programmes. Previous work has indicated conflicting evidence regarding the capacity for migratory species to change migratory programmes in order to colonise new regions (Böhning-Gaese et al. 1998, Henningsson & Alerstam 2005, Sutherland 1998, Thorup 2006). The wider capacity for such changes across taxa, and the mechanisms by which they can happen, remain poorly understood.

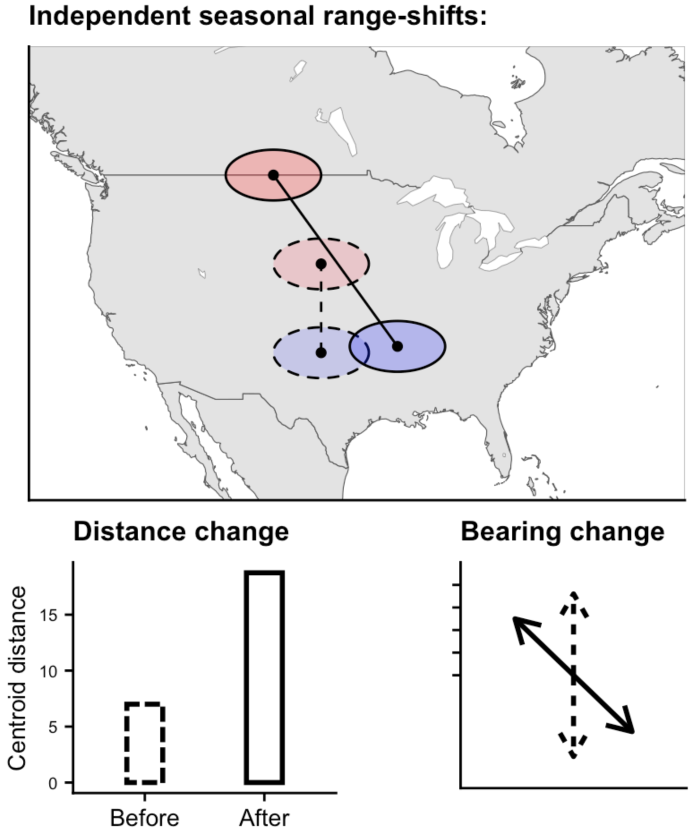


Figure 1. Theoretical example of independent shifts in seasonal distributions, whereby zones of climatic suitability for breeding and non-breeding ranges (red and blue respectively) shift at different rates and in different directions (dashed line ellipses denote ranges prior to shift, solid line ellipses after shifts). In order to track such shifts, populations would need to change the distance and direction of their migratory movements.

Simulation modelling has demonstrated a requirement for heritable changes in migratory programmes where season-independent range shifts occur (Chapter 3). The potential for these inter-generational changes in migratory programmes will depend in part on how organisms navigate between their seasonal ranges, particularly in early life. The mechanics of migratory navigation are complex and vary considerably between species (Åkesson et al. 2022, Mouritsen 2018), but there is strong evidence that heritable clock-and-compass navigation mechanisms are widespread across many taxa, whereby juveniles inherit a genetically-encoded program that determines migratory distance and direction in their first year (Berthold 2003, Liedvogel et al. 2011, Mouritsen 1998), or in some cases an inherited navigational map based on geomagnetic information (Thorup et al. 2020). This may be combined with varying levels of cultural learning, where juveniles follow experienced conspecifics on their initial migratory journey (Harrison et al. 2010). Species can thus be assumed to fall upon a gradient between obligate genetic and obligate cultural systems of migratory programme inheritance.

For species such as the Common Cuckoo *Cuculus canorus* that migrate alone as juveniles after adults have departed, and therefore lack any ability for cultural inheritance of migratory programmes (Vega et al. 2016), the transfer of novel migratory programmes (i.e. altered distance and direction) between generations could only occur through genetic mechanisms. The genetic basis for migratory programmes has only partially been elucidated (Bingman & Ewry 2020), but recent evidence suggests that the genes underpinning migration distance and orientation may differ between bird species (Delmore et al. 2020), and that heritable changes in these genes may arise relatively infrequently (with the possible exception of wholesale route reversal; Wynn et al. unpubl.). Conversely, species such as the Caspian tern *Hydroprogne caspia* that migrate in mixed-age parent-offspring flocks have the potential to transfer novel migration routes between generations directly through route-learning (Byholm et al. 2022, Teitelbaum et al. 2016).

Importantly, whilst ‘vagrant’ individuals frequently migrate to new areas as a result of misorientation or wind-drift, the novel routes pioneered by such individuals are unlikely to be inherited by their offspring unless the misorientation arose from a heritable genetic trait, in the absence of a cultural inheritance mechanism. For species that do have the capacity for cultural migratory inheritance, however, novel migration routes that arise from any stochastic pathway – including wind drift - still have the potential to be transferred to offspring via direct learning, if those species migrate in flocks (Teitelbaum et al. 2016). Population-wide shifts in migratory programmes may therefore be able to progress faster where cultural inheritance pathways are present.

We hypothesise that flocking behaviour during migration is a key determinant of the degree of genetic or cultural inheritance of migratory programmes, and that this behaviour in turn will strongly influence the speed at which populations can colonise new areas, and thus expand or shift their ranges. We further expect the link between flocking and range shift capability to vary across seasonal life-stages. In the breeding range, any successful dispersal movement can allow a novel site to be colonised by subsequent generations by default, as offspring are then born in the new location. Conversely in the non-breeding range, future use of newly-colonised sites by the offspring of colonists can only occur if they inherit (culturally or genetically) an appropriate migratory program to bring them to the new non-breeding site from their natal location. We predict that flock-migrating species – and in particular those species that migrate in mixed-age flocks – will show higher rates of population-scale change in non-breeding ranges than solitary migrants with wholly genetic migratory program inheritance. We test these predictions using long-term monitoring data for 122 North American bird species, controlling for phylogenetic autocorrelation and demographic traits likely to influence range-shift capacity.

Results

We assessed shifts in centre of abundance (COA) as an index of range shift rates across migratory North American birds. COA shifts were measured separately in the breeding season using Breeding Bird Survey data and in the non-breeding season using Christmas Bird Count data, both spanning a 50-year period (1970–2019). From an initial pool of 409 migratory species, we built a trait database encompassing migratory flocking behaviour, demographic traits, and biological traits. Complete trait data were available for 122 species (across 14 orders) where migratory flocking was defined as ‘solo’ or ‘flocking’, and a subset of 81 species (11 orders) where flocking species could be further refined to ‘age-separated’ or ‘mixed-age’ flocking (Figure 2).

Across the suite of demographic and biological traits tested for the full species sample, migratory flocking behaviour had the strongest effect on annual COA displacement in the non-breeding range (Figures 2 & 3), with annual COA displacement being significantly higher in flocking species than those that migrate solo (Coefficient = 1970.70 ± 510.60SE, p = 0.0002, SM Table 10, Figure 3A). Range-shift rates in the breeding range were best predicted by absolute population trends over the time period and migration distance, but were not significantly related to flocking behaviour (Figure 4).

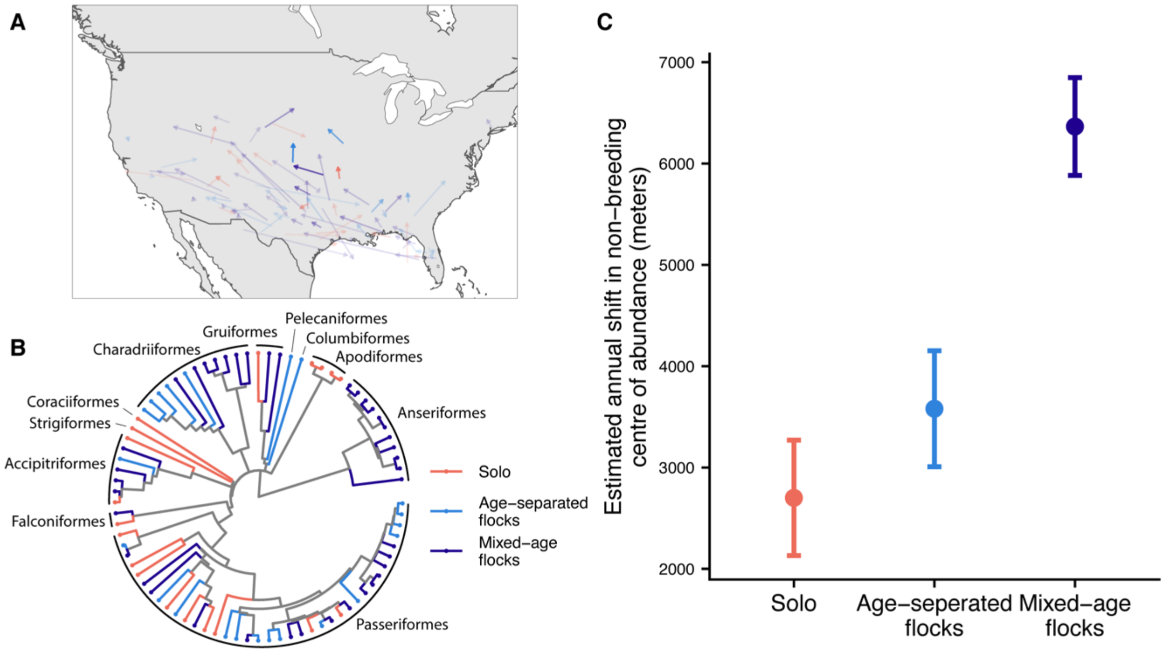


Figure 2. A. Approximate shifts in Christmas Bird Count centre of abundance 1970–2019 for 81 analysed species. Arrows are coloured by migratory flocking behaviour – age-separated flocks (red), mixed-age flocks (dark-blue) and solo (light blue) and transparency is set according to reciprocal error in estimated shift. **B.** Phylogenetic tree of the 81 species analysed for shifts in Christmas Bird Count annual centre of abundance and incorporated into the Phylogenetic Generalised Least Squares (PGLS) model. Nodes are coloured by migratory flocking behaviour – age-separated flocks (red), mixed-age flocks (dark-blue) and solo (light blue). **C.** Estimated marginal mean annual shifts in Christmas Bird Count centre of abundance 1970–2019 for migratory flocking behaviour based upon 81 species of North America migratory birds in a Phylogenetic Generalised Least Squares (PGLS) model incorporating uncertainty in shift rates and controlling for biological and demographic traits.

In our reduced pool of 81 species that could be characterised in terms of the extent of adult-juvenile mixing in flocks, we found that rates of non-breeding range shift were highest in species that migrate in mixed-age flocks (Coefficient = 3664.67 ± 508.76SE, p < 0.0001, SM Table 14, Figure 3B), and thus have potential for juveniles to learn migratory routes from experienced migrants. Range-shift rates in this sample were again lowest in species that migrate solo, though these did not differ significantly from species migrating in age-separated flocks (Coefficient = 879.34 ± 495.46SE, p = 0.08, SM Table 14, Figure 3B). This may reflect the relatively limited potential for cultural inheritance in age-separated flocks, where juveniles rarely interact with experienced individuals on migration, limiting capacity for inter-generational transfer of migration programmes. No further significant effects were found across the control variables of demographic and biological traits (SM Tables 10 and 14, Figure 3).

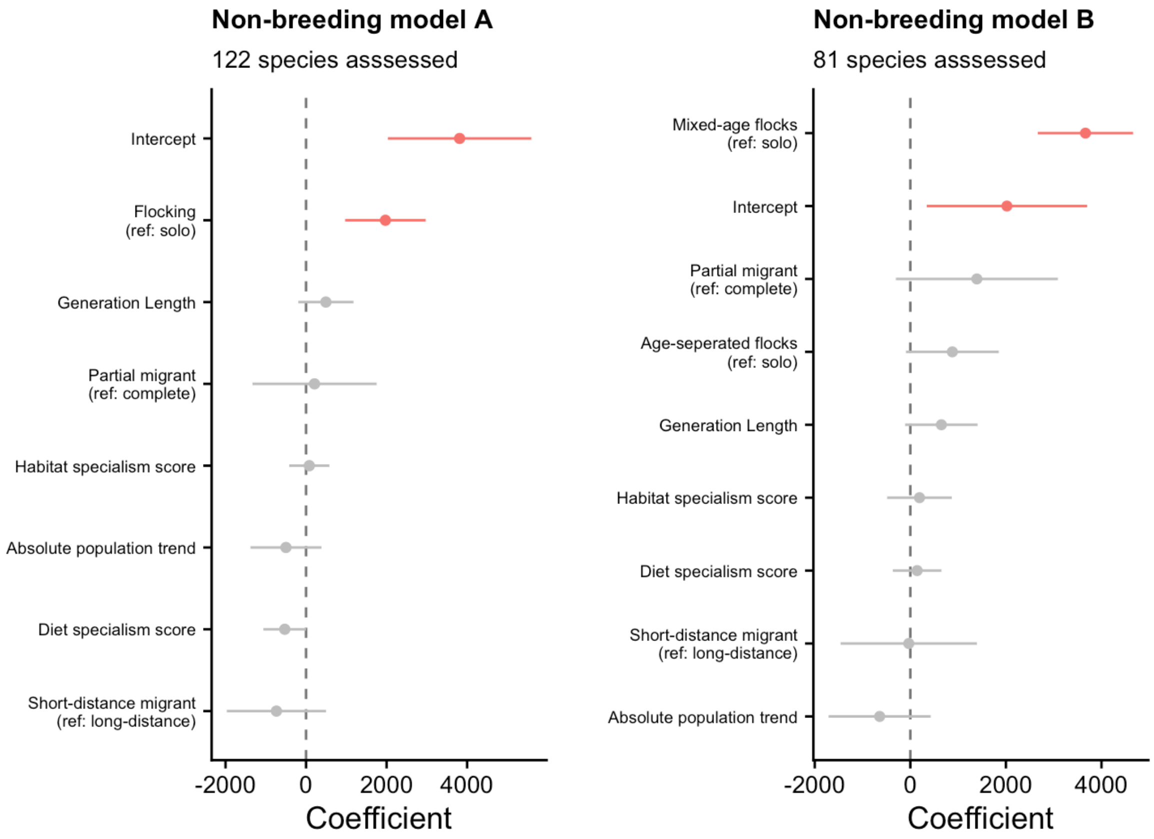


Figure 3. Phylogenetic Generalised Least Squares (PGLS) model coefficients for predictors of annual shift rates of Christmas Bird Count centre of abundance (in metres) 1970–2019. Model A assessed migratory flocking as a binary flocking vs. solo migrants for 122 species. Model B refined the assessment of migratory flocking differentiating between species that flock in age-separated and mixed-age flocks, for a reduced pool of 81 species. Red points indicate significant results inferred from credible 95th percentiles (error bars) that exclude zero.

Migratory flocking behaviour showed no significant relationship with annual displacement of breeding range COA in either of our models assessing breeding COA shifts in BBS data (SM Tables 2 and 6, Figure 4). Species experiencing faster rates of population change (absolute linear BBS trends) shifted their breeding COA at the fastest rates (Model A Coefficient = 1866.83 ± 457.16SE, Model A $p = 0.0001$, SM Table 2, Model B Coefficient = 2632.06

± 540.28SE, Model B $p < 0.0001$, SM Table 6, Figure 4). Short-distance migrants showed significantly lower breeding range shift rates than long-distance migrants within our wider species pool (Coefficient = -803.86 ± 392.22SE, $p = 0.04$, SM Table 2, Figure 4A), though this effect was non-significant in our reduced species pool (Coefficient = -224.26 ± 468.73SE, $p = 0.63$, SM Table 6, Figure 4B), indicating that this result was sensitive to the species analysed.

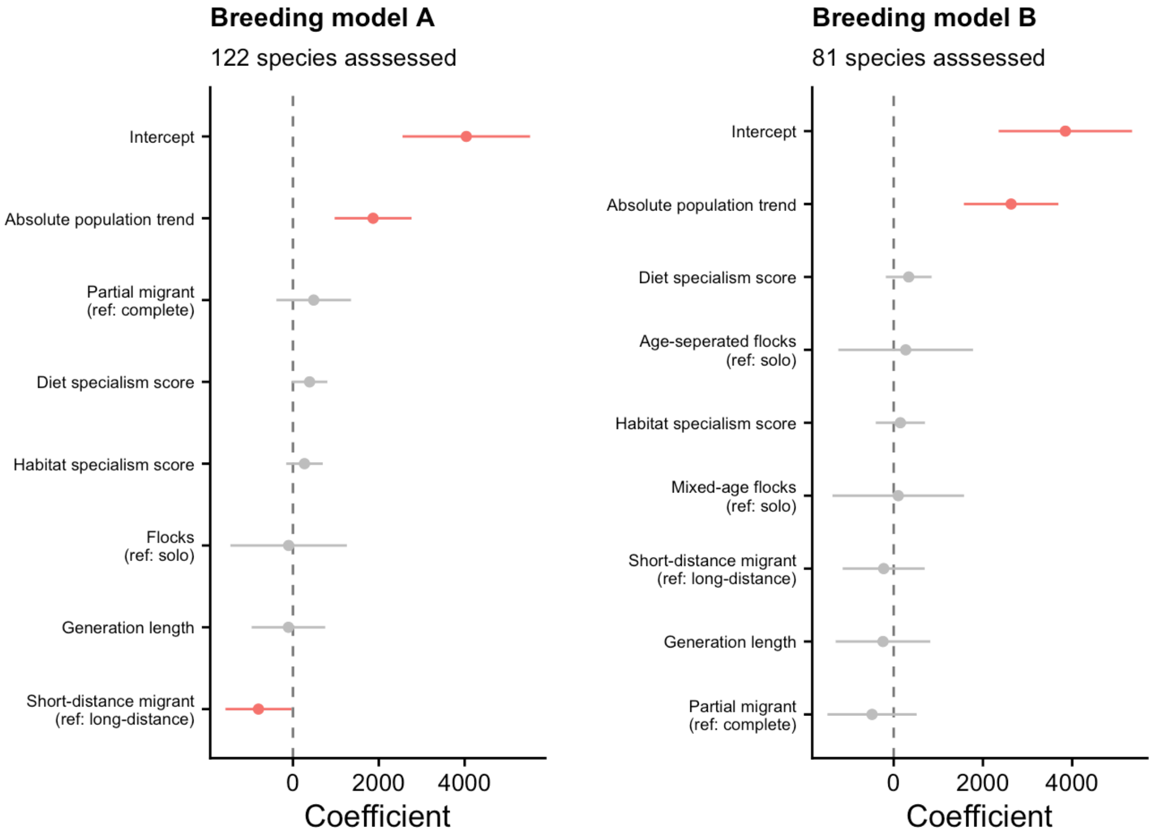


Figure 4. Phylogenetic Generalised Least Squares (PGLS) model coefficients for predictors of annual shift rate of Breeding Bird Survey centre of abundance (in metres) 1970–2019. Model A assessed migratory flocking as a binary flocking vs. solo migrants for 122 species. Model B refined the assessment of migratory flocking differentiating between species that flock in age-separated and mixed-age flocks, for a reduced pool of 81 species. Red points indicate significant results based upon credible 95th percentiles excluding zero (error bars).

Model results reported here are for our global model without model refinement in order to retain control variables, however results were broadly consistent across two model refinement processes (backwards stepwise deletion and information-theoretic model-averaging). All model results can be found in the supplemental materials (SM3).

Discussion

Across 50 years of Christmas Bird Count data, we found evidence for significant differences in centre of abundance (COA) shifts between migratory flocking behaviour classifications, with this being the strongest trait predictor of shift rates. A corresponding significant effect was however lacking for Breeding Bird Survey COA shifts, indicating processes driving observed range shift rates are likely to be season-dependent. These results support our hypothesis that migratory flocking behaviour may play an important role in facilitating migratory programme inheritance, and thus in determining rates of population-scale migratory change over time.

It is well understood that dispersal ability is a key limiting factor in a species ability to colonise new ranges (Brooker et al. 2007, Williams 2018), but previous work has largely failed to consider how these processes operate in the non-breeding ranges of migrant species (i.e. non-reproductive dispersal; Chapter 3). The movement mechanisms determining dispersal around non-breeding ranges are poorly understood, but likely include behavioural and stochastic phenomena such as itinerant sampling movements, misorientation and weather-drift during migration, and over-shooting or short-stopping along the historical migration axis (Sutherland 1998; Chapter 3). Significantly higher non-breeding COA shifts for species migrating in flocks, especially those that are mixed-age, does not necessarily suggest a greater propensity for dispersal movements in these species *per se* – rather, this result implies a greater capacity for the outcomes of dispersal to be transferred between generations. Indeed, we might expect levels of non-breeding dispersal, vagrancy and itinerant movement to be highest in solitary migrants that rely entirely on inherited compass mechanisms to navigate (Lees & Gilroy 2021). Our findings support the hypothesis that the probability of newly-colonised non-breeding sites being utilised by future generations will be lower in such species than those that migrate in flocks, particularly where younger and older individuals intermix.

Our understanding of the mechanics of inter-generational change in migratory programmes remains limited, despite improved understanding of the genetic basis for migratory traits (Delmore et al. 2020, Pulido 2007). In particular, it remains difficult to accurately estimate how rapidly the gene complexes underpinning migratory navigation may mutate, and the extent of heritability in novel phenotypes. Our results strengthen the increasing evidence for the importance of cultural inheritance pathways for migratory programmes (Byholm et al. 2022), particularly in the context of rapid changes in the mechanisms by which species may colonise new non-breeding ranges. Vagrancy events and rapid adoption of novel migratory routes have been linked to genetic mutations (Berthold et al. 1992, Thorup et al. 2012), but such events appear to be rare, and involve relatively distinct step changes (e.g. route reversal; Delmore et al. 2020) rather than gradual changes required for populations to track shifting climate niches.

Despite significant advances in species monitoring technology, including increasingly widespread use of remote-tracking (Tibbetts 2017) and other technologies such as radar (Nilsson et al. 2018), we still lack a clear understanding of the nature of migratory flocking behaviour for many species. The relative paucity of data for this behavioural trait can be partially attributed to the prevalence of nocturnal migration, making it difficult to ascertain group size and age cohort timing. Some species may also experience ‘fall’ events (Birds of the World 2022) whereby outsized collections of individuals may gather during migration staging, however it may not be the case that this represents true migratory flocking if those flocks then disperse into solo migratory journeys. Thus, maximum migratory flock size may not always be the best approximation of flocking behaviour. Age cohort timing is also difficult to estimate for many species, due to varying degrees of overlap between cohorts. This may explain the slightly higher rates of COA shifts we observed in age-separated flocking species compared to solo migrants. Whilst species that migrate in what we define as age-separated flocks may be assumed to have no avenue for cultural inheritance of migration from experienced individuals, this may not always be the case. Our quantification for both elements of migratory flocking behaviour (flock size and age-cohort timing) aimed to limit potential biases, but future studies are needed to better quantify the prevalence and mechanisms of cultural learning during migration across taxa.

Quantification of range shifts can also be difficult to achieve in practice, particularly for species with stochastic or patchy distributions (Loehle 2020). Centres of abundance alleviate some of these issues by focussing on the overall mass of a population. Previous work has demonstrated clear trends in COA shifts for many North-American species (Huang et al. 2017), including latitudinal COA shifts associated with increases in non-breeding range climate (Niven et al. 2010). However, COA shift metrics can arise from multiple mechanisms, including regional changes in population abundance within a static range, rather than shifts arising from colonisation-extinction dynamics (Huang et al. 2015). Furthermore, apparent low rates of range-shift do not necessarily indicate a limited capacity to colonise new areas, as suitable new areas may not be available, or populations may be adapting in-situ (Bradshaw & Holzapfel 2006, Crick et al. 1997, Holt 1990).

The limited influence of migratory flocking behaviour on breeding range shifts is in line with our hypothesis that persistent colonisation of new breeding areas is less likely to require heritable changes in migratory programmes than new non-breeding areas. Reproductive dispersal allows novel breeding sites to be occupied directly by subsequent generations without any heritable change in migratory programmes, as long as offspring exhibit natal philopatry (as is typical in migratory species; Cava et al. 2016). Our models demonstrated that breeding COA shifts are related most strongly to changes in population size (either through declines or increases), which is expected given the potential for spatially-structured abundance changes to strongly influence COA metrics even in the absence of range expansion (Loehle 2020). We failed to find any significant effect of absolute population trend in our non-breeding COA assessments, suggesting that patterns of change in non-breeding ranges are more indicative of colonisation-extinction dynamics which are known to have been more prevalent for species non-breeding distributions (Curley et al. 2020).

We found a significant difference between long- and short-distance migrants within breeding COA shifts, but this effect was limited to our wider species pool. Long-distance migrants here were found to generally be shifting their breeding COA at a faster rate, which is broadly consistent with trends in latitudinal shift rates among North American species (Rushing et al. 2020). The reasons for this relationship are unclear, and the lack of a significant effect in our more limited species pool suggests the pattern may be highly dependent on species assessed.

Conclusions

We uncover evidence that species flocking, particularly in mixed-age groups, is an important predictor of variation in range-shift capacity across species, particularly for the areas occupied during non-breeding life stages. This indicates a central role of cultural inheritance in enabling migratory programme adaptation, which is likely to be crucial for species experiencing seasonally-independent spatial shifts in zones of suitable bioclimate. Gaps remain in our understanding of migratory programme inheritance, but significant advances are likely to come from improving our understanding of how these mechanisms interact with and influence species capacities for dispersal. Understanding how migratory program inheritance influences species responses to climate change will have important consequences for conservation planning (Alagador et al. 2015, Lawler & Hepinstall-Cymerman 2010), particularly in enabling more realistic forecasts of future range shifts that account for limitations imposed by the adaptive capacity of migratory life histories.

Methods

Migratory flocking strategy and species traits

We built a migratory flocking strategy database building upon data collected by Beauchamp (2011), with additional traits drawn from Birds of the World (2022), Evans and O'Brien (2002), Sauer et al. (2020), Bird et al. (2020), and analysis of United States Geological Survey banding data (Celis-Murillo et al. 2021). Where disagreements were found between sources, Birds of the World (2022) was used, this being the most recent literary source aggregating current literature. Migration distance was taken from Beauchamp (2011) where the distinction between short- and long-distance species was dependent upon whether one leg of the migratory journey covered 15 degrees of latitude or more. We also extracted flocking information from Beauchamp (2011), whereby a maximum flock size whilst travelling greater than 1 indicated presence of flocking on migration. We augmented and refined this binary flocking metric through a systematic appraisal of species accounts in Birds of the World (2022), collating information on migration type (complete or partial migrant), flocking during migration (binary measure) and cohort timing (whether juveniles migrate before, concurrently, or after adults). Quantification of cohort timing was further refined and expanded to a wider species pool through analysis of United States Geological Survey banding data 1960–2019 (Celis-Murillo et al. 2021) for 34 species that had at least 1000 banding records.

To evaluate cohort timing from banding data, we fitted generalised additive models (GAM; package mgcv, Wood 2011) for each species whereby the latitude of banding events was explained by a thin-plate regression spline term of Julian day in an interaction with age class (hatch-year and after hatch-year). In each model the default basis dimension (k) value of -1 was used to give 10 basis functions for spline fitting, and Generalised Cross-Validation was used to estimate smoothness parameters. An initial model was fit to the entire dataset for each species to visually assess appropriate start and end dates of autumn migration (i.e. a clear trend of changing latitude). We then fitted a second model identical in structure to this limited time period, and categorised cohort timing by assessing the proportionate overlap in area under for the normalised fitted smoothed lines for each cohort over the migration period (Figure 5). We used a threshold of overlap greater than 0.85 to classify species as having mixed-age migration timing, as this value maximised agreement between model-derived classifications and those from accounts of migration behaviour in Birds of the World (2022) (SM1).

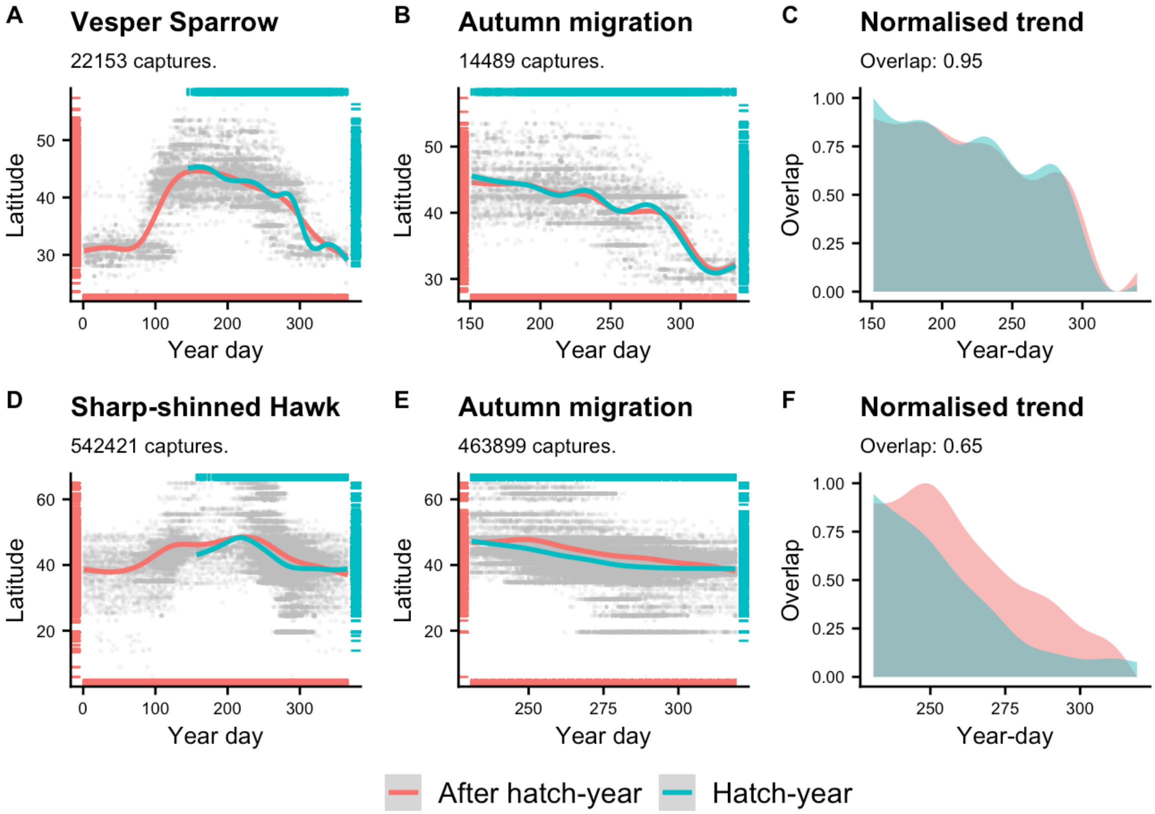


Figure 5. Example methodology for assessing overlap in timing of migration between age cohorts using banding data, showing examples of a species with high cohort overlap and thus concurrent migration timing of age classes (Vesper Sparrow *Pooecetes gramineus*, **A–C**) and a species with relatively low overlap and thus non-concurrent migratory timing (Sharp-shinned Hawk *Accipiter striatus*, **D–F**). After initially fitting GAMs to latitudes of banding events across the year for hatch-year and after hatch-year age cohorts of a given species across all USGS banding events 1960–2019 (**A** and **D**), we restricted the dataset to the autumn migration period (assessed as the temporal region where latitude shows a clear negative trend), and refit the GAM models (autumn migration; **B** and **E**). We then normalised the GAM-predicted mean latitudes for each age class to a 0–1 scale and calculated the overlap in area under the curve as an index of cohort temporal overlap during migration (**C** and **F**).

We subsequently refined the resulting information on flocking and cohort timing to a single categorical variable, where 'mixed-age flocking' are species that typically migrate in conspecific flocks containing adults and juveniles (i.e. species with and without prior migratory experience), 'age-separated flocking' are those that migrate in conspecific flocks but adults and juveniles are typically separated temporally and thus do not migrate together, and finally ‘solo’ migrants are those that migrate alone and seldom or never join flocks.

We accounted for other traits deemed likely to influence range-shift rates. To control for the influence of changes in overall population size, we took the linear breeding population size trend estimate (1966–2019) for each species from publicly-available USGS breeding bird survey results (see Sauer et al. 2020). We converted this to an absolute value to measure population change rather than directional trend, as both positive and negative trends may lead to higher rates of shift in COA. We included generation length (years) to control for the influence of life history characteristics associated with pace of life and body size, taking values from Bird et al. (2020) calculations incorporating model-estimated age of first reproduction, maximum longevity, and annual adult survival. Finally, we also derived a measure of habitat and dietary specialism (0–100) by taking the maximum score across habitat and dietary classes respectively from the Elton Traits Database 1.0 (Wilman et al. 2014).

Table 1. Migratory traits and how the data was collated.

Trait	Description	Source
Migration type	Is the species a partial or complete migrant? (Yes/No)	Birds of the World 2022
Migration distance	Description of migratory distance (Short/Long)	Beauchamp 2011
Cohort timing	Do juveniles migrate before, concurrently, or after adults?	Celis-Murillo et al. 2021 (see SM2), Birds of the World 2022
Flocking	Does the species flock on migration? (Yes/no)	Beauchamp 2011, Birds of the World 2022
Flocking behaviour	Species flocking behaviour (mixed-age flocks, age-separated flocks, or solo)	Based upon Cohort timing and Flocking variables
Absolute population trend	Survey-wide linear population trend based upon Breeding Bird Survey data (%/yr 1966–2019 for the Core Survey Area). Absolute value taken.	Sauer et al. 2020
Generation length	Modelled generation length based upon age of first reproduction, maximum longevity, and annual adult survival.	Bird et al. 2020
Habitat specialism score	How specialised is the species to a certain habitat (0–100)	Derived from Wilman et al. (2014) as maximum score across habitat classes
Diet specialism score	How specialised is the species to a dietary niche (0–100)	Derived from Wilman et al. (2014) as maximum score across diet classes

We were able to derive complete trait data for 81 species, and partial data (lacking age cohort information due to paucity of USGS banding or Birds of the World 2022 data) for 122 species. Where taxonomic nomenclature has been revised over time, manual revisions of taxonomic names were required to combine data from separate sources ensuring nomenclature remained consistent across datasets (SM Table 1).

Calculating annual centres of abundance

We estimated annual centres of abundance (COAs) for breeding and non-breeding periods for each species using Breeding Bird Survey (BBS) and Christmas Bird Count (CBC) data respectively. BBS surveys comprised >4000 39.3km linear routes throughout the United States and Canada (see Bystrak 1981 for detail), while CBC surveys comprised of >2400 count circles across North America where all birds detected within a 24.1km diameter circle, on a single day (between 14 December and 5 January) are counted (see Soykan et al. 2016 for detail).

Raw count metrics from these surveys may be liable to spatial sampling biases, particularly over time. We therefore use model-derived metrics at the stratum level, where strata refer to intersections between Bird Conservation Regions (BCRs) and states or provinces across North America (Sauer et al. 2003). Stratum-based metrics help to alleviate issues of imbalanced spatiotemporal sampling that are present in BBS and CBC surveys (Huang et al. 2016). To further limit spatial bias, we limited analysis to strata across well-sampled BCRs 5 and 9–39 (Figure 6). For stratum-level BBS annual indices, we used posterior median and 95th percentile values from Bayesian hierarchical GAMs (GAMYE model) provided by Smith and Edwards (2021). For stratum-level CBC annual indices, a Bayesian log-linear hierarchical model was used following the method described in Soykan et al. (2016), with posterior median and 95th percentile values drawn from Meehan et al. (2020).

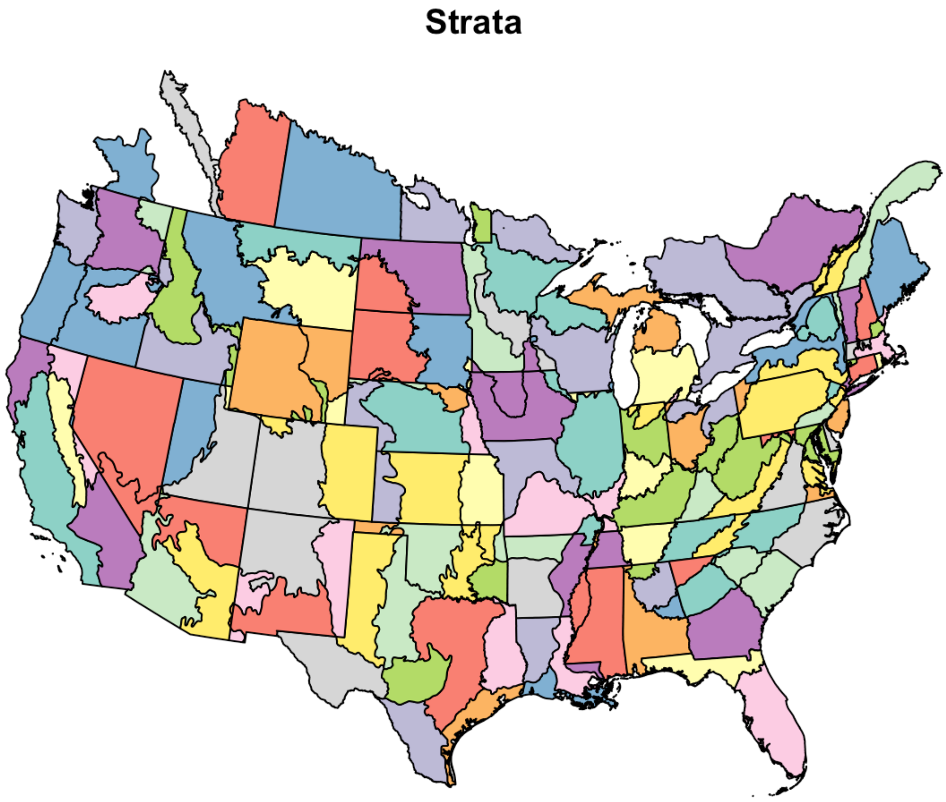


Figure 6. Breeding Bird Survey and Christmas Bird Count analysis strata used to calculate annual centres of abundance 1970–2019. Strata refer to intersections between Bird Conservation Regions (BCRs) and states or provinces across North America.

To calculate the location of an annual centre of abundance (longitude and latitude, separately) for a species, the yearly mean of strata centroid locations (longitude and latitude) were weighted by the Bayesian posterior strata abundance indices (Equation 1).

Equation 1.

$$COA_{Latitude} = \frac{\sum Population\ Index_{Stratum} * \ Latitude_{Stratum}}{\sum Population\ Index_{Stratum}}$$

$$COA_{Longitude} = \frac{\sum Population\ Index_{Stratum} * \ Longitude_{Stratum}}{\sum Population\ Index_{Stratum}}$$

We calculated COAs across the period 1970–2019 as this avoided early periods of both surveys where spatial sampling coverage was sparse. As Bayesian posteriors can be assumed to follow an approximately normal distribution around the median for sufficiently large samples (Gelman et al. 2013), standard deviation (SD) can be calculated using the 95th percentiles (Equation 2).

Equation 2.

$$SD = \frac{Upper\ 95^{th}\ Percentile - Lower\ 95^{th}\ Percentile}{3.92}$$

We used classical error propagation to incorporate error into COA calculations. Error around each posterior stratum abundance estimate was propagated using the first-order Taylor series method from package methods (Ucar et al. 2018).

Centre of abundance trends

We calculated linear trend coefficients separately for both latitudinal and longitudinal components of the annual COA metrics for each species (Equation 3), representing estimates of annual latitudinal and longitudinal displacement in the COA, again propagating errors using the first-order Taylor series method.

Equation 3.

$$Linear\ trend\ coefficient = \frac{\sum(Year_n - mean(Year)) \times (COA_n - mean(COA))}{\sum(Year_n - mean(Year))^2}$$

A single vector of annual COA displacement was then calculated using Pythagorean theorem (Equation 4). Once again, error was propagated using the first-order Taylor series method.

Equation 4.

$$COA\ displacement = \sqrt{Latitudinal\ displacement^2 + Longitudinal\ displacement^2}$$

Trait analysis

We built phylogenetic generalised least squares (PGLS) models to test for the effects of species traits on annual centre of abundance shift rates for each season, controlling for potential phylogenetic collinearity. Explanatory variables of migration type (complete or partial), migration distance (long or short), habitat specialism score (numeric), diet specialism score (numeric), absolute population trend (numeric), and generation length (numeric) were used within all models. The first model for each season included flock behaviour as a binary variable (flocking or solo) for a species pool of 122. We then fitted a second model for each season using a refined flock behaviour variable (mixed-age flocks, age-separated flocks, or solo) for the reduced species pool of 81 for which this trait information was available. Numeric variables were first scaled to Z-scores to ensure comparable effect coefficients. The pgls.SEy function from package phytools (Revell 2012) was used to fit the PGLS models, allowing uncertainty within our dependent variable to be accounted for using the propagated errors attained during shift rate calculations. Models were checked for collinearity between predictor variables using variance inflation factor scores, with no variables exceeding a threshold of 5 in any model. We report results for the global models without model refinement, ensuring we account for all potential variables we believe to be important in influencing shift-rates. To evaluate whether model coefficients are influenced by retention of non-significant variables, we also performed model refinement using two competing methodologies. Firstly, backwards stepwise deletion using ANOVA comparisons to reach the most parsimonious model with the fewest number of parameters that needed to be estimated. Secondly, model averaging across all nested models within 2 AICc units of our global model using the package MuMIn (Bartoń 2022).

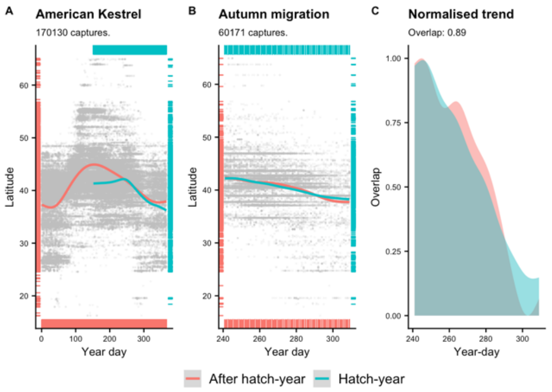
For all models, we used a consensus phylogenetic tree derived from the posterior distribution of complete trees produced by Jetz et al. (2012) available at http://www.birdtree.org and provided by Holtmann et al. (2017). The tree was prepared on the basis of a Hackett backbone (Hackett tree; Hackett et al. 2008). Trees were trimmed based upon species names within our dataset for each model.

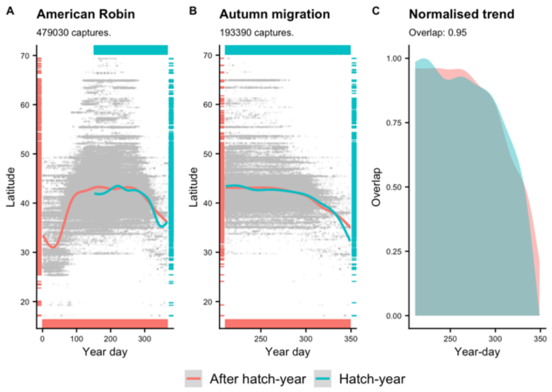
All statistical analyses were performed with R 4.1.2 (R Core Team 2021). Scripts for the completed analysis are available as supplementary material.

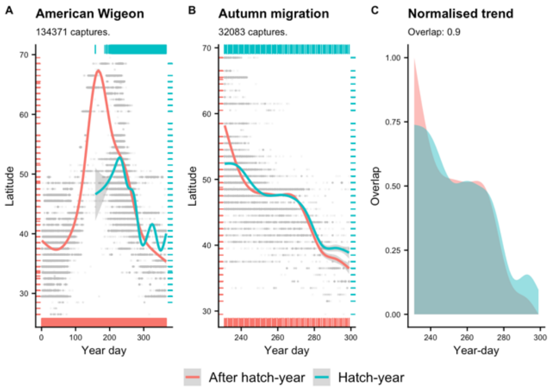
Supplementary material

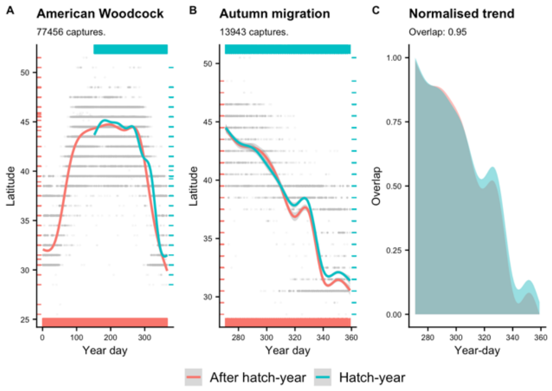
SM1. Migratory timing banding analysis

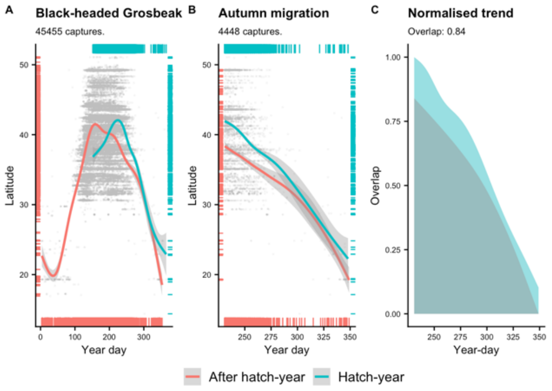
Species timing plots for 34 species that had sufficient data to allow cohort-timing assessment through banding analysis. Start and end dates used for autumn migration period can be found in the full trait database dataset.

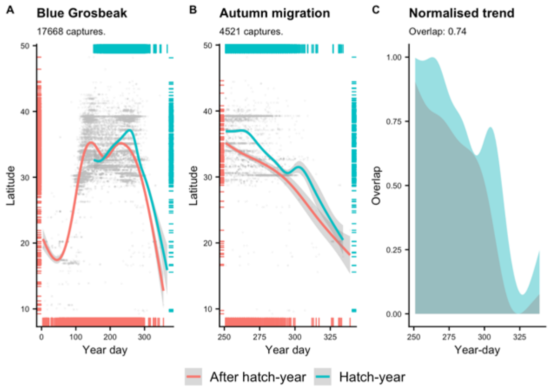


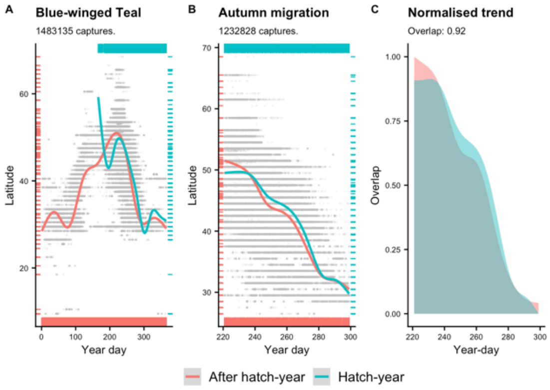


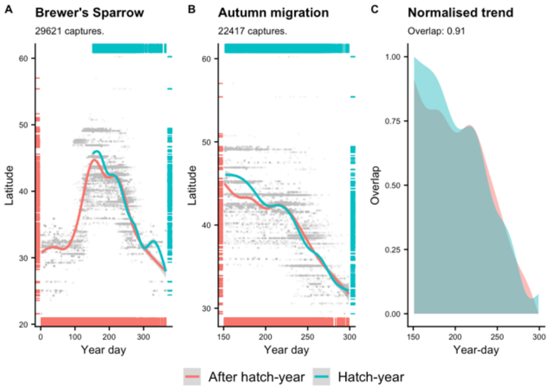


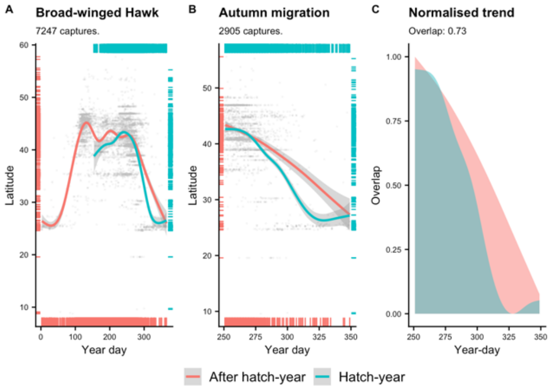


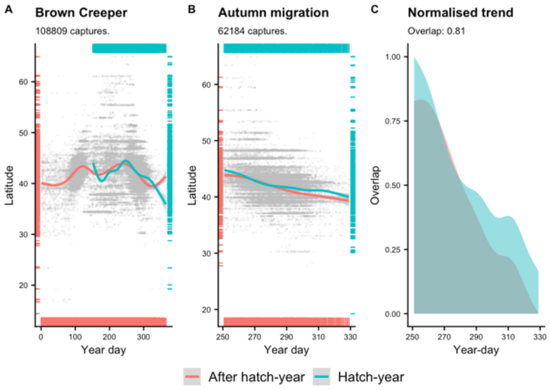


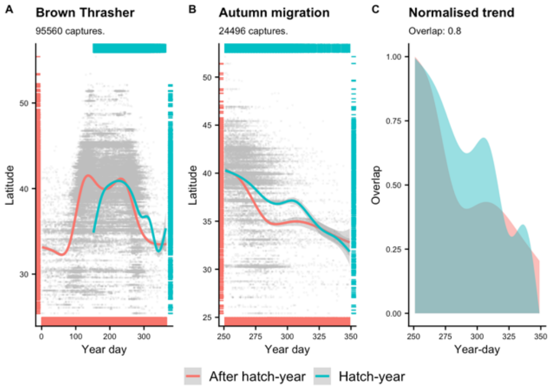


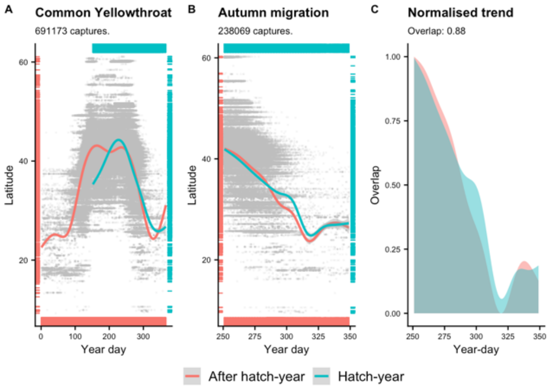

A
Blue-winged Teal
1483135 captures.
Latitude
20
40
60
0
100
200
300
Year day
B
Autumn migration
1232828 captures.
Latitude
30
40
50
60
70
220
240
260
280
300
Year day
C
Normalised trend
Overlap: 0.92
Overlap
0.00
0.25
0.50
0.75
1.00
220
240
260
280
300
Year-day
After hatch-year
Hatch-year

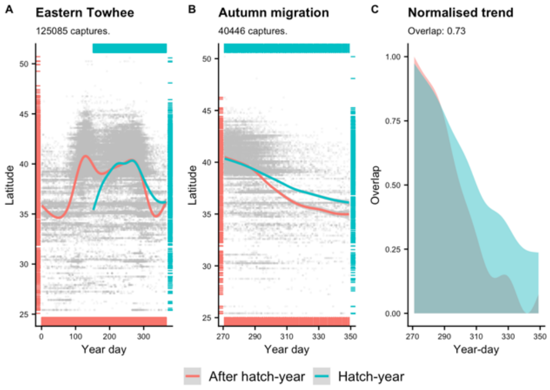

A
Brewer's Sparrow
29621 captures.
Latitude
20
30
40
50
60
0
100
200
300
Year day
B
Autumn migration
22417 captures.
Latitude
30
40
50
60
150
200
250
300
Year day
C
Normalised trend
Overlap: 0.91
Overlap
0.00
0.25
0.50
0.75
1.00
150
200
250
300
Year-day
After hatch-year
Hatch-year

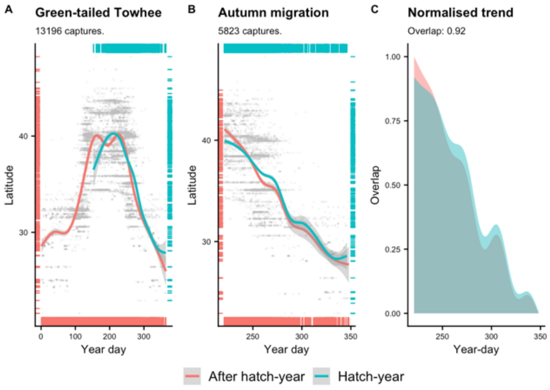

A
Broad-winged Hawk
7247 captures.
Latitude
10
20
30
40
50
60
0
100
200
300
Year day
B
Autumn migration
2905 captures.
Latitude
10
20
30
40
50
250
275
300
325
350
Year day
C
Normalised trend
Overlap: 0.73
Overlap
0.00
0.25
0.50
0.75
1.00
250
275
300
325
350
Year-day
After hatch-year
Hatch-year

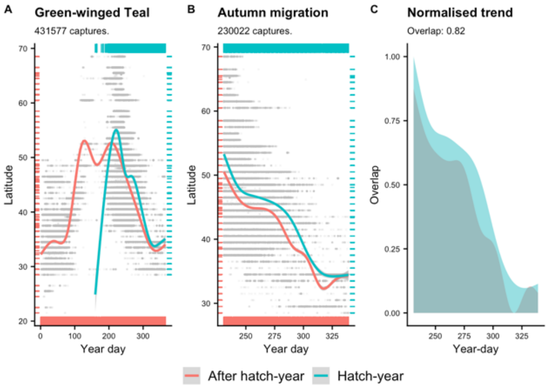

A
Brown Creeper
108809 captures.
Latitude
20
30
40
50
60
0
100
200
300
Year day
B
Autumn migration
62184 captures.
Latitude
20
30
40
50
60
250
270
290
310
330
Year day
C
Normalised trend
Overlap: 0.81
Overlap
0.00
0.25
0.50
0.75
1.00
250
270
290
310
330
Year-day
After hatch-year
Hatch-year

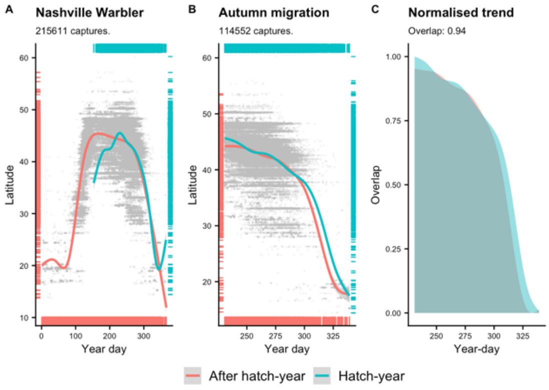

A
Brown Thrasher
95560 captures.
Latitude
30
40
50
0
100
200
300
Year day
B
Autumn migration
24496 captures.
Latitude
25
30
35
40
45
50
250
275
300
325
350
Year day
C
Normalised trend
Overlap: 0.8
Overlap
0.00
0.25
0.50
0.75
1.00
250
275
300
325
350
Year-day
After hatch-year
Hatch-year

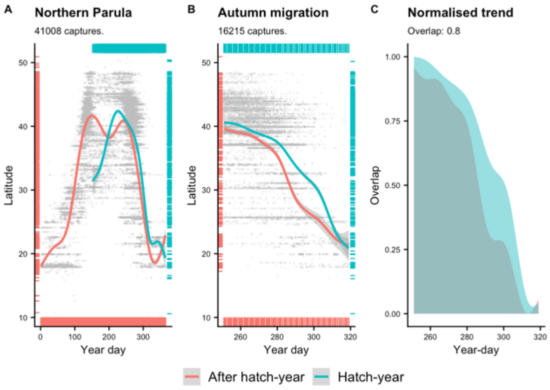

A
Common Yellowthroat
691173 captures.
Latitude
20
40
60
0
100
200
300
Year day
B
Autumn migration
238069 captures.
Latitude
20
40
60
250
275
300
325
350
Year day
C
Normalised trend
Overlap: 0.88
Overlap
0.00
0.25
0.50
0.75
1.00
250
275
300
325
350
Year-day
After hatch-year
Hatch-year

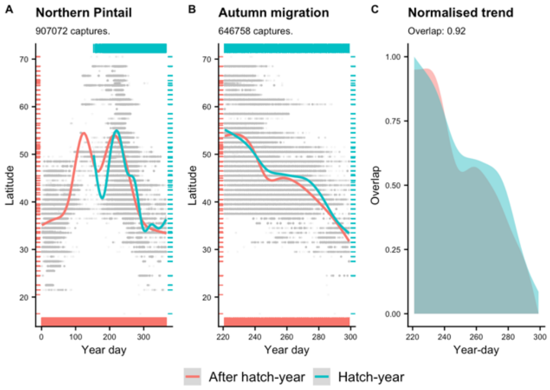

A
Eastern Towhee
125085 captures.
Latitude
25
30
35
40
45
50
0
100
200
300
Year day
B
Autumn migration
40446 captures.
Latitude
25
30
35
40
45
50
270
290
310
330
350
Year day
C
Normalised trend
Overlap: 0.73
Overlap
0.00
0.25
0.50
0.75
1.00
270
290
310
330
350
Year-day
After hatch-year
Hatch-year

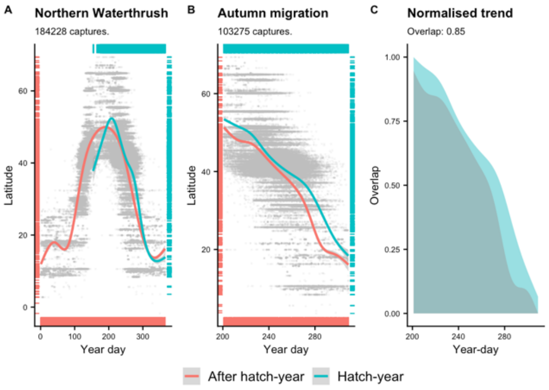

A
Green-tailed Towhee
13196 captures.
Latitude
30
40
0
100
200
300
Year day
B
Autumn migration
5823 captures.
Latitude
30
40
250
300
350
Year day
C
Normalised trend
Overlap: 0.92
Overlap
0.00
0.25
0.50
0.75
1.00
250
300
350
Year-day
After hatch-year
Hatch-year

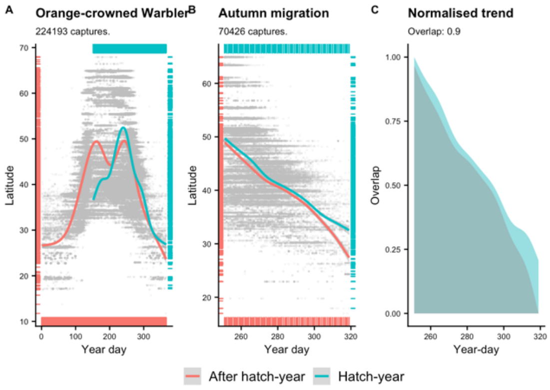

A
Green-winged Teal
431577 captures.
Latitude
Year day
B
Autumn migration
230022 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.82
Overlap
Year-day
After hatch-year
Hatch-year

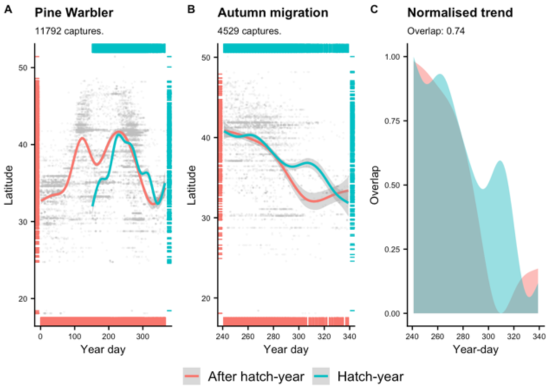

A
Nashville Warbler
215611 captures.
Latitude
Year day
B
Autumn migration
114552 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.94
Overlap
Year-day
After hatch-year
Hatch-year

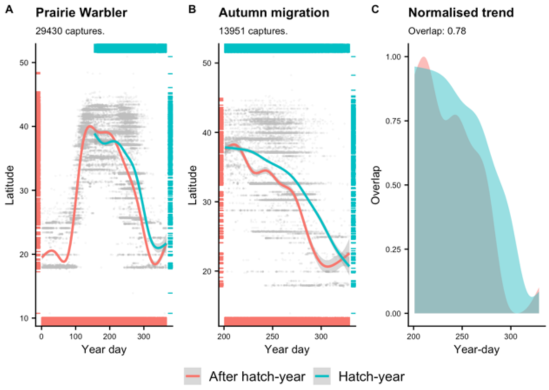

A
Northern Parula
41008 captures.
Latitude
Year day
B
Autumn migration
16215 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.8
Overlap
Year-day
After hatch-year
Hatch-year

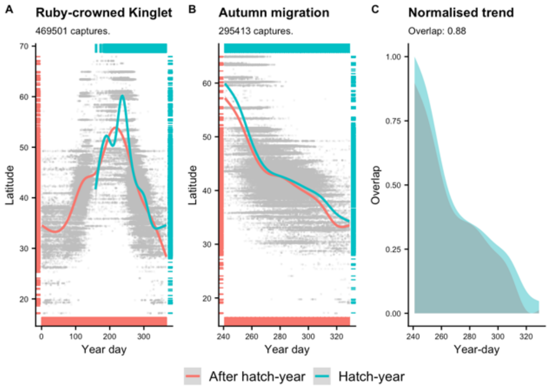

A
Northern Pintail
907072 captures.
Latitude
Year day
B
Autumn migration
646758 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.92
Overlap
Year-day
After hatch-year
Hatch-year

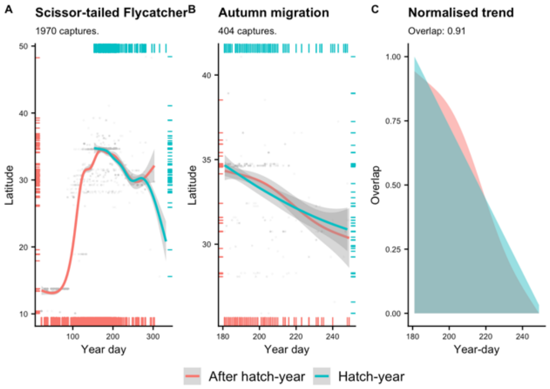

A
Northern Waterthrush
184228 captures.
Latitude
Year day
B
Autumn migration
103275 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.85
Overlap
Year-day
After hatch-year
Hatch-year

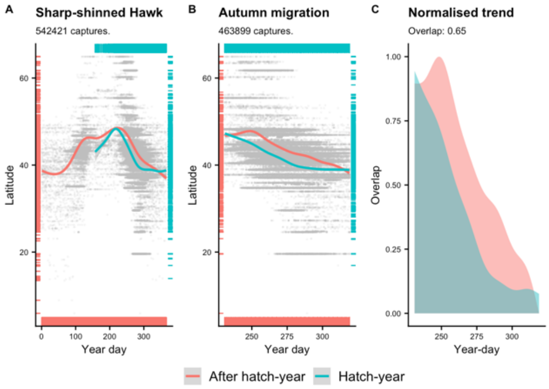

A
Orange-crowned Warbler
224193 captures.
Latitude
Year day
B
Autumn migration
70426 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.9
Overlap
Year-day
After hatch-year
Hatch-year

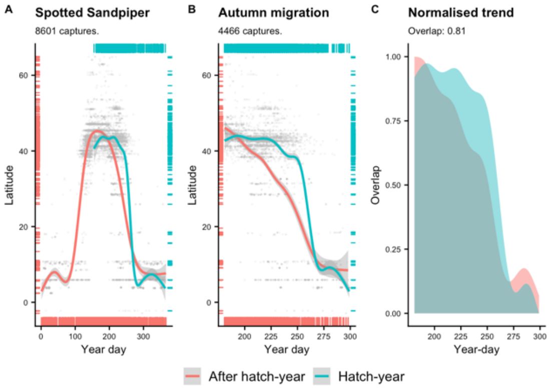

A
Pine Warbler
11792 captures.
Latitude
Year day
B
Autumn migration
4529 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.74
Overlap
Year-day
After hatch-year
Hatch-year

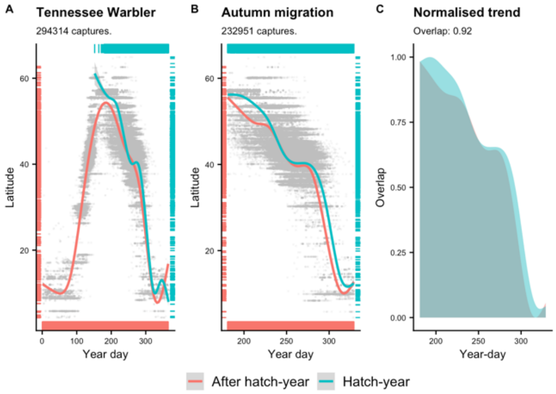

A
Prairie Warbler
29430 captures.
Latitude
Year day
B
Autumn migration
13951 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.78
Overlap
Year-day
After hatch-year
Hatch-year

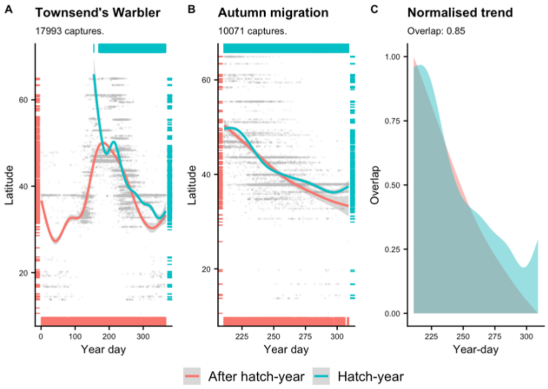

A
Ruby-crowned Kinglet
469501 captures.
Latitude
Year day
B
Autumn migration
295413 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.88
Overlap
Year-day
After hatch-year
Hatch-year

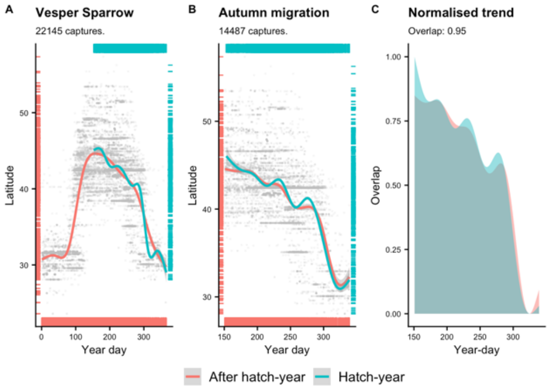

A
Scissor-tailed Flycatcher
1970 captures.
Latitude
Year day
B
Autumn migration
404 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.91
Overlap
Year-day
After hatch-year
Hatch-year

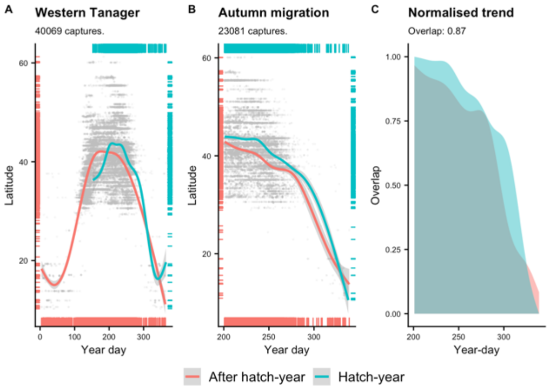

A
Sharp-shinned Hawk
542421 captures.
Latitude
Year day
B
Autumn migration
463899 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.65
Overlap
Year-day
After hatch-year
Hatch-year


A
Spotted Sandpiper
8601 captures.
Latitude
Year day
B
Autumn migration
4466 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.81
Overlap
Year-day
After hatch-year
Hatch-year


A
Tennessee Warbler
294314 captures.
Latitude
Year day
B
Autumn migration
232951 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.92
Overlap
Year-day
After hatch-year
Hatch-year


A
Townsend's Warbler
17993 captures.
Latitude
Year day
B
Autumn migration
10071 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.85
Overlap
Year-day
After hatch-year
Hatch-year


A
Vesper Sparrow
22145 captures.
Latitude
Year day
B
Autumn migration
14487 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.95
Overlap
Year-day
After hatch-year
Hatch-year


A
Western Tanager
40069 captures.
Latitude
Year day
B
Autumn migration
23081 captures.
Latitude
Year day
C
Normalised trend
Overlap: 0.87
Overlap
Year-day
After hatch-year
Hatch-year

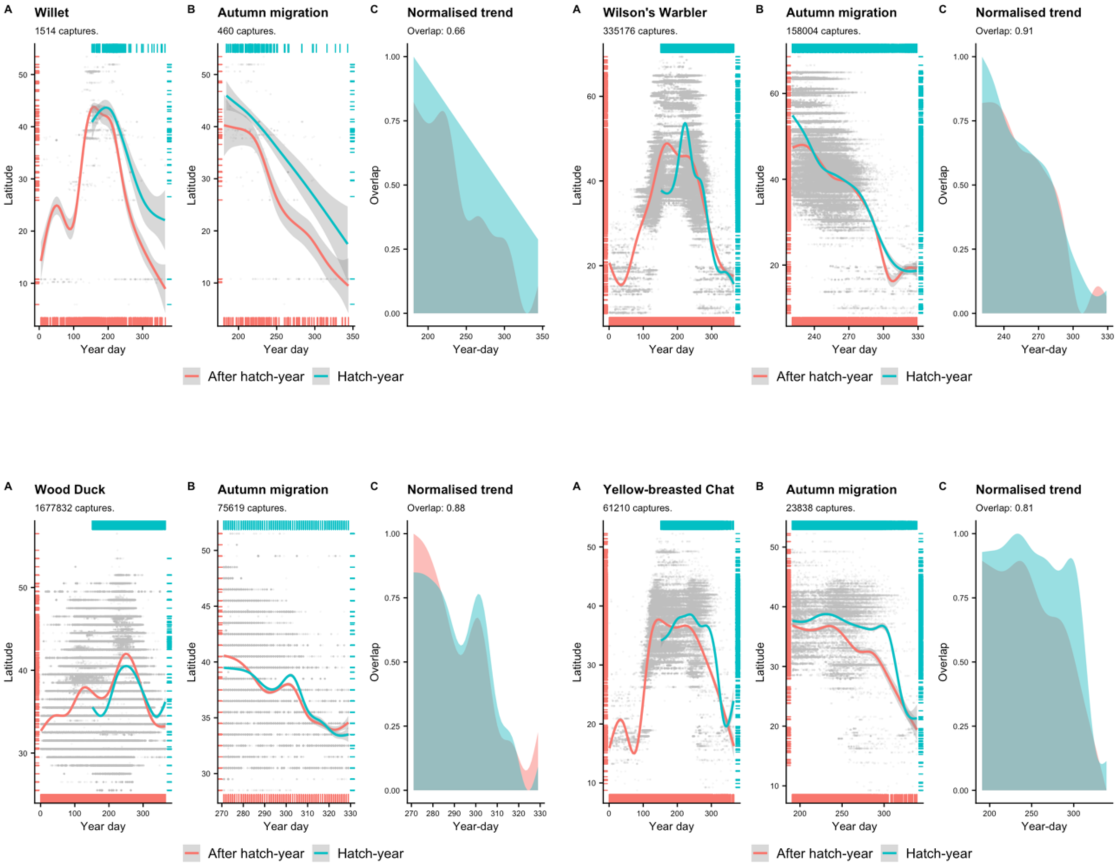


Figure SM1. All 34 species methodology for assessing overlap in timing of migration between age cohorts. Generalised Additive Model (GAM) model predicted average latitude of banding events across year-day for hatch-year and after hatch-year age cohorts across all USGS banding events 1960–2019 (plots lebelled A). Time period was cropped to the autumn migration period where latitude is showing a clear negative trend (southward migration) (plots labelled B). Latitudes are normalised to a 0–1 scale and area under the curve overlap is calculated (plots labelled C).

SM2. Trait database

The full trait database used for analysis (precursor variables and further information is available on request).

Table SM1. Trait database used for Phylogenetic Generalised Least Squares analysis of centre of abundance shifts 1970–2019.

AOU	Tree species	Flock	Flock behav.	Mig. type	Mig. dist.	Trend	Hab. spec.	Diet spec.	GenFLS
1770	Dendrocygna autumnalis	Yes	Mixed-age flock	Partial	long	6.25	50	90	2.075
1780	Dendrocygna bicolor	Yes		Partial	short	2.24	80	60	2.326
1400	Anas discors	Yes	Mixed-age flock	Complete	short	0.26	100	60	2.026
1410	Anas cyanoptera	Yes	Mixed-age flock	Partial	short	-0.89	100	50	1.736
1430	Anas acuta	Yes	Mixed-age flock	Complete	long	-2.61	70	50	3.307
1390	Anas crecca	Yes	Mixed-age flock	Partial	short	0.15	100	50	2.144
1350	Anas strepera	Yes	Mixed-age flock	Partial	short	1.7	80	70	2.616
1370	Anas americana	Yes	Mixed-age flock	Complete	short	-1.51	50	100	3.081
1500	Aythya collaris	Yes	Mixed-age flock	Complete	long	1.85	100	60	2.544
1490	Aythya affinis	Yes	Mixed-age flock	Complete	long	-0.37	100	50	3.233
1440	Aix sponsa	Yes	Mixed-age flock	Partial	short	1.15	80	50	2.124
1310	Lophodytes cucullatus	Yes		Partial	long	4.91	80	40	4.514
1290	Mergus merganser	Yes		Complete	long	-0.44	80	70	3.511
1510	Bucephala clangula	Yes		Complete	short	0.47	80	70	4.827
1530	Bucephala albeola	Yes	Mixed-age flock	Complete	long	3.43	100	70	4.122
640	Sterna caspia	Yes	Mixed-age flock	Partial	long	0.18	80	80	9.749
650	Sterna maxima	Yes	Mixed-age flock	Partial	long	0.08	100	80	10.508
690	Sterna forsteri	Yes	Mixed-age flock	Partial	long	-1.3	80	80	7.166
580	Larus atricilla	Yes		Partial	short	1.11	50	40	7.567
590	Larus pipixcan	Yes		Complete	short	-1.13	40	40	7.124
470	Larus marinus	Yes	Mixed-age flock	Partial	long	-1.57	80	20	11.453
800	Rynchops niger	Yes	Mixed-age flock	Partial	long	-1.38	100	70	5.713
2640	Numenius americanus	Yes	Mixed-age flock	Complete	long	0.03	80	90	6.748
2280	Scolopax minor	Yes	Mixed-age flock	Partial	long	-0.73	80	100	2.298
2580	Catoptrophorus semipalmatus	Yes	Age-separated flock	Complete	short	-0.64	70	80	3.533

2550	Tringa flavipes	Yes	Age-separated flock	Complete	short	-1.04	50	100	4.061
2540	Tringa melanoleuca	Yes	Age-separated flock	Complete	short	0.68	80	80	4.857
2560	Tringa solitaria	Yes		Complete	short	0.23	50	80	3.038
2630	Actitis macularius	Yes	Age-separated flock	Complete	long	-1.49	80	80	3.283
2490	Limosa fedoa	Yes	Age-separated flock	Complete	long	-0.54	80	100	7.439
2730	Charadrius vociferus	Yes		Partial	long	-0.57	100	90	3.924
2250	Recurvirostra americana	Yes		Partial	short	0.3	50	80	4.551
2260	Himantopus mexicanus	Yes		Partial	long	1.1	100	100	5.599
3600	Falco sparverius	Yes	Mixed-age flock	Partial	short	-1.41	50	60	2.406
3550	Falco mexicanus	Yes		Partial	long	1.15	70	100	4.374
3560	Falco peregrinus	No	Solo	Partial	short	2.17	20	80	5.712
4480	Tyrannus vociferans	Yes		Partial	short	-0.14	80	80	2.725
4470	Tyrannus verticalis	Yes	Age-separated flock	Complete	short	-0.13	40	90	2.647
4430	Tyrannus forficatus	Yes	Mixed-age flock	Complete	long	-1.03	60	60	2.347
4540	Myiarchus cinerascens	No	Solo	Partial	long	0.71	70	70	2.989
6280	Vireo flavifrons	No	Solo	Complete	long	0.9	50	70	2.353
6220	Lanius ludovicianus	No	Solo	Partial	long	-2.56	80	70	2.275
6170	Stelgidopteryx serripennis	Yes		Partial	short	-0.22	70	100	2.027
7260	Certhia americana	Yes	Age-separated flock	Partial	short	0.34	30	70	1.664
7190	Thryomanes bewickii	No	Solo	Partial	short	-0.42	50	80	1.784
7080	Toxostoma bendirei	Yes		Partial	long	-2.75	100	50	2.536
7050	Toxostoma rufum	Yes	Age-separated flock	Partial	long	-0.88	80	50	2.681
7540	Myadestes townsendi	No	Solo	Partial	short	0.33	60	50	2.564
7610	Turdus migratorius	Yes	Mixed-age flock	Partial	short	0.12	40	50	3.147
7550	Hylocichla mustelina	No	Solo	Complete	long	-1.3	80	60	2.335
6200	Phainopepla nitens	Yes	Mixed-age flock	Complete	short	1.23	40	60	2.328
7490	Regulus calendula	Yes	Mixed-age flock	Complete	long	0.7	50	80	1.565
6070	Piranga ludoviciana	Yes	Age-separated flock	Complete	short	0.55	40	80	2.230
5950	Pheucticus ludovicianus	Yes	Mixed-age flock	Complete	long	-0.25	30	50	2.402

5960	Pheucticus melanocephalus	Yes	Age-separated flock	Partial	long	0.42	50	70	2.596
5970	Passerina caerulea	Yes	Age-separated flock	Partial	long	0.72	100	40	3.086
6040	Spiza americana	Yes		Complete	short	-0.6	100	100	2.079
6050	Calamospiza melanocorys	Yes	Age-separated flock	Complete	long	-3.66	50	60	2.030
5520	Chondestes grammacus	Yes	Age-separated flock	Partial	long	-1.18	80	70	2.047
5620	Spizella breweri	Yes	Mixed-age flock	Complete	short	-0.89	100	50	2.118
5650	Spizella atrogularis	Yes		Partial	short	-2.08	100	50	2.389
5730	Amphispiza bilineata	Yes	Mixed-age flock	Partial	long	-0.44	100	50	2.202
5870	Pipilo erythrophthalmus	Yes	Age-separated flock	Partial	short	-1.4	80	40	2.611
5900	Pipilo chlorurus	Yes	Mixed-age flock	Complete	short	0.08	70	40	2.780
5450	Ammodramus bairdii	Yes		Complete	short	-0.92	90	50	2.135
5480	Ammodramus leconteii	No	Solo	Complete	long	-0.41	80	80	1.851
5400	Pooecetes gramineus	Yes	Mixed-age flock	Partial	short	-0.83	80	50	2.215
5540	Zonotrichia leucophrys	No	Solo	Partial	short	-0.2	80	70	1.976
5011	Sturnella neglecta	Yes		Partial	long	-0.88	100	50	2.641
6830	Icteria virens	Yes	Age-separated flock	Complete	short	-0.73	100	80	2.242
6810	Geothlypis trichas	Yes	Mixed-age flock	Partial	long	-0.58	80	100	2.344
6750	Seiurus noveboracensis	Yes	Mixed-age flock	Complete	long	1.04	80	90	2.215
6480	Parula americana	Yes	Age-separated flock	Complete	long	1.22	80	70	1.916
6730	Dendroica discolor	Yes	Age-separated flock	Partial	short	-1.93	60	80	2.035
6680	Dendroica townsendi	Yes	Age-separated flock	Complete	long	-0.14	80	100	1.955
6690	Dendroica occidentalis	Yes		Complete	short	0.09	80	100	2.018
6720	Dendroica palmarum	Yes		Complete	long	0.37	100	70	1.892
6710	Dendroica pinus	Yes	Age-separated flock	Partial	short	1.3	80	70	2.060
6850	Wilsonia pusilla	Yes	Mixed-age flock	Complete	short	-1.72	80	80	1.808
6460	Vermivora celata	Yes	Mixed-age flock	Partial	short	-0.59	50	70	1.846
6450	Vermivora ruficapilla	Yes	Mixed-age flock	Complete	long	-0.23	40	80	1.803

6470	Vermivora peregrina	Yes	Mixed-age flock	Complete	long	-0.58	40	70	1.618
5390	Calcarius mccownii	Yes		Complete	long	-2.12	80	80	2.362
7000	Anthus spragueii	No	Solo	Complete	long	-3.24	70	80	1.941
3900	Megaceryle alcyon	No	Solo	Partial	short	-0.89	40	70	2.277
3670	Asio flammeus	No	Solo	Partial	short	-1.69	90	100	2.458
3260	Coragyps atratus	Yes		Partial	short	3.37	100	70	14.199
3250	Cathartes aura	Yes		Partial	short	1.78	100	100	6.797
3320	Accipiter striatus	Yes	Age-separated flock	Partial	short	0.35	25	100	3.616
3420	Buteo swainsoni	Yes	Mixed-age flock	Complete	long	1.08	20	60	7.660
3480	Buteo regalis	No	Solo	Partial	short	0.9	100	100	6.860
3430	Buteo platypterus	Yes	Mixed-age flock	Complete	long	0.64	100	70	5.771
3520	Haliaeetus leucocephalus	Yes	Mixed-age flock	Partial	short	3.97	40	30	13.343
3490	Aquila chrysaetos	Yes	Mixed-age flock	Partial	short	0.19	100	80	13.850
3640	Pandion haliaetus	No	Solo	Partial	long	1.96	60	100	7.955
3160	Zenaida macroura	Yes		Partial	short	-0.42	60	90	2.638
3190	Zenaida asiatica	Yes	Age-separated flock	Partial	short	0.46	60	60	2.980
3120	Patagioenas fasciata	Yes		Partial	short	-1.27	50	70	3.826
40	Podiceps nigricollis	Yes		Partial	long	1.43	60	80	5.028
20	Podiceps grisegena	Yes		Complete	long	1.28	70	50	5.627
1860	Plegadis falcinellus	Yes	Age-separated flock	Partial	short	4.43	50	80	4.607
2000	Egretta caerulea	Yes		Partial	short	-1.23	100	60	2.814
2010	Butorides virescens	Yes		Partial	short	-1.32	80	40	4.210
1960	Casmerodius albus	Yes		Partial	long	1.52	50	40	5.184
2001	Bubulcus ibis	Yes		Partial	short	-1.04	70	60	4.961
1900	Botaurus lentiginosus	Yes		Partial	short	-0.74	70	60	3.525
1260	Pelecanus occidentalis	Yes		Partial	short	3.55	100	80	8.562
1250	Pelecanus erythrorhynchos	Yes		Partial	long	3.17	100	100	10.248
1230	Phalacrocorax pelagicus	Yes		Partial	short	-0.72	100	80	6.459
2140	Porzana carolina	Yes		Partial	long	0.96	40	40	1.266
2210	Fulica americana	Yes	Mixed-age flock	Partial	long	-0.92	50	40	1.967
2120	Rallus limicola	No	Solo	Partial	long	0.32	50	20	2.141
2080	Rallus elegans	Yes		Partial	long	-3.82	50	30	3.269
2060	Grus canadensis	Yes	Mixed-age flock	Partial	short	4.1	50	30	11.455

4290	Archilochus alexandri	No	Solo	Partial	long	0.31	50	90	1.759
4280	Archilochus colubris	No	Solo	Complete	long	0.94	40	60	1.737
4340	Selasphorus sasin	No	Solo	Partial	short	-2.89	60	90	1.927
4330	Selasphorus rufus	No	Solo	Complete	long	-2.13	60	90	1.953
4250	Aeronautes saxatalis	Yes		Partial	long	-0.75	90	100	2.447
4210	Chordeiles acutipennis	Yes		Partial	short	0.15	70	100	3.361
4171	Caprimulgus vociferus	Yes		Complete	long	-1.75	50	100	3.696
4160	Caprimulgus carolinensis	Yes		Partial	short	-1.61	40	90	4.056

SM3. PGLS analysis

SM3.1. *Breeding Bird Survey analysis*

Table SM2. Phylogenetic generalised least squares analysis global model results for Breeding Bird Survey centre of abundance analysis 1960–2019 across 122 species. Flocking behaviour assessed as binary variable (flocking/solo).

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		4039.05	758.05	5.33	<0.0001
Migration type (Partial)	1.12	483.35	443.46	1.09	0.28
Migration distance (short)	1.13	-803.86	392.22	-2.05	0.04
Flocking behaviour (flocking)	1.36	-100.81	691.91	-0.15	0.88
Habitat specialism score	1.29	268.31	216.80	1.24	0.22
Diet specialism score	1.46	387.64	210.45	1.84	0.07
Generation length	1.56	-105.43	437.07	-0.24	0.81
Absolute population trend	1.32	1866.83	457.16	4.08	0.0001

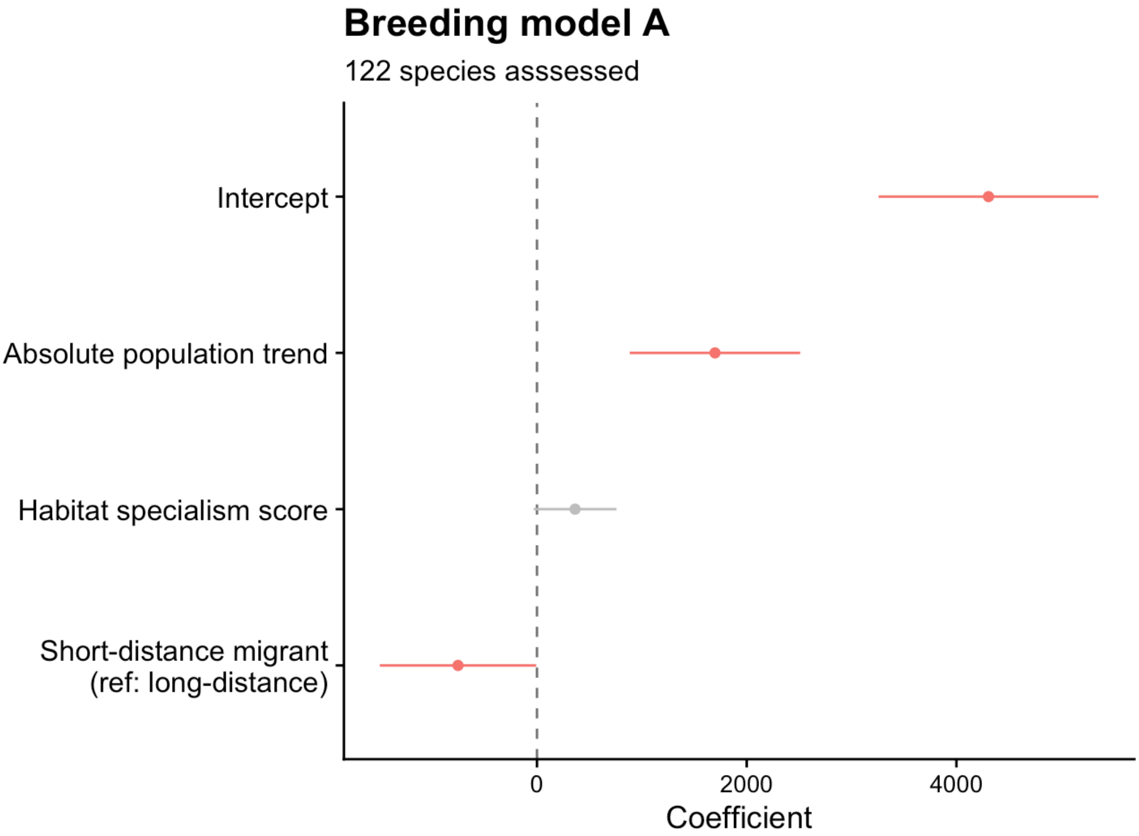


Figure SM2. Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Breeding Bird Survey centre of abudance (in metres) 1970–2019. Model refinement undertaken through backwards stepwise deletion. Model assessed migratory flocking as a binary flocking vs. solo migrants for 122 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM3. Phylogenetic generalised least squares analysis model results for Breeding Bird Survey centre of abundance analysis 1960–2019 across 122 species. Model refinement undertaken through backwards stepwise deletion. Flocking behaviour assessed as binary variable (flocking/solo). Final model results after backwards stepwise deletion.

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		4039.05	534.79	8.05	<0.0001
Migration distance (short)	1.06	-753.04	380.48	-1.98	0.05
Habitat specialism score	1.11	363.24	201.51	1.80	0.07
Absolute population trend	1.08	1697.69	414.90	4.09	0.0001

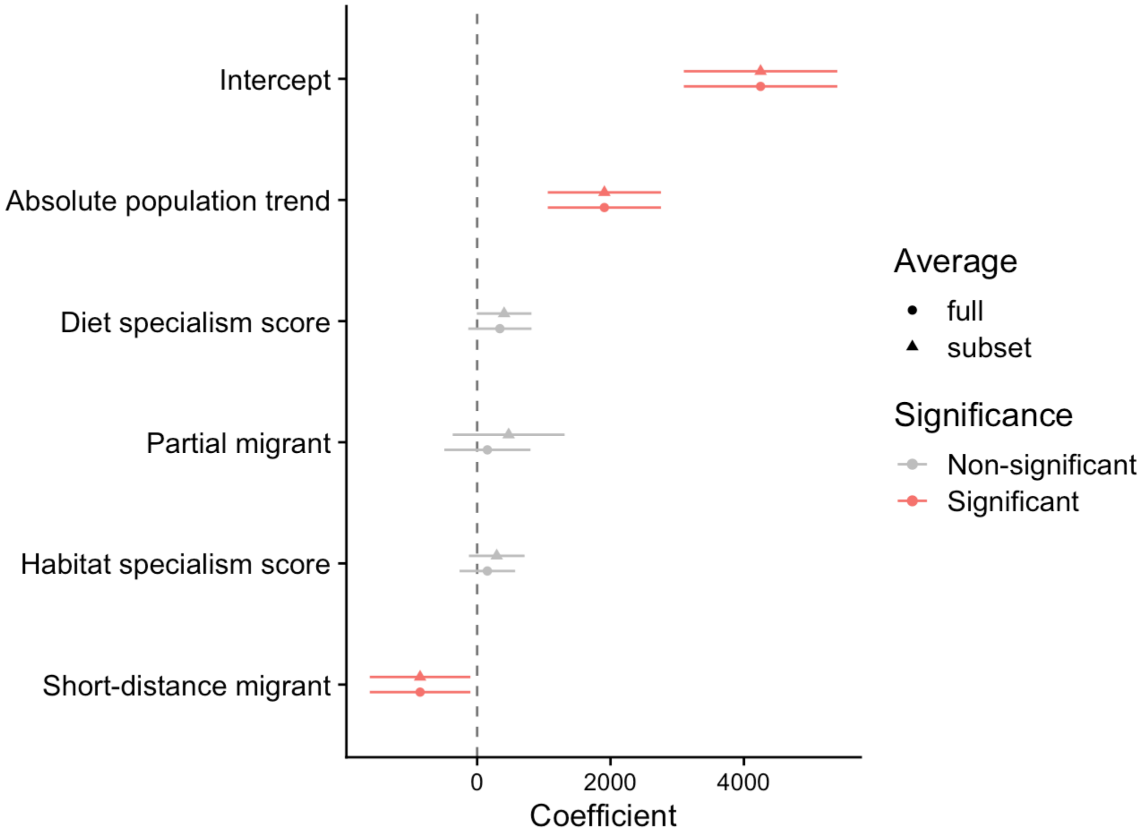


Figure SM3. Model-averaged Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Breeding Bird Survey centre of abundance (in metres) 1970–2019. Model refinement undertaken through model averaging. Model assessed migratory flocking as a binary flocking vs. solo migrants for 122 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM4. Phylogenetic generalised least squares analysis model coefficients, delta AICc, and model weights for averaging across the best performing nested models within the global model. Model set includes all models within 2 AICc units of best performing model. Models assess Breeding Bird Survey centre of abundance analysis 1960–2019 across 122 species. Flocking behaviour assessed as binary variable (flocking/solo).

Model	Int.	Mig. Type	Mig. Dist.	Hab. Spec.	Diet Spec.	Pop. trend	Delta AICc	Weight
1	4396.33		-914.46		420.02	2009.44	0.00	0.29
2	4343.64		-810.98	270.28	349.42	1857.34	0.45	0.23
3	4037.03	488.63	-924.31		458.29	2014.32	0.83	0.19
4	4305.90		-753.04	363.24		1697.69	1.22	0.16
5	4016.18	449.74	-826.41	253.67	388.98	1871.18	1.52	0.13

Table SM5. Phylogenetic generalised least squares analysis model results for Breeding Bird Survey centre of abundance analysis 1960–2019 across 122 species. Flocking behaviour assessed as binary variable (flocking/solo). Model averaged results across model set in SM Table 4.

Variable	Coefficient (Full)	SE (Full)	Z-value (Full)	P-value (Full)	Coefficient (Subset)	SE (Subset)	Z-value (Subset)	P-value (Subset)
Intercept	4250.40	581.70	7.24	<0.0001	4250.40	581.70	7.24	<0.0001
Migration type(Partial)	153.60	327.60	0.47	0.64	472.50	423.50	1.10	0.27
Migration distance (short)	-855.40	381.10	2.22	0.03	-855.40	381.10	2.22	0.03
Habitat specialism score	153.20	211.40	0.72	0.47	293.90	210.70	1.38	0.17
Diet specialism score	341.10	240.00	1.41	0.16	404.5	206.6	1.94	0.05
Absolute population trend	1908.00	428.90	4.41	<0.0001	1908.0	428.9	4.41	<0.0001

Table SM6. Phylogenetic generalised least squares analysis global model results for Breeding Bird Survey centre of abundance analysis 1960–2019 across 81 species. Flocking behaviour assessed as three-level variable (mixed-age flocking/ager-separated flocking/solo).

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		3847.47	763.00	5.04	<0.0001
Migration type(Partial)	1.06	-484.82	509.86	-0.95	0.35
Migration distance (short)	1.11	-224.26	468.73	-0.48	0.63
Flocking behaviour (Age-separated flocks)	1.16	269.00	769.77	0.3	0.73
Flocking behaviour (Mixed-age flocks)	1.16	102.25	751.88	0.14	0.90
Habitat specialism score	1.23	149.60	281.15	0.53	0.60
Diet specialism score	1.08	336.68	261.41	1.29	0.20
Generation length	1.04	-239.69	540.79	-0.44	0.66
Absolute population trend	1.18	2632.06	540.28	4.87	<0.0001

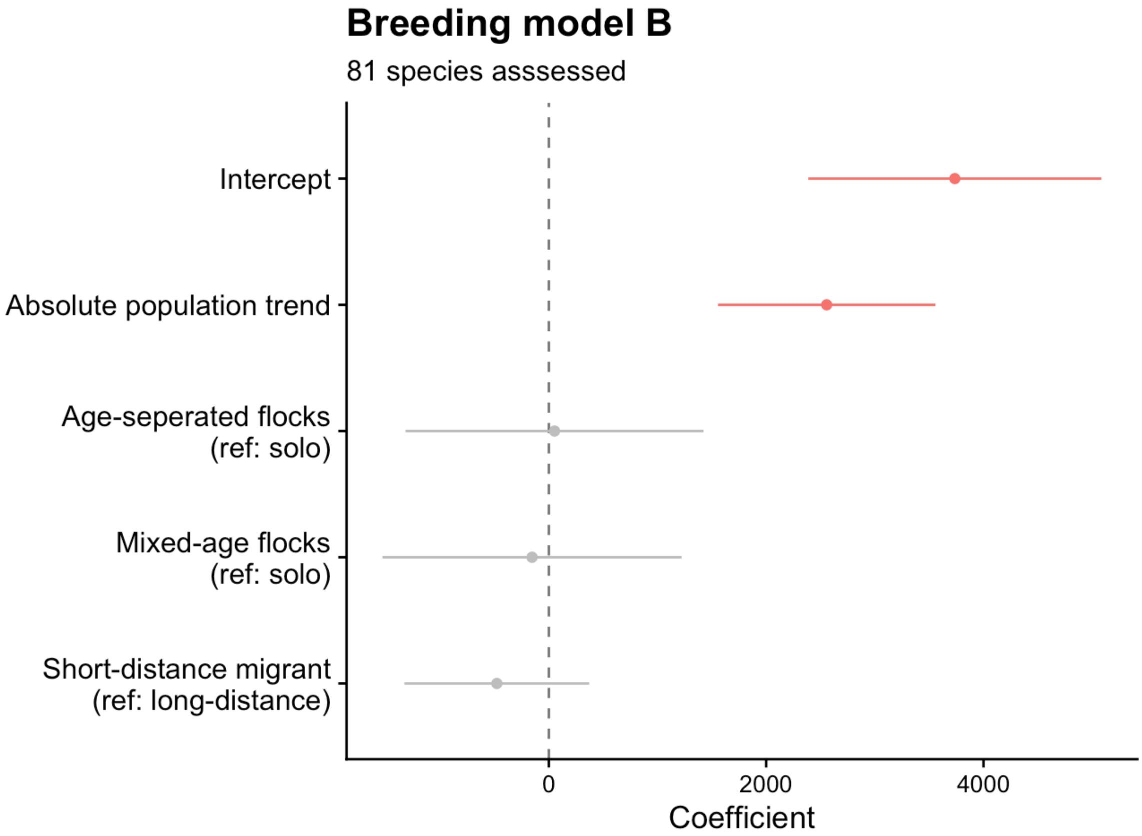


Figure SM4. Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Breeding Bird Survey centre of abundance (in metres) 1970–2019. Model refinement undertaken through backwards stepwise deletion. Model assessed migratory flocking as a three-level variable (mixed-age flocking/age-separated flocking/solo) for 81 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM7. Phylogenetic generalised least squares analysis model results for Breeding Bird Survey centre of abundance analysis 1960–2019 across 81 species. Model refinement undertaken through backwards stepwise deletion. Flocking behaviour assessed as three-level variable (mixed-age flocking/age-separated flocking/solo).

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		3736.32	688.08	5.43	<0.0001
Migration distance (short)	1.03	-478.21	433.83	-1.10	0.27
Flocking behaviour (Age-separated flocks)	1.06	52.63	699.57	0.08	0.94
Flocking behaviour (Mixed-age flocks)	1.06	-154.23	702.35	-0.22	0.83
Absolute population trend	1.12	2556.84	510.34	5.01	<0.0001

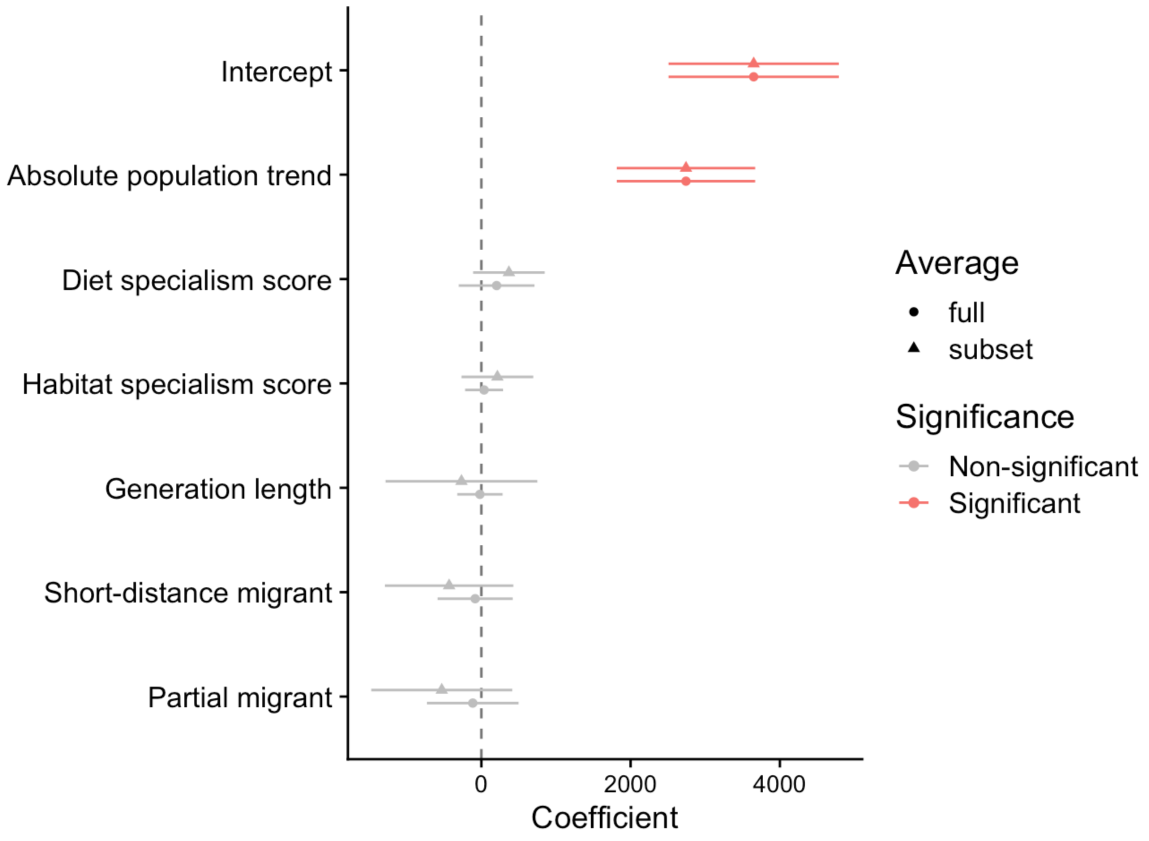


Figure SM5. Model-averaged Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Breeding Bird Survey centre of abundance (in metres) 1970–2019. Model refinement undertaken through model averaging. Model assessed migratory flocking as a three-level variable (mixed-age flocking/age-separated flocking/solo) for 81 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM8. Phylogenetic generalised least squares analysis model coefficients, delta AICc, and model weights for averaging across the best performing nested models within the global model. Model set includes all models within 2 AICc units of best performing model. Models assess Breeding Bird Survey centre of abundance analysis 1960–2019 across 81 species. Flocking behaviour assessed as three-level variable (mixed-age flocking/age-separated flocking/solo).

Model	Int.	Mig. Type	Mig. Dist.	Hab. Spec.	Diet Spec.	Pop. trend	Gen. Length	Delta AICc	Weight
1	3591.11				385.46	2832.43		0.00	0.19
2	3473.14					2741.08		0.45	0.15
3	3895.72	-500.04			363.21	2814.28		1.10	0.11
4	3823.69	-562.86				2726.59		1.21	0.11
5	3700.71		-489.91			2633.74		1.29	0.10
6	3748.62		-366.93		343.22	2742.03		1.52	0.09
7	3625.67			192.93	361.76	2692.52		1.60	0.09
8	3524.53			237.09		2576.05		1.66	0.08
9	3521.58				376.86	2818.67	-266.73	1.99	0.07

Table SM9. Phylogenetic generalised least squares analysis model results for Breeding Bird Survey centre of abundance analysis 1960–2019 across 81 species. Flocking behaviour assessed as a three-level variable (mixed-age flocking/age-separated flocking/solo). Model averaged results across model set in SM Table 8.

Variable	Coefficient (Full)	SE (Full)	Z-value (Full)	P-value (Full)	Coefficient (Subset)	SE (Subset)	Z-value (Subset)	P-value (Subset)
Intercept	3649.12	573.66	6.27	<0.0001	3649.10	573.70	6.27	<0.0001
Migration type(Partial)	-115.09	310.85	0.37	0.71	-530.60	474.40	1.10	0.27
Migration distance (short)	-82.95	254.59	0.32	0.75	-431.90	432.20	0.98	0.33
Habitat specialism score	36.78	128.60	0.28	0.78	214.70	241.50	0.88	0.38
Diet specialism score	204.52	256.62	0.79	0.43	369.20	241.00	1.51	0.13
Absolute population trend	2741.97	465.90	5.80	<0.0001	2742.00	465.90	5.80	<0.0001
Generation length	-19.10	152.95	0.12	0.90	-266.70	510.60	0.51	0.61

SM3.2. *Christmas Bird Count analysis*

Table SM10. Phylogenetic generalised least squares analysis global model results for Christmas Bird Count centre of abundance analysis 1960–2019 across 122 species. Flocking behaviour assessed as binary variable (flocking/solo).

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		3813.57	909.21	4.19	0.0001
Migration type(Partial)	1.15	210.10	786.35	0.27	0.78
Migration distance (short)	1.74	-735.78	628.26	-1.17	0.24
Flocking behaviour (flocking)	1.15	1970.70	510.60	3.86	0.0002
Habitat specialism score	1.64	80.50	254.15	0.32	0.75
Diet specialism score	1.73	-528.88	270.56	-1.96	0.05
Generation length	2.00	492.21	349.43	1.41	0.16
Absolute population trend	3.15	-499.59	449.70	-1.11	0.27

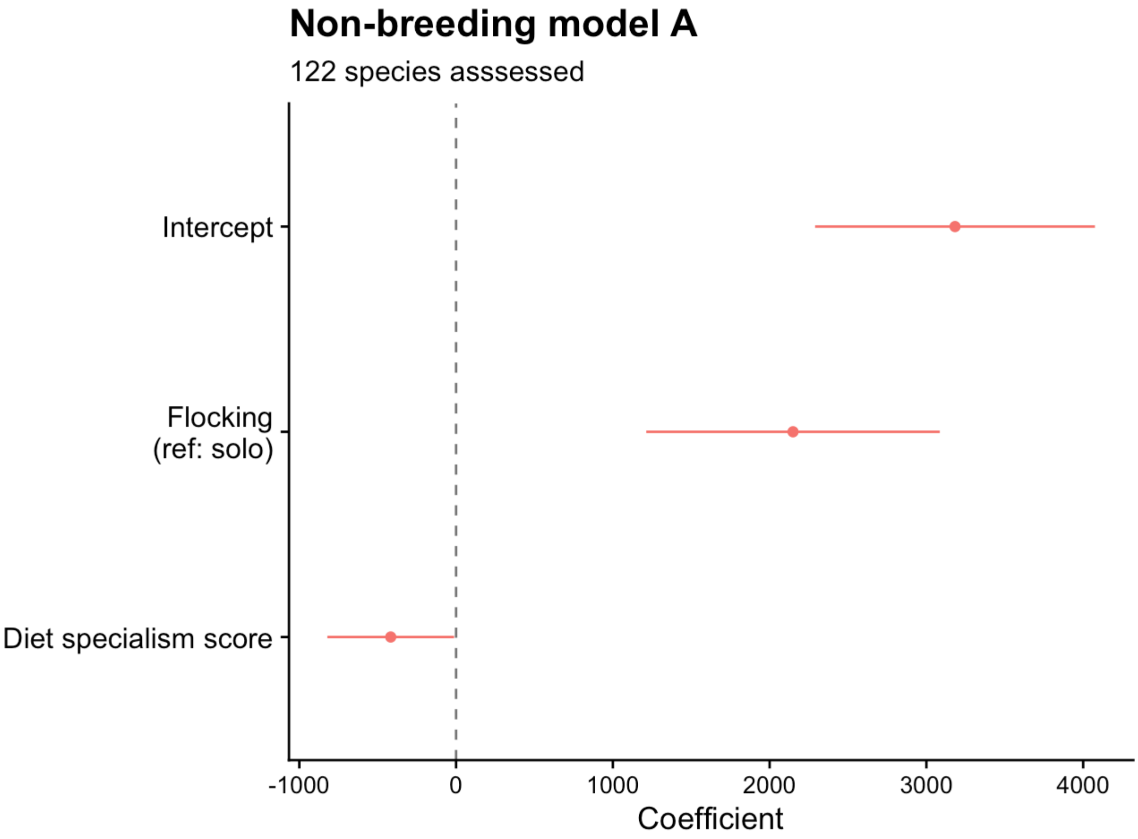


Figure SM6. Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Christmas Bird Count centre of abundance (in metres) 1970–2019. Model refinement undertaken through backwards stepwise deletion. Model assessed migratory flocking as a binary flocking vs. solo migrants for 122 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM11. Phylogenetic generalised least squares analysis model results for Christmas Bird Count centre of abundance analysis 1960–2019 across 122 species. Model refinement undertaken through backwards stepwise deletion. Flocking behaviour assessed as binary variable (flocking/solo). Final model results after backwards stepwise deletion.

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		3182.62	455.42	6.99	<0.0001
Flocking behaviour (flocking)	1.02	2149.25	477.64	4.50	<0.0001
Diet specialism score	1.02	-416.84	206.19	-2.02	<0.05

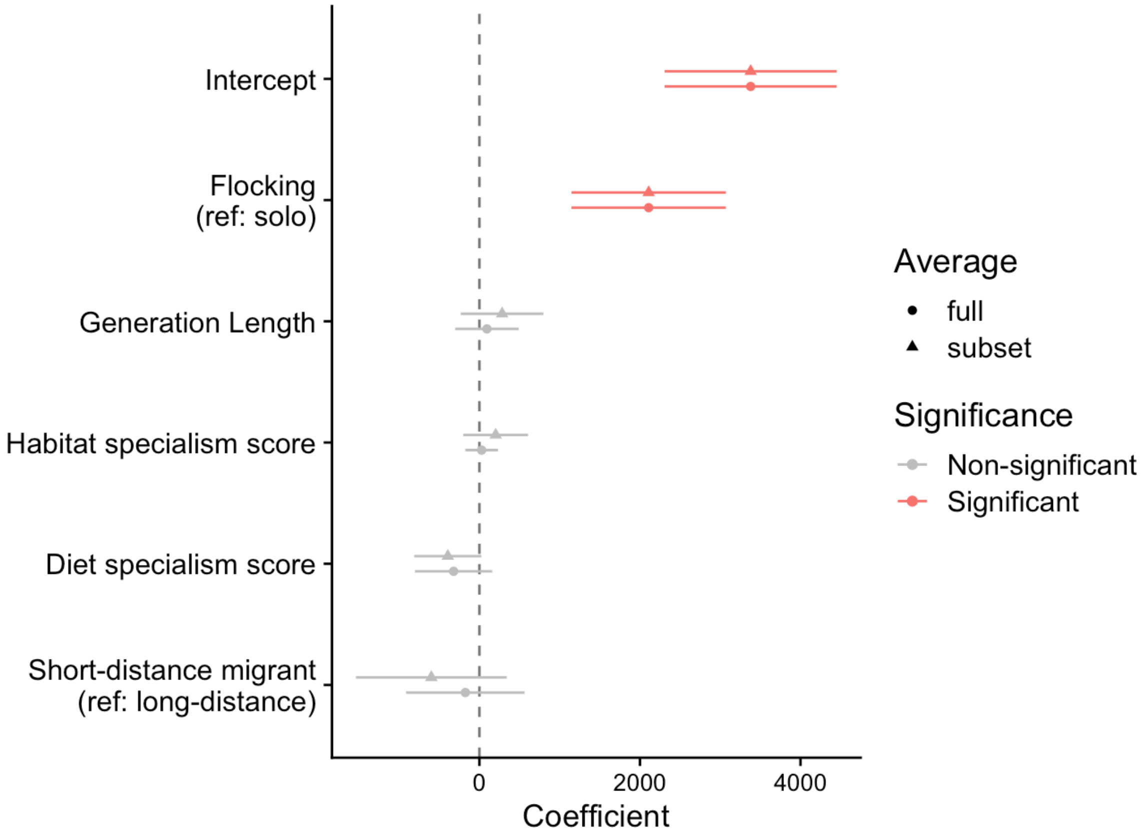


Figure SM7. Model-averaged Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Christmas Bird Count centre of abundance (in metres) 1970–2019. Model refinement undertaken through model averaging. Model assessed migratory flocking as a binary flocking vs. solo migrants for 122 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM12. Phylogenetic generalised least squares analysis model coefficients, delta AICc, and model weights for averaging across the best performing nested models within the global model. Model set includes all models within 2 AICc units of best performing model. Models assess Christmas Bird Count centre of abundance analysis 1960–2019 across 122 species. Flocking behaviour assessed as binary variable (flocking/solo).

Model	Int.	Gen. Length	Mig. Dist.	Hab. Spec.	Diet Spec.	Flock. Behav.	Delta AICc	Weight
1	3182.62				-416.84	2149.25	0.00	0.25
2	3633.78		-601.62		-419.12	2182.56	0.52	0.19
3	3347.24			202.50	-367.28	2158.08	1.16	0.14
4	3300.94	253.87			-363.50	2064.63	1.17	0.14
5	3743.52	248.29	-593.64		-366.92	2099.36	1.76	0.10
6	3343.84	364.93				1929.02	1.97	0.09
7	3171.77					2028.44	1.98	0.09

Table SM13. Phylogenetic generalised least squares analysis model results for Breeding Bird Survey centre of abundance analysis 1960–2019 across 122 species. Flocking behaviour assessed as binary variable (flocking/solo). Model averaged results across model set in SM Table 12.

Variable	Coefficient (Full)	SE (Full)	Z-value (Full)	P-value (Full)	Coefficient (Subset)	SE (Subset)	Z-value (Subset)	P-value (Subset)
Intercept	3378.94	542.04	6.18	<0.0001	3378.90	542.00	6.18	<0.0001
Flocking Behaviour (Flocks)	2108.62	485.88	4.30	<0.0001	2108.62	485.88	4.30	<0.0001
Migration distance (short)	-175.33	374.23	0.47	0.64	-598.80	474.00	1.25	0.21
Habitat specialism score	28.05	103.13	0.27	0.79	202.50	203.60	0.98	0.33
Diet specialism score	-321.19	243.94	1.31	0.19	-393.70	210.70	1.85	0.06
Generation Length	94.08	200.67	0.47	0.64	283.00	260.10	1.08	0.28

Table SM14. Phylogenetic generalised least squares analysis global model results for Christmas Bird Count centre of abundance analysis 1960–2019 across 81 species. Flocking behaviour assessed as three-level variable (mixed-age flocking/age-separated flocking/solo).

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		2020.92	855.93	2.36	0.02
Migration type(Partial)	1.22	1392.40	864.49	1.61	0.11
Migration distance (short)	1.50	-32.77	727.16	-0.05	0.96
Flocking behaviour (Age-separated flocks)	1.23	879.34	495.46	1.78	0.08
Flocking behaviour (Mixed-age flocks)	1.23	3664.67	508.76	7.20	<0.0001
Habitat specialism score	1.72	191.70	345.06	0.56	0.58
Diet specialism score	1.54	142.27	259.09	0.55	0.59
Generation length	1.55	649.37	386.71	1.68	0.10
Absolute population trend	2.12	-641.93	545.10	-1.18	0.24

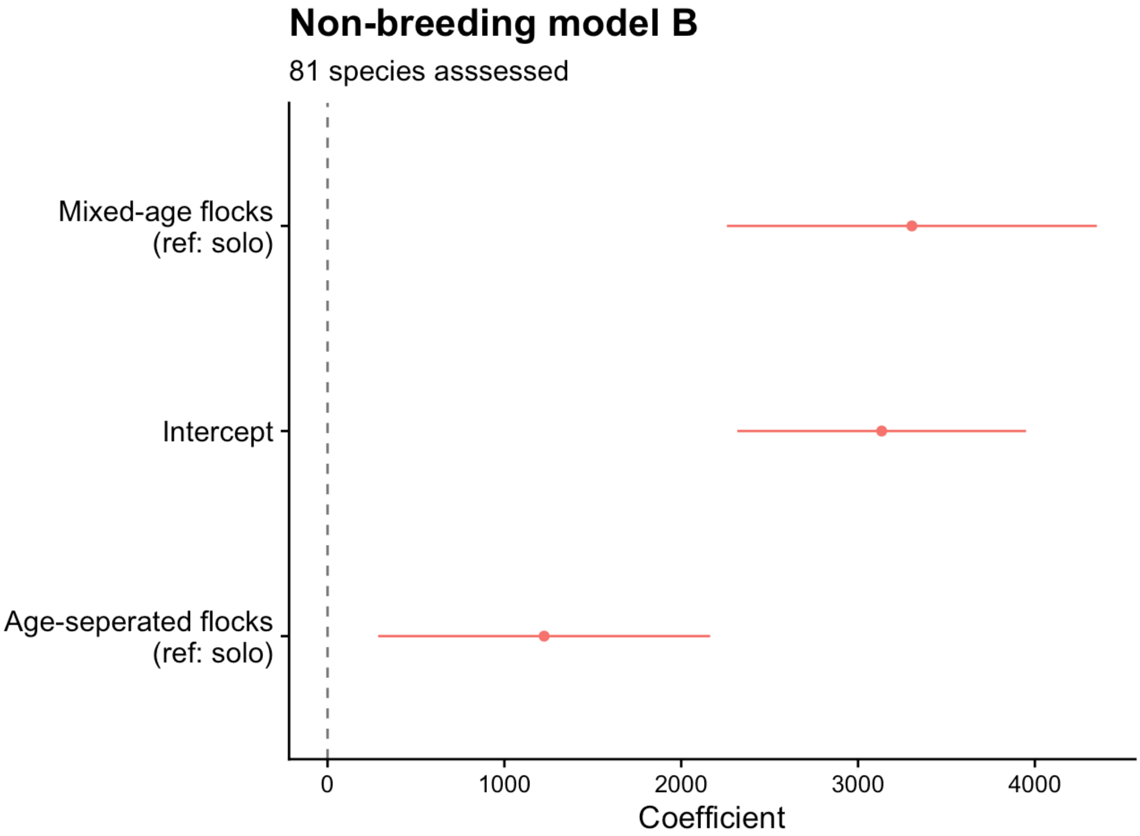


Figure SM8. Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Christmas Bird Count centre of abundance (in metres) 1970–2019. Model refinement undertaken through backwards stepwise deletion. Model assessed migratory flocking as a three-level variable (mixed-age flocking/age-separated flocking/solo) for 81 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM15. Phylogenetic generalised least squares analysis model results for Christmas Bird Count centre of abundance analysis 1960–2019 across 122 species. Model refinement undertaken through backwards stepwise deletion. Flocking behaviour assessed as three-level variable (mixed-age flocking/age-separated flocking/solo). Final model results after backwards stepwise deletion.

Variable	Variable VIF	Coefficient	SE	T-value	P-value
Intercept		3133.65	416.46	7.52	<0.0001
Flocking behaviour (Age-separated flocks)		1224.92	478.95	2.56	0.01
Flocking behaviour (Mixed-age flocks)		3304.49	533.75	6.19	<0.0001

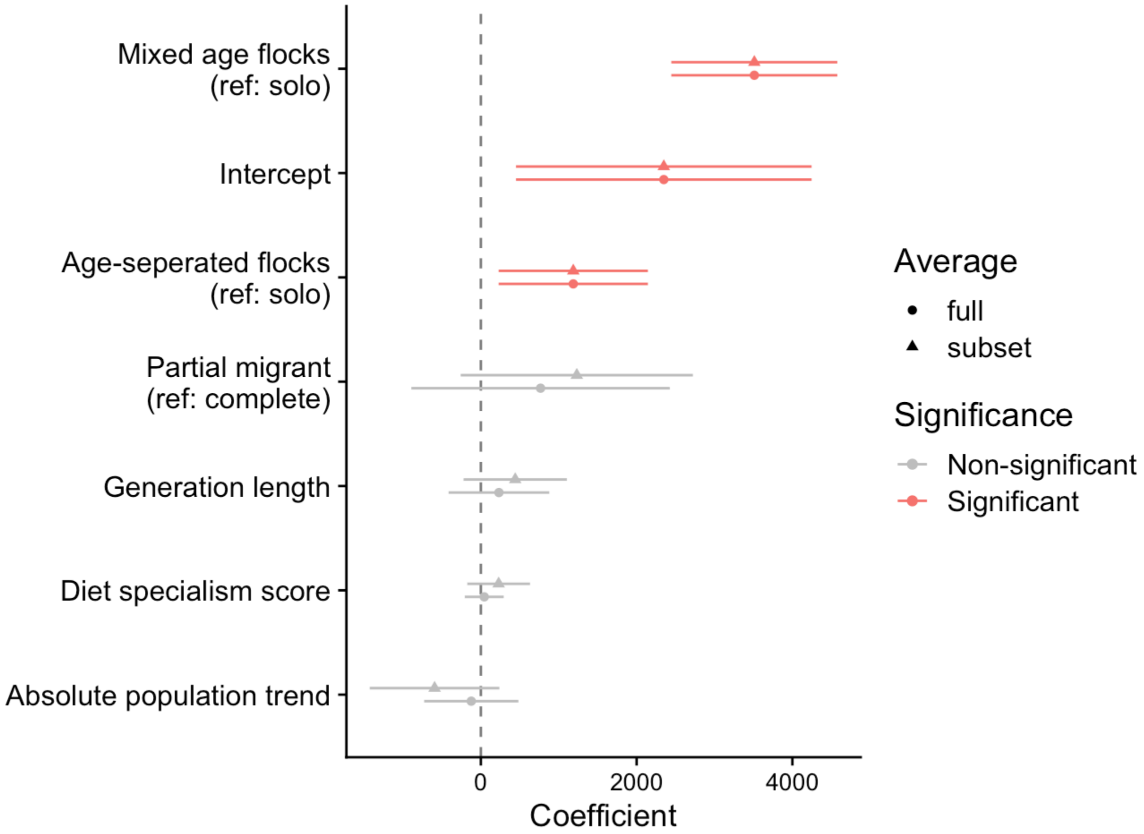


Figure SM9. Model-averaged Phylogenetic Generalised Least Squares (PGLS) model derived estimated coefficients describing effects on annual shift rate of Christmas Bird Count centre of abundance (in metres) 1970–2019. Model refinement undertaken through model averaging. Model assessed migratory flocking as a three-level variable (mixed-age flocking/age-separated flocking/solo) for 81 species. Red points indicate significant results based upon credible 95th percentiles (error bars).

Table SM16. Phylogenetic generalised least squares analysis model coefficients, delta AICc, and model weights for averaging across the best performing nested models within the global model. Model set includes all models within 2 AICc units of best performing model. Models assess Christmas Bird Count centre of abundance analysis 1960–2019 across 81 species. Flocking behaviour assessed as three-level variable (mixed-age flocking/age-separated flocking/solo).

Model	Int.	Flock. Behav. (mixed-age)	Flock. Behav. (age-sep.)	Mig. type.	Gen. Length	Pop. Trend	Diet Spec. Score	Delta AICc	Weight
1	1754.92	3665.50	1382.63	1235.86				0.00	0.20
2	3133.65	3304.49	1224.92					0.38	0.16
3	3124.83	3335.92	1293.83		352.75			0.92	0.12
4	2015.01	3541.33	1314.74	1099.70	292.10			0.96	0.12
5	1602.85	3772.40	1193.09	1383.03			224.91	1.03	0.12
6	2005.13	3616.77	899.02	1200.67	592.09	-594.77		1.07	0.12
7	3391.19	3170.79	803.40		677.95	-593.04		1.49	0.09
8	1866.99	3647.76	1114.45	1247.60	303.87		234.42	1.92	0.08

Table SM17. Phylogenetic generalised least squares analysis model results for Christmas Bird Count centre of abundance analysis 1960–2019 across 81 species. Flocking behaviour assessed as a three-level variable (mixed-age flocking/age-separated flocking/solo). Model averaged results across model set in SM Table 16.

Variable	Coefficient (Full)	SE (Full)	Z-value (Full)	P-value (Full)	Coefficient (Subset)	SE (Subset)	Z-value (Subset)	P-value (Subset)
Intercept	2349.05	960.40	2.43	0.02	2349.10	960.40	2.43	0.02
Flocking Behaviour (mixed-age)	3511.24	536.33	6.46	<0.0001	3511.24	536.33	6.46	<0.0001
Flock. Behaviour (age-separated)	1186.70	482.20	2.43	0.02	1186.70	482.20	2.43	0.02
Migration type (Partial)	766.76	839.86	0.91	0.37	1232.00	748.40	1.62	0.11
Generation length	232.25	327.48	0.70	0.48	441.20	334.00	1.30	0.19
Absolute population trend	-123.08	306.79	0.40	0.69	-594.00	417.80	1.40	0.16
Diet specialism score	43.83	126.24	0.34	0.73	228.60	202.20	1.11	0.27

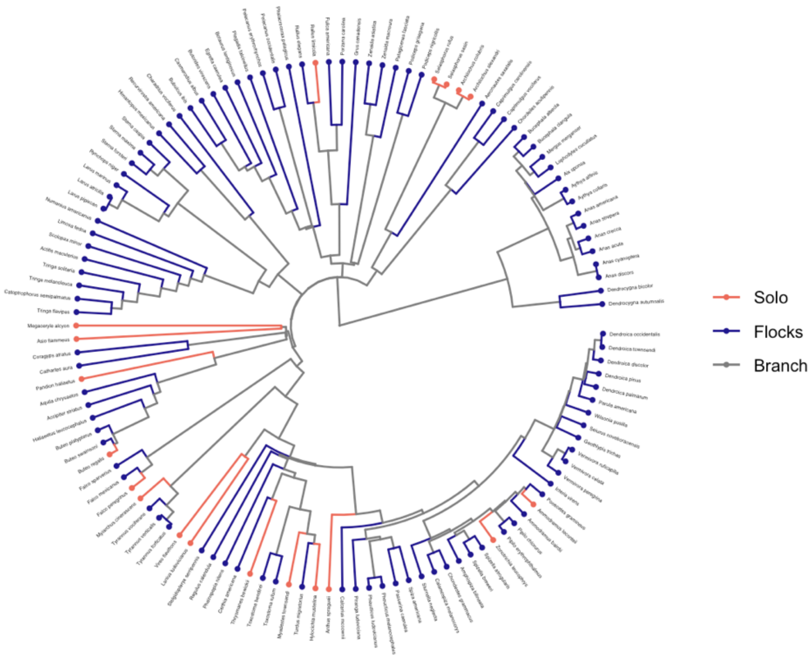


Figure SM10. Phylogenetic tree of the 122 species analysed for shifts in annual centres of abundance and incorporated into the Phylogenetic Generalised Least Squares (PGLS) models assessing migratory flocking behaviour as a binary variable (flocks/solo). Nodes are coloured by migratory flocking behaviour – solo (red) and flocks (dark-blue).

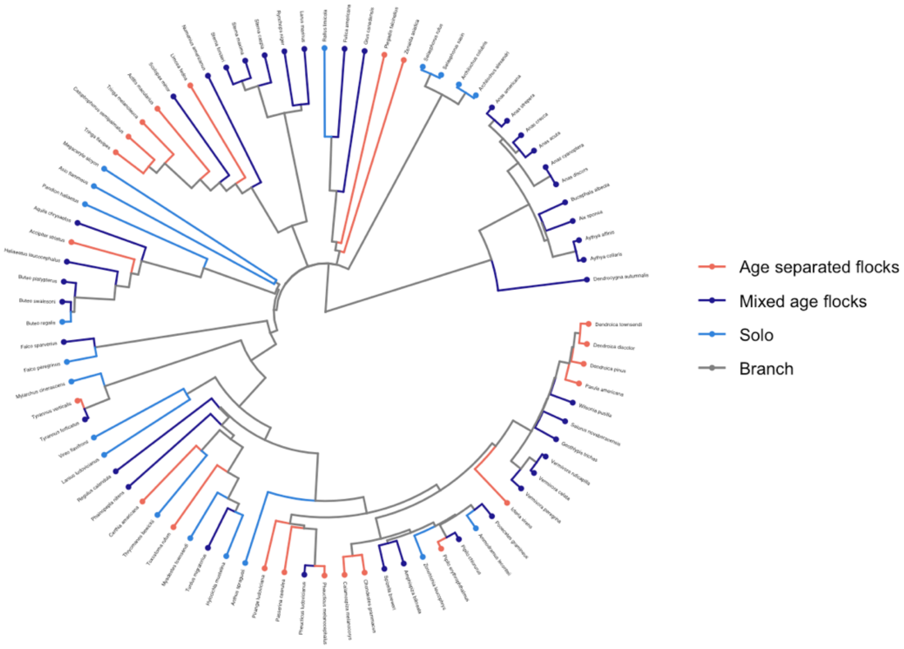


Figure SM11. Phylogenetic tree of the 81 species analysed for shifts in annual centres of abundance and incorporated into the Phylogenetic Generalised Least Squares (PGLS) models assessing migratory flocking behaviour as a three-level variable (mixed-flocks/age-separated flocks/solo). Nodes are coloured by migratory flocking behaviour – age-separated flocks (red), mixed-age flocks (dark-blue) and solo (light blue).

5

Limited effects of breeding and non-breeding climate anomalies on inter-annual population changes in North American birds

Vickers, S.H., Meehan, T.D., Michel, N.L., Franco, A.M.A., & Gilroy, J.J. (In review). Limited effects of breeding and non-breeding climate anomalies on inter-annual population changes in North American birds. Ornithological applications.

Abstract

Climatic change is increasingly impacting avian populations, but the effects of short-term climate fluctuations on year-to-year population change are poorly understood, particularly concerning the relative impacts of climate at different stages of the annual cycle. Here, we used North American Breeding Bird Survey data from 1968–2015 to assess the effects of temperature and precipitation anomalies in summer and winter on year-to-year population growth rates across 177 North American breeding bird species. Effect sizes of climate variables were generally small for most species, with significant climate relationships found in only 30.5% of species. Winter temperatures had the strongest standardized mean effect size on average, with summer temperature and winter precipitation marginally lower, and summer precipitation having the lowest by a significant margin. Between-species variation in population sensitivity to climate was poorly explained by species traits. The lack of strong climate effects across species may reflect the importance of spatial scale in identifying impacts of climate change, with effects of climate on annual population growth potentially being inconsistent across species ranges, and thus harder to detect at large spatial scales. The lack of clear relationships between climate sensitivity and species traits makes broad generalizations about climate impacts across species groups more difficult to achieve.

Keywords

Climate change, population trends, breeding, non-breeding, North America, birds, Breeding Bird Survey, temperature variability

Lay summary

Understanding how birds respond to fluctuations in weather and climate are key if we are to accurately predict future response to climate change.

We used 47 years of North American Breeding Bird Survey to assess the impacts of temperature and precipitation on annual population change of 177 species.

The impact of climate on year-to-year population change was generally small, with significant effects only found in 30.5% of species tested. This may be

because temperature and rainfall effects are often inconsistent across large areas, resulting in limited concordance with range-wide population changes. Targeted species-specific studies can be costly and time-consuming, so shared traits may be used to predict response across species groups. However, species traits proved to be a poor predictor of species reponses to climate in our study, making trait-based generlizations difficult.

Future studies should take care when generalizing effects across these large spatial scales.

Introduction

Broad-scale climatic change, driven by anthropogenic activity, has already been found to affect key demographic parameters in birds, but a better understanding of species sensitivities to climate is still required (Crick 2004). In North America, bird abundance is estimated to have declined by 29% since 1970, with climate change exacerbating the negative impacts of other drivers such as habitat loss, land-use change, and other anthropogenic activities (Rosenberg et al. 2019). Various studies have identified strong relationships between climate change and long-term population trends (Stephens et al. 2016, Howard et al. 2020), but less is known about the sensitivity of inter-annual population growth rates to season-specific climate fluctuation (but see e.g., Reed et al. 2013). Identifying the climatic drivers of short-term population growth can help us understand how climate variability may impact the demographic rates that underpin long-term changes. Short-term changes in climate (i.e. weather) can have significant effects on avian population growth rates, modulating both survival and reproduction in direct and indirect ways (Jenouvrier 2013, Sæther et al. 2004). Further significant change in climate is predicted over the next 100 years (Collins et al. 2013, IPCC 2014); therefore, a detailed understanding of how population growth rates respond to variation in climate is urgently needed to inform conservation prioritization and management.

Weather- and climate-driven impacts on survival and reproductive success produce strong associations between climate and population trends, observable both within species and across guilds (Betts et al. 2019, Eglington and Pearce-Higgins 2012, Mason et al. 2019, Pearce-Higgins et al. 2015). Weather-driven impacts on population growth are often associated with variation in temperature and precipitation (Pearce-Higgins et al. 2015, Robinson et al. 2007), and species can vary widely in their sensitivity to these variables in different seasons (Leech et al. 2004). Recent research on European migratory birds has suggested that long-term population trends were more closely associated with climate change on the breeding grounds than the non-breeding range (Howard et al. 2020). It is unclear whether this pattern is mirrored in other regions or avifauna, but the relative sensitivity of populations to season-specific climates is a key question for conservationists interested in pinpointing the stages of the annual cycle where species are most vulnerable to anthropogenic change (Sæther et al. 2004; Williams et al. 2015).

The conditions encountered by populations at each stage of the annual cycle can impact different components of population growth, e.g., survival rates and productivity (Nott et al. 2002, Robinson et al. 2007). Effects of climate on breeding success are thought to be predominantly driven by conditions within the breeding period, but there is also growing evidence for carryover effects from pre-breeding periods (Finch et al. 2014, Rockwell et al. 2012, Sorensen et al. 2009). For example, unfavourable conditions during the winter may lead to adults entering the breeding season in poorer condition, negatively impacting subsequent breeding success. Survival rates can be directly affected by climate throughout the annual cycle (Robinson et al. 2007), and there is some evidence that direct effects are stronger during the non-breeding period (Salewski et al. 2013). However, this has predominantly been shown in relatively restricted species pools or species-specific studies (e.g., Robinson et al. 2008, Stokke et al. 2005) and the effects of climate may have relatively low explanatory power in some species (Salewski et al. 2013). We thus lack a general understanding of the primacy of breeding and non-breeding season climates as drivers of both short- and long-term population trends across avifaunas.

Another key question concerns whether the relative sensitivity of species to season-specific climate variability can be explained or predicted by their traits. Understanding trait-dependence in sensitivity to climate can greatly aid in conservation efforts by improving our ability to effectively target conservation efforts towards species groups based upon shared traits and assumed shared risk profiles (Foden et al. 2013). Broad generalized conservation actions based upon trait-driven species assemblages may in turn be cheaper and quicker to enact than species-specific conservation planning (Nadeau and Fuller 2016). Trait-based associations also underpin elements of species-level climate change vulnerability assessments (CCVA's) that have been used to inform global conservation priorities (Foden et al. 2018). Migratory species are expected to be disproportionately impacted by changing climate (Robinson et al. 2009), and understanding season-specific climate sensitivity may enable practitioners to target limited resources and efforts to mitigate seasonal effects. This is likely to be beneficial for resident species conservation but will be particularly important in migratory species where targeted seasonal efforts may require drastically different approaches and potentially require international efforts (Runge et al. 2014).

Here, we utilize 47 years of Breeding Bird Survey data collected across continental North America to assess broad-scale effects of annual weather patterns on annual population growth rates in 177 avian species, spanning a broad spectrum of trait characteristics and occupying a wide variety of biogeographic regions of North America. We assess direct effects of season-specific climate anomalies (temperature and rainfall) on interannual population changes, with a focus on evaluating the generality of range-scale, season-specific responses across species. We evaluate trends in the relative importance of summer and winter climates based upon relative effect sizes of seasonal climatic variables and assess whether species-level responses to climate over broad scales are trait-dependent.

Methods

Population growth rates

The North American Breeding Bird Survey (BBS) (Pardieck et al. 2020) is a yearly road-based transect survey conducted at thousands of sites across North America, operating since 1966. Observers count the number of birds detected of each species at 0.8-km intervals along a 39.4-km survey route. Surveys are undertaken in late-May to early July and thus counts, for the most part, are representative of adult breeding populations. From these observer counts, yearly abundance indices are modelled by the United States Geological Survey (USGS) for more than 420 bird species using hierarchical Bayesian generalized linear mixed models with random terms controlling for year, stratum, and observer effects (Sauer et al. 2013). We used these annual abundance index values to calculate yearly relative population growth rates (*Lambda*) for each species using the following equation:

Equation 1.

$$Lambda_{year\ t} = \frac{BBS\ index_{year\ t}}{BBS\ index_{year\ t-1}}$$

Due to limited sampling conducted in the first BBS years and availability of climatic data, we used *Lambda* values only for the period 1968–2015.

Selection of species pool

We considered several factors in selecting species for inclusion in the analysis. The BBS yearly transect surveys are conducted across much of North America, but the distribution of survey locations is non-uniform, being linked to human population density and road infrastructure. In particular, northern Canada and Alaska have relatively poor spatiotemporal coverage, such that annual population indices for species with breeding ranges that include these sparsely-surveyed areas may suffer from low precision. To account for this, we restricted analyses to species with breeding ranges largely restricted to a contiguous region with sufficient spatial BBS coverage across the time period ('core BBS range'; Figure 1). Species with breeding ranges (based on Birdlife extant range maps (BirdLife 2019)) that overlap less than 75% with this region were then excluded from analysis. Further exclusions were also made for nocturnal species as they are unlikely to be well captured by daytime BBS surveys, and species with a marine non-breeding distribution as these species may be particularly transient in their non-breeding distributions between years. This produced a final pool of 177 species for analysis (Table SM1). For subsequent trait-based analysis, the species pool was further limited by the availability of some species trait data, leaving a maximum of 154 species.

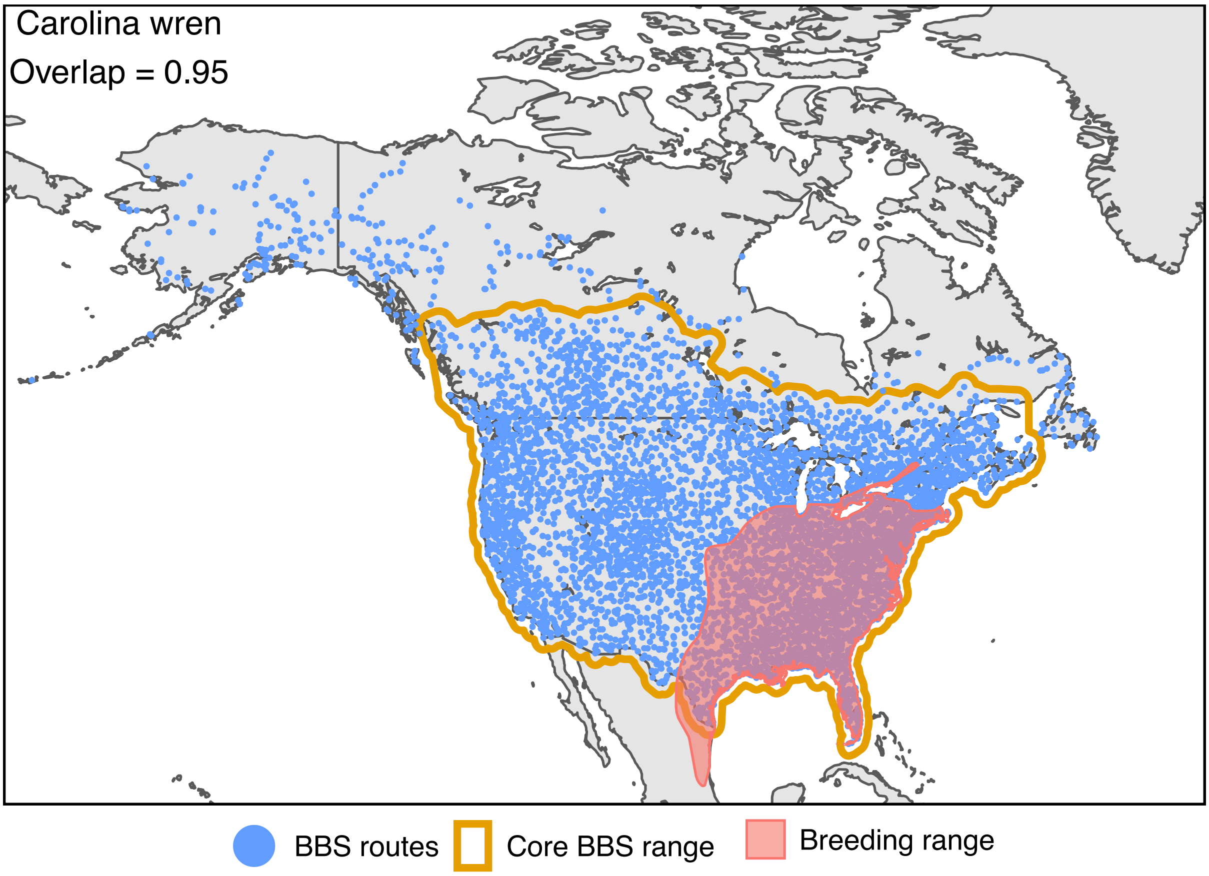


Figure 1. Map of North America depicting the location of all Breeding Bird Survey (BBS) routes (both active and inactive, blue points). The zone bounded in orange represents the 'core' BBS range where BBS route coverage was considered sufficient for robust inter-annual trend analysis. As an example, the breeding range of Carolina Wren Thryothorus ludovicianus is shown as the shaded red region; the degree of overlap between the core BBS range and the species' breeding range was used to determine whether species were retained for analysis.

Climatic variables

Monthly gridded temperature and precipitation data from CRU TS (Climatic Research Unit gridded Time Series, Harris et al. 2020) were used to create spatial raster layers of temperature and precipitation anomalies for North and South America with a cell resolution of 0.5° latitude by 0.5° longitude. Climate data was extracted for the entirety of North and South America to ensure complete coverage of the full annual range of the North American breeding birds studied. Each layer represented average May–August (summer) or November–February (winter) values for each year between 1967–2015 (Figure SM1). For temperature, this average was calculated from daily maximum temperatures (Celsius), and for precipitation as an average of total monthly rainfall values (mm). Anomalies were calculated at the cell level by taking the difference between each grid cell annual value (e.g., May–August year *t*) and the mean seasonal value for that cell across the entire 1967–2015 period. BirdLife extant range maps (BirdLife 2019) for breeding and non-breeding ranges were then overlaid onto these raster layers to extract annual mean climate anomaly values from across each range polygon (breeding and non-breeding) for each year and season. For species with ranges extending beyond the Americas, extant range maps were cropped to exclude these additional regions.

Modelling the effects of climate on year-to-year population growth rate

For each species, we modelled annual range-wide rates of population change (*Lambda*) as a function of mean breeding-range temperature and precipitation anomalies in the summer period of the preceding year, and non-breeding-range temperature and precipitation anomalies in the preceding winter period (Figure SM1). Annual weather values from the preceding year were used as BBS surveys take place at the start of or during the breeding period, and the summer weather of the previous year is therefore expected to have the most direct effect on observed annual population changes through its impacts on reproductive success and post-fledging survival. A separate general linear model was fitted for each of the 177 species including linear effects of all four climate variables (summer and winter temperature anomaly, summer and winter precipitation anomaly). We selected a Gaussian error family and an identity link function for these species-level global models based on visual goodness of fit checks and normalized fitted residuals. All regression predictors (climatic variables) were standardized by centering and dividing by 2 standard deviations (Gelman 2008). Model simplification was achieved through mutli-model averaging (*MuMin*; Barton 2020). We considered all possible combinations of predictors within a global model describing *Lamda* in association with the four climatic variables using the *dredge* function (*car*, Fox and Weisberg 2019) to produce candidate models. Collineariy was assessed through variance inflation factor scores, however no variables exceeded our cutoff value of 4 for variable exclusion (Pan and Jackson 2008). Models within 2 AIC_c units from the model with the lowest AIC_c (Burnham and Anderson 2002) were then averaged and the ‘full’ average output was used (Nakagawa and Freckleton, 2010).

We used a generalized linear mixed model with gamma error family and a log link function to test whether the model-averaged slope coefficients (i.e. climate variable effect) from the species-level models were significantly different between seasons (winter vs. summer), and climatic variables (temperature vs. precipitation). The model also included a two-way interaction between season and weather to evaluate seasonal differences in climate effects. A gamma error family with log link function was selected based on visual goodness of fit checks, normalized fitted residuals, and AIC_c values. For this model, the absolute values of the standardized slope coefficients were used in order to focus on magnitude of climate effect rather than direction, and species was treated as a random variable. To limit the influence of climate responses with high statistical uncertainty, the model was weighted by the reciprocal standard error of the response variable (i.e. the standard error of the slope coefficient derived from species-level climatic effect models).

Trait-based analysis of climate responses

We examined whether between-species variation in responses to climatic effects was explained by a range of species biological (e.g., body mass and clutch size) and geographical (e.g., range size and latitude) traits. Traits were selected to include physical, behavioral, and spatial characteristics of each species that might plausibly influence species sensitivity to climate (see Table 1 for details), and where species-level trait data was available across the species pool. We fitted linear regression models using these traits to explain between-species variation in slope coefficients for each of the four climatic variables, with the models weighted by the reciprocal standard error of the response variable. Gaussian error family and an identity link function was selected for these species-level global models based on visual goodness of fit checks, normalized fitted residuals, and lowest AIC_c values.

For each analysis, model refinement was undertaken through multi-model averaging (MuMin; Barton 2020). The global model consisted of the dependent variable and ten explanatory variables (Table 1). Species range size, range centroid latitude, and range-wide climatic variation were matched with the relevant season-specific climatic variables (i.e. summer range size was used as explanatory variable for summer climatic variables). Excessive collineariy was assessed through variance inflation factor scores, however no variables exceeded our cutoff value of 4 (Pan and Jackson 2008).

Table 1. Species trait variables used for the trait-based analysis.

Variable	Description	Source
Clutch size	Average number of eggs laid in a breeding attempt.	Cooke et al. 2019
Habitat specialism score	Score from 0–100 describing how specialized the species is in terms of habitat selection. 0 being a generalist, and 100 being a strict specialist.	Derived from Wilman et al. 2014 as the maximum proportion from the habitat usage categories.
Breeding range size	Total size of breeding range (km^2) based on BirdLife range map.	BirdLife 2019
Non-breeding range size	Total size of non-breeding range (km^2) based on BirdLife range map.	BirdLife 2019
Proportion of invertebrates in diet	Proportion of diet estimated to constitute of invertebrates.	Wilman et al. 2014
Diet specialism score	Score from 0–100 describing how specialized the species diet is. 0 being a generalist, and 100 being a strict specialist.	Derived from Wilman et al. 2014 as the maximum proportion from the diet categories.
Body mass	Average body mass in grams.	Wilman et al. 2014
Migrant	Does the species undertake a yearly migration.	Derived from BirdLife 2019 range maps.
Maximum longevity	Maximum lifespan in years.	Bird et al. 2020
Summer range centroid latitude	Centroid latitude of the breeding range based on BirdLife range maps.	BirdLife 2019

Non-breeding range centroid latitude	Centroid latitude of the non-breeding range based on BirdLife range maps.	BirdLife 2019
Range wide climatic variation	The average (across the 1969–2015 period) standard deviation in the relevant climatic variable across the range. Based on variation between grid cell values.	Derived from CRU TS (Climatic Research Unit gridded Time Series, Harris et al. 2020) and BirdLife 2019 range maps.

All statistical analyses were performed with R 4.0.3 (R Core Team 2020). Scripts for the completed analysis are available as electronic supplementary material.

Results

Effects of weather on year-to-year population growth rate

All four climatic variables were retained within the top candidate model set for 13% (23) of the 177 species considered. Winter and summer temperature were each retained in the top models of 63% of species, whilst winter and summer precipitation were retained for 60% and 58% of species respectively. For all four climatic variables tested, species-level model-averaged slope coefficients were clustered around zero, with 95% of the 433 standardized slope coefficients produced having absolute values less than 0.05 (Figure 2). No slope coefficients were produced in a further 275 cases due to the variables being dropped from the models in the model averaging process. Model-averaged slope coefficients were significant ($P<0.05$) in a relatively small number of cases overall, with summer precipitation being significant for 8 species (7.8%), summer temperature being significant for 14 species (12.5%), winter precipitation being significant for 18 species (16.8%), and winter temperature being significant for 23 species (20.5%). Explanatory power of species-level models were generally very low with an average adjusted R^2 of 0.042 (±0.008SE, range: -0.087–0.433) for global models.

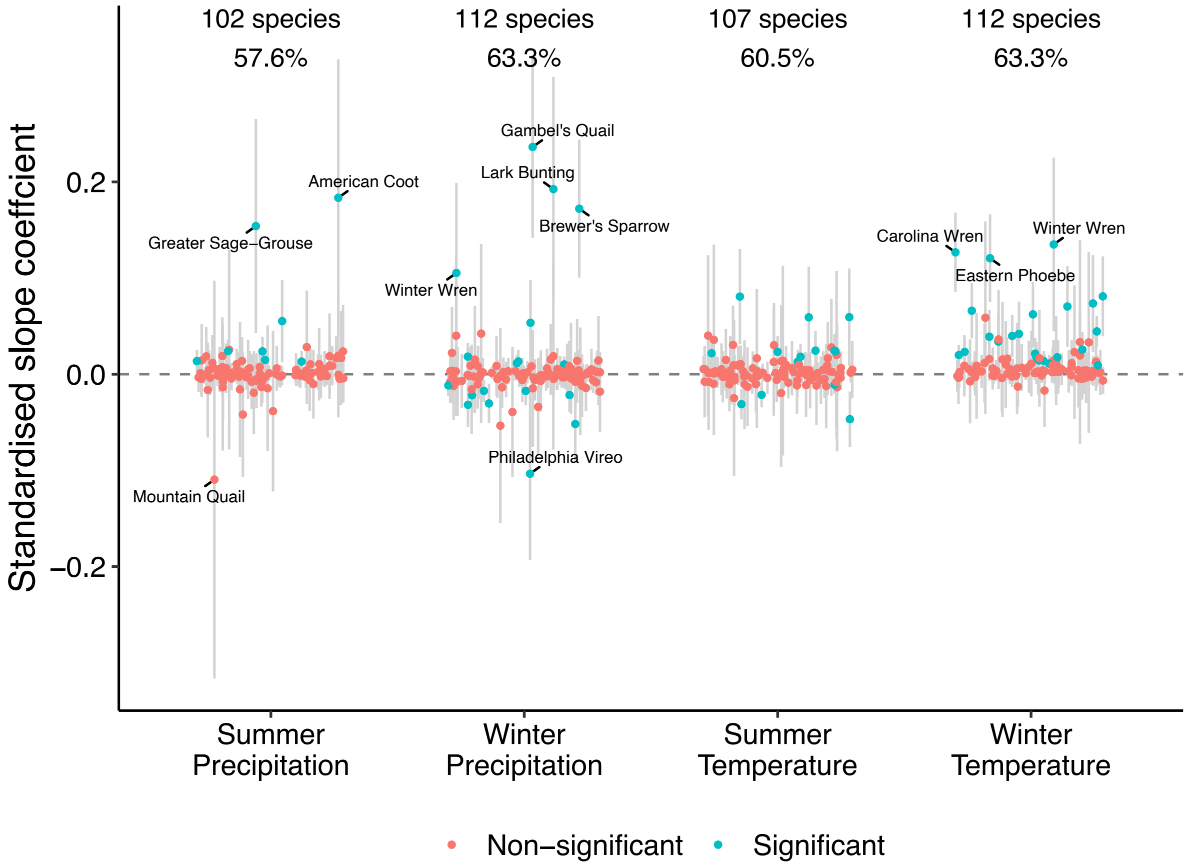


Figure 2. Standardized slope coefficients from 177 individual species-level models assessing summer and winter precipitation and temperature on yearly population growth rates. Inset numbers along the top of each variable indicate the number of species where the corresponding variable was included in the final averaged model for that species. Blue points indicate significant slope coefficients (P<0.05), red points indicant non-significant slope coefficients (P>0.05), and error bars indicate 95% CI. Species names are given only for species with strong effects (slope > 0.1 or < -0.1).

Across all species, the mean of all absolute values of model slope coefficients was lowest for summer precipitation, and significantly higher for winter precipitation and both summer and winter temperature (Table 2, Figure 3). However, this model had extremely low explanatory power (trigamma Pseudo R^2; marginal: <0.001, conditional: 0.02), suggesting a lack of generality in the strength of climate effects between seasons. The average effect size of season in explaining the magnitude of climate effects across seasons was also low (<0.01).

Table 2. Model summary results assessing seasonal (winter and summer) and climatic (temperature and precipitation) differences in absolute slope coefficients from the individual species-level models.

	Estimate	Standard error	t-value	P-value
Intercept*	-5.30	0.08	-64.4	<0.001
Season	0.38	0.01	38.4	<0.001
Climate	0.45	0.01	44.4	<0.001
Season : Climate	-0.35	0.01	-24.0	<0.001

* Reference levels of Season (Summer) and Climate (Precipitation)

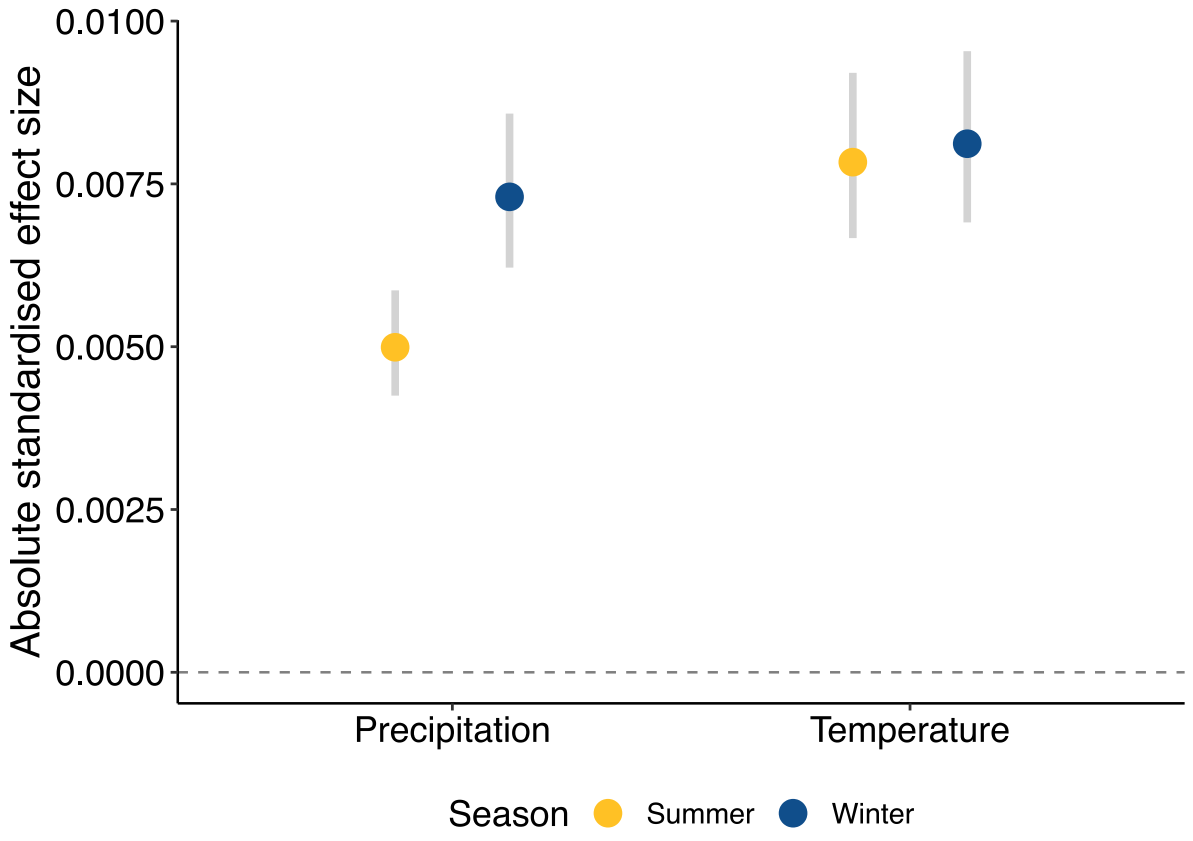


Figure 3. Across-species average of absolute standardized effect sizes for summer and winter precipitation and temperature based upon model predictions. Error bars indicate 95% confidence intervals of slope means across species.

Trait-based analysis of species climate responses

Species traits overall had limited power in explaining between-species variation in slope coefficients across the four climatic variables considered (mean R^2: 0.05 ± 0.01SE). Whilst many traits were retained within the candidate model sets in the averaging process (i.e. were present in at least one of the top performing candidate models), there were no significant associations found within the 'full' averaged model coefficients for any climate response (Figure 4). However, an association between winter temperature coefficients and non-breeding range latitude only fell just short of the significance threshold, as did winter precipitation coefficients and clutch size. With the heavy clustering of slope estimates around zero across all climatic variables, trait-based associations are likely to be difficult to ascertain and may partially explain the lack of significant associations.

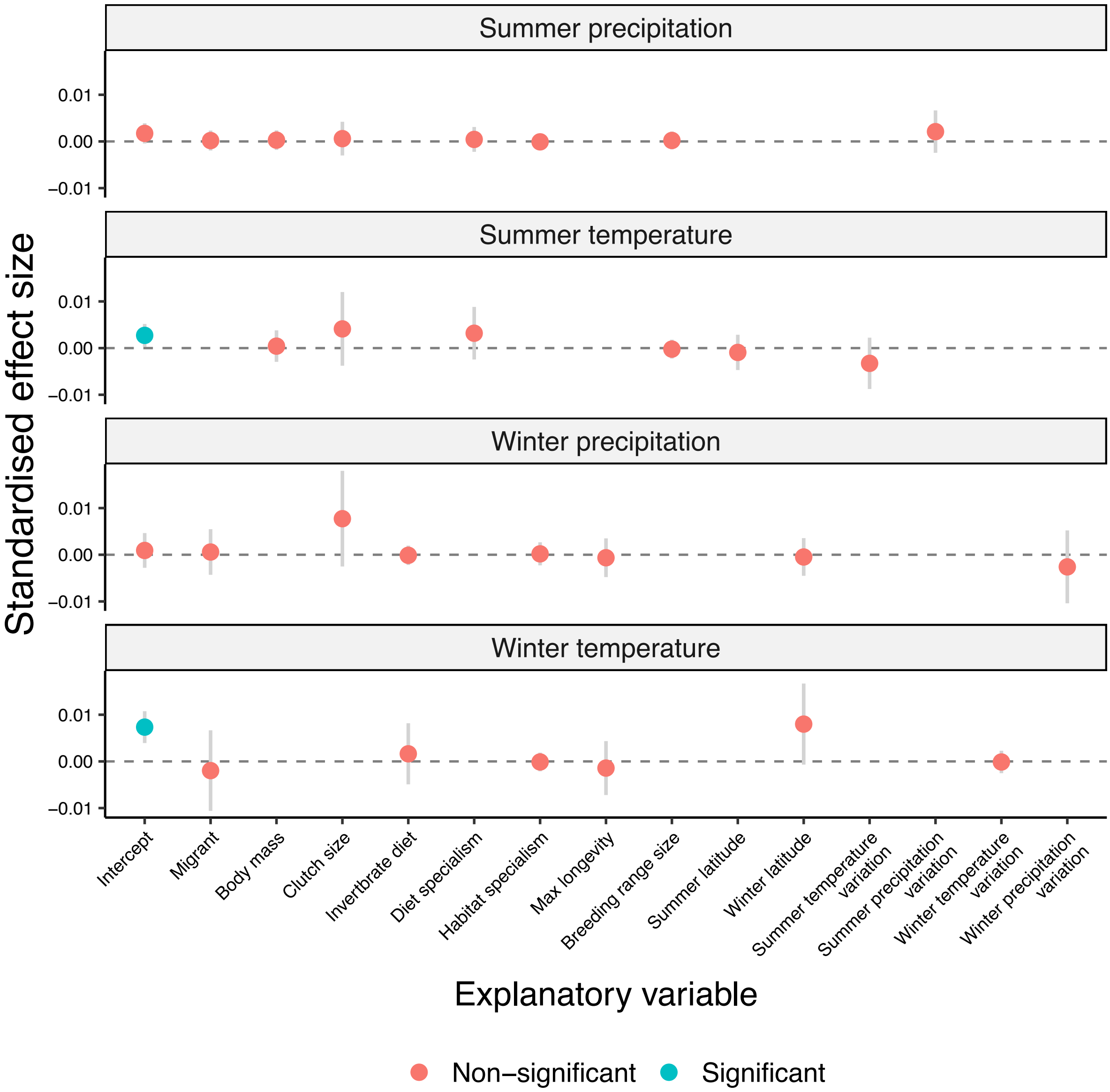


Figure 4. Standardized effect sizes for species traits from the four trait-based models assessing associations with the standardized slope coefficients from the 177 individual species-level models assessing summer and winter precipitation and rainfall on yearly population growth rates. Where there is no standardized effect size shown, the variable had been dropped within the model averaging process or was not included for that model (e.g., winter temperature variation was only included within the winter temperature global model). Blue points indicate significant slope coefficients (P<0.05), red points indicant non-significant slope coefficients (P>0.05), and error bars indicate 95% confidence interval.

Discussion

Our long-term, large-scale analyses suggest that the effects of climatic conditions on year-to-year population changes are generally weak in the majority of the 177 species we assessed, with direct climate associations being statistically significant for relatively few species and explaining little variation. More species showed significant associations with winter climate variables than summer variables overall, although absolute effect sizes were similar on average for winter precipitation, winter temperature, and summer temperature - only summer precipitation showed a significantly lower mean overall effect. The explanatory power of climate variables was almost universally very low across species, suggesting that annual population changes are generally relatively insensitive to large-scale climate variability across our studied species assemblage. We also found no significant relationships between sensitivity to climate variables and species traits, suggesting that generalizations about the effects of climate across species groupings may be difficult to make.

The observed clustering of effect sizes around zero from the four climate variables tested may have arisen through many methodological factors. Our analysis considered inter-annual variation in mean climate conditions across species' seasonal ranges, but many species may experience significant spatial heterogeneity in climate across their range in any given season, and thus may have varying responses across their range (Ashcroft et al. 2009, Senner et al. 2017). Our range-scale analysis may therefore 'smooth' any resultant effects across large geographic spaces, reducing observable effect size. Significant effects may be thus limited to those species that show particularly strong climate associations or have ranges with more spatially homogeneous climates. However, we found that spatial heterogeneity in yearly climate (measured as the range-wide standard deviation in cell-level values for each climate variable) was not significantly associated with the strength of climatic responses (Figure 4), suggesting that homogeneity of climate across the range alone is not a significant predictor of climate sensitivity.

The clustering of climate effect sizes around zero may also reflect short-term population resilience to the effects of climate, or dominance of non-climatic influences in driving short-term population changes (Jiguet et al. 2006). Broad climate effects have been shown in studies of both long-term population trends (Illán et al. 2014; Pearce-Higgins and Crick 2019) and in some cases inter-annual fluctuations in population size (Eglington and Pearce-Higgins 2012, Sæther et al. 2004) – the limited sensitivity of annual population changes to climate across our large species pool is therefore surprising. Whilst we did find strong associations in some species, indicating short-term response to climate can sometimes be strong, these effects could not be broadly generalized. Significant long-term impacts of climate could plausibly still arise where relatively modest short-term changes in climate have small population-level effects that accumulate over time or reach critical thresholds. For example, chronic sublethal effects of high temperatures and decreased precipitation are an expected outcome of climate change, potentially resulting in long-term population declines particularly in hot, arid zones (Conradie et al. 2019, Iknayan and Beissinger 2012), although the short-term signal of such impacts may be difficult to detect.

Previous work has come to varying conclusions on the relative importance of conditions during different seasons in determining rates of population change (Howard et al. 2020, Illán et al. 2014). Here we found relatively small differences in the overall strength of climate effects between seasons, and average absolute standardized effect sizes were consistently low across the four climatic variables. These results diverge from those of Howard et al. (2020), who found that climate suitability trends on the breeding grounds had a larger effect on long-term population trends than those of the non-breeding grounds for a suite of migratory European birds. Our lack of clear seasonal differences in average effect sizes, with the small differences that were present indicating a larger effect of winter climates, further reflect the disconnect between short-term annual effects and how they translate into general long-term trends.

Whilst long-term trends are clearly important for understanding the effects of climate change on birds, direct year-to-year effects have the potential to better inform us about the mechanisms driving impacts, and pinpoint ranges of conditions that are most likely to pose threats. Climate change is not only expected to lead to long-term trends of change in mean temperature and precipitation, but also lead to greater variability in climate between years on a continental scale, leading to greater and more common extremes (IPCC 2019). Understanding how this year-to-year variation may impact upon vulnerable species in the short-term is paramount in understanding the risk that these species may face at the range-wide scale. The weak signal of range-scale year-to-year climate impacts in our study also suggests that other methods may be necessary to explore these effects, particularly accounting for spatial climate heterogeneity within ranges, shorter term within-season climate fluctuations, longer term carryover effects and interactions with other drivers (e.g., land cover).

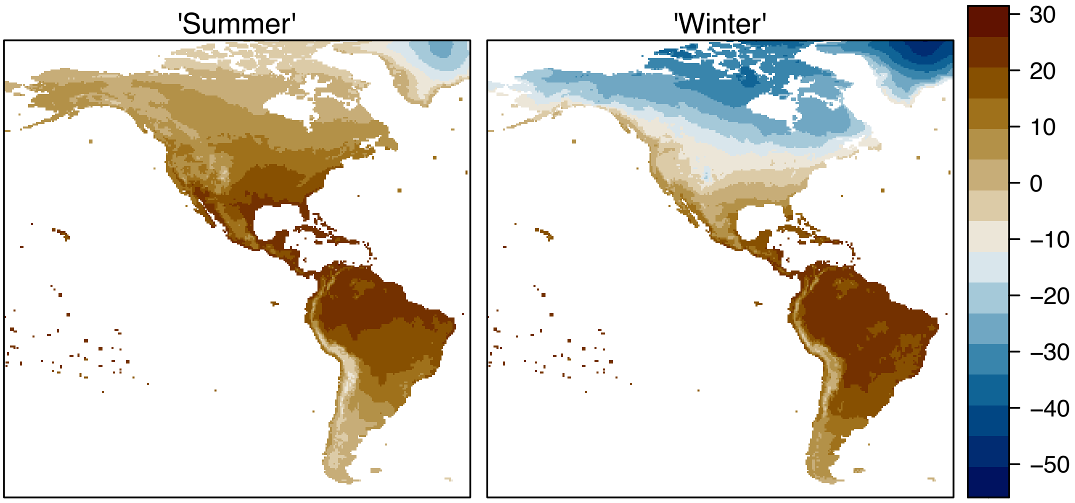
When applying conservation actions, practitioners may make certain assumptions in terms of extinction risk, effective strategy, and responses based upon shared traits between target species (Butt and Gallagher 2018). This is particularly the case with species that are hard to study or rare. Our results suggest that the species traits tested here are relatively poor predictors of species sensitivity to yearly climate variation, indicating a lack of consistency across species with shared characteristics. This may indicate that broad generalizations about climate sensitivity for species groupings (e.g., migratory insectivores) are unlikely to be accurate, further highlighting the importance of species-specific knowledge and bespoke conservation planning. Previous work has particularly focused upon the importance of habitat and/or dietary specialism in predicting long-term effects of climate change (Jiguet et al. 2010, Colles et al. 2009, Crick 2004), both of which were poor predictors in our analysis, with no clear directionality in effect on year-to-year climatic effects. This may be an indication that short-term effects of climate do not disproportionately impact specialists, though the weak climate effects left little variation to be explained by differences in specialization.

One pattern suggested by our trait analysis was that species with a more northerly non-breeding range tended to have more positive associations with warmer winter temperatures, although this effect fell just short of the usual significance threshold. The relatively small number of species that did show strong effects for winter temperature tended to be small-bodied species with more northerly non-breeding ranges, particularly insectivores such as Winter Wren (*Troglodytes hiemalis*), Carolina Wren (*Thryothorus ludovicianus*), and Eastern Phoebe (*Sayornis phoebe;* Figure 2). Over-winter survival of these species may be highly dependent on the availability of invertebrate prey, which in turn may be very sensitive to winter climate (Bowler et al. 2019, Cox et al. 2019, Nebel et al. 2010). Winter and Carolina Wrens, in particular, are notably sensitive to severe winter weather, with complete population loss following a severe storm in southern Illinois (Graber and Graber 1979). Similarly, a non-significant positive association between species with larger clutch sizes and wetter winters was apparently driven by small number of outlier species such as Gambel's Quail (*Callipepla gambelii*) that had a strong positive slope coefficient for winter precipitation (Figure 2) and a large clutch size (13; Wilman et al. 2014). These associations, whilst strong for certain species groups, were not found to be universal and likely point towards a more complex form of trait dependence where multiple traits may interact. Our trait-based analysis was also further limited by the heavy clustering of effects around zero for most species.

Overall, our analyses suggest a notably weak signal of range-wide climatic drivers for inter-annual population changes at the continental scale, with strong effects being limited to a handful of species. This suggests that climate effects on short-term population dynamics may be complex and operate over finer spatial scales, or accumulate over longer temporal scales, than those considered here. Researchers should be cautious in making generalizations about climate sensitivity across species groups at such scales, particularly if those generalizations are based on the assumption of shared outcomes for species with similar traits. As highlighted by Howard et al. (2020), further research is particularly required to understand how migratory connectivity might influence seasonal climate sensitivity, requiring a focus on effects operating at a more granular scale that accounts for geographic linkages within and between species seasonal ranges.

Supplementary material

Mean temperature (°C) in 2014



Mean precipitation (mm, log scale) in 2014

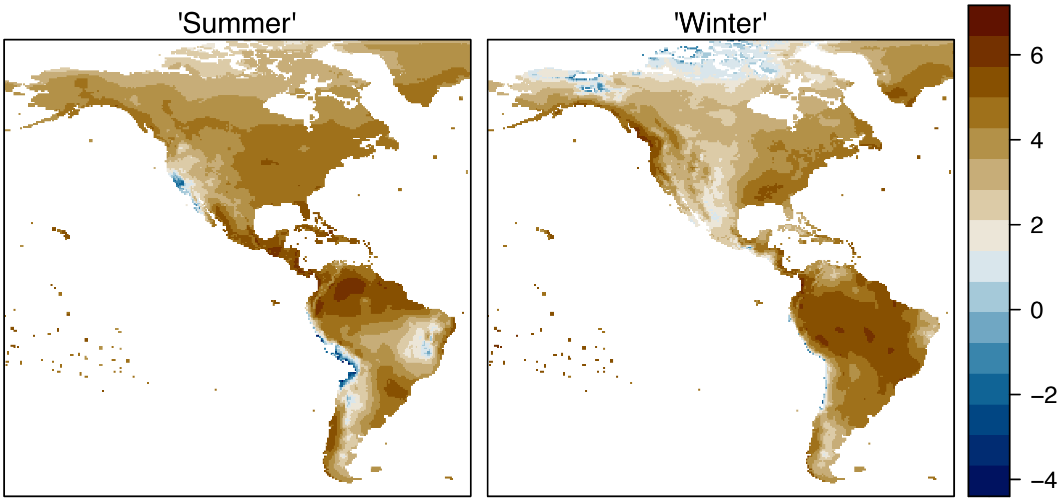


Figure SM1. Patterns of mean season-specific temperature and precipitation values across the Americas in 2014 (‘Summer’ = May–August, ‘Winter’ = November–February).

Table SM1. Systematic list of species where species-level model assessing effect of climatic variables were undertaken.

Species	***Latin***	**Species**	**Latin**	**Species**	**Latin**
Abert's Towhee	*Pipilo aberti*	Connecticut Warbler	*Oporornis agilis*	Oak Titmouse	*Baeolophus inornatus*
Acadian Flycatcher	*Empidonax virescens*	Cooper's Hawk	*Accipiter cooperii*	Orchard Oriole	*Icterus spurius*
Allen's Hummingbird	*Selasphorus sasin*	Dickcissel	*Spiza americana*	Ovenbird	*Seiurus aurocapilla*

American Avocet	*Recurvirostra americana*	Double-crested Cormorant	*Phalacrocorax auritus*	Painted Bunting	*Passerina ciris*
American Bittern	*Botaurus lentiginosus*	Dusky Flycatcher	*Empidonax oberholseri*	Philadelphia Vireo	*Vireo philadelphicus*
American Coot	*Fulica americana*	Eastern Bluebird	*Sialia sialis*	Pine Warbler	*Setophaga pinus*
American Crow	*Corvus brachyrhynchos*	Eastern Kingbird	*Tyrannus tyrannus*	Pinyon Jay	*Gymnorhinus cyanocephalus*
American Goldfinch	*Spinus tristis*	Eastern Phoebe	*Sayornis phoebe*	Prairie Falcon	*Falco mexicanus*
American Redstart	*Setophaga ruticilla*	Eastern Towhee	*Pipilo erythrophthalmus*	Prairie Warbler	*Setophaga discolor*
Anna's Hummingbird	*Calypte anna*	Eastern Wood-Pewee	*Contopus virens*	Prothonotary Warbler	*Protonotaria citrea*
Bachman's Sparrow	*Peucaea aestivalis*	Eurasian Tree Sparrow	*Passer montanus*	Purple Finch	*Carpodacus purpureus*
Baltimore Oriole	*Icterus galbula*	Ferruginous Hawk	*Buteo regalis*	Purple Martin	*Progne subis*
Barn Swallow	*Hirundo rustica*	Field Sparrow	*Spizella pusilla*	Pygmy Nuthatch	*Sitta pygmaea*
Bell's Vireo	*Vireo bellii*	Fish Crow	*Corvus ossifragus*	Red-bellied Woodpecker	*Melanerpes carolinus*
Bendire's Thrasher	*Toxostoma bendirei*	Gadwall	*Anas strepera*	Red-breasted Nuthatch	*Sitta canadensis*
Bewick's Wren	*Thryomanes bewickii*	Gambel's Quail	*Callipepla gambelii*	Red-headed Woodpecker	*Melanerpes erythrocephalus*
Black-and-white Warbler	*Mniotilta varia*	Golden-winged Warbler	*Vermivora chrysoptera*	Red-naped Sapsucker	*Sphyrapicus nuchalis*
Black-billed Cuckoo	*Coccyzus erythropthalmus*	Grasshopper Sparrow	*Ammodramus savannarum*	Red-shouldered Hawk	*Buteo lineatus*
Black-billed Magpie	*Pica hudsonia*	Gray Catbird	*Dumetella carolinensis*	Red-winged Blackbird	*Agelaius phoeniceus*
Black-chinned Hummingbird	*Archilochus alexandri*	Gray Flycatcher	*Empidonax wrightii*	Ring-necked Pheasant	*Phasianus colchicus*

Black-headed Grosbeak	*Pheucticus melanocephalus*	Gray Partridge	*Perdix perdix*	Rock Wren	*Salpinctes obsoletus*
Black-throated Blue Warbler	*Setophaga caerulescens*	Gray Vireo	*Vireo vicinior*	Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Black-throated Gray Warbler	*Setophaga nigrescens*	Great Blue Heron	*Ardea herodias*	Ruby-throated Hummingbird	*Archilochus colubris*
Black-throated Green Warbler	*Setophaga virens*	Great Crested Flycatcher	*Myiarchus crinitus*	Rufous Hummingbird	*Selasphorus rufus*
Blackburnian Warbler	*Setophaga fusca*	Greater Sage-Grouse	*Centrocercus urophasianus*	Sage Thrasher	*Oreoscoptes montanus*
Blue Grosbeak	*Passerina caerulea*	Green-tailed Towhee	*Pipilo chlorurus*	Scarlet Tanager	*Piranga olivacea*
Blue Jay	*Cyanocitta cristata*	Hermit Warbler	*Setophaga occidentalis*	Scissor-tailed Flycatcher	*Tyrannus forficatus*
Blue-gray Gnatcatcher	*Polioptila caerulea*	Hooded Warbler	*Setophaga citrina*	Song Sparrow	*Melospiza melodia*
Blue-headed Vireo	*Vireo solitarius*	House Finch	*Carpodacus mexicanus*	Sooty Grouse	*Dendragapus fuliginosus*
Blue-winged Teal	*Anas discors*	Indigo Bunting	*Passerina cyanea*	Spotted Towhee	*Pipilo maculatus*
Blue-winged Warbler	*Vermivora cyanoptera*	Juniper Titmouse	*Baeolophus ridgwayi*	Sprague's Pipit	*Anthus spragueii*
Boat-tailed Grackle	*Quiscalus major*	Kentucky Warbler	*Geothlypis formosa*	Summer Tanager	*Piranga rubra*
Bobolink	*Dolichonyx oryzivorus*	Lark Bunting	*Calamospiza melanocorys*	Swainson's Hawk	*Buteo swainsoni*
Brewer's Blackbird	*Euphagus cyanocephalus*	Lark Sparrow	*Chondestes grammacus*	Swainson's Thrush	*Catharus ustulatus*
Brewer's Sparrow	*Spizella breweri*	Lawrence's Goldfinch	*Spinus lawrencei*	Swainson's Warbler	*Limnothlypis swainsonii*
Broad-winged Hawk	*Buteo platypterus*	Lazuli Bunting	*Passerina amoena*	Tricolored Blackbird	*Agelaius tricolor*

Brown Creeper	*Certhia americana*	LeConte's Thrasher	*Toxostoma lecontei*	Tufted Titmouse	*Baeolophus bicolor*
Brown Thrasher	*Toxostoma rufum*	Least Flycatcher	*Empidonax minimus*	Upland Sandpiper	*Bartramia longicauda*
Brown-headed Cowbird	*Molothrus ater*	Lewis's Woodpecker	*Melanerpes lewis*	Veery	*Catharus fuscescens*
Brown-headed Nuthatch	*Sitta pusilla*	Loggerhead Shrike	*Lanius ludovicianus*	Vesper Sparrow	*Pooecetes gramineus*
Bullock's Oriole	*Icterus bullockii*	Long-billed Curlew	*Numenius americanus*	Warbling Vireo	*Vireo gilvus*
California Quail	*Callipepla californica*	Louisiana Waterthrush	*Parkesia motacilla*	Western Kingbird	*Tyrannus verticalis*
California Thrasher	*Toxostoma redivivum*	MacGillivray's Warbler	*Geothlypis tolmiei*	Western Meadowlark	*Sturnella neglecta*
Calliope Hummingbird	*Stellula calliope*	Marbled Godwit	*Limosa fedoa*	Western Tanager	*Piranga ludoviciana*
Canada Warbler	*Cardellina canadensis*	Marsh Wren	*Cistothorus palustris*	White-breasted Nuthatch	*Sitta carolinensis*
Carolina Chickadee	*Poecile carolinensis*	McCown's Longspur	*Rhynchophanes mccownii*	White-eyed Vireo	*Vireo griseus*
Carolina Wren	*Thryothorus ludovicianus*	Mississippi Kite	*Ictinia mississippiensis*	Wild Turkey	*Meleagris gallopavo*
Cassin's Finch	*Carpodacus cassinii*	Mountain Bluebird	*Sialia currucoides*	Willet	*Tringa semipalmata*
Cassin's Vireo	*Vireo cassinii*	Mountain Chickadee	*Poecile gambeli*	Williamson's Sapsucker	*Sphyrapicus thyroideus*
Cedar Waxwing	*Bombycilla cedrorum*	Mountain Plover	*Charadrius montanus*	Winter Wren	*Troglodytes hiemalis*
Cerulean Warbler	*Setophaga cerulea*	Mountain Quail	*Oreortyx pictus*	Wood Duck	*Aix sponsa*
Chestnut-backed Chickadee	*Poecile rufescens*	Mourning Dove	*Zenaida macroura*	Wood Thrush	*Hylocichla mustelina*
Chestnut-collared Longspur	*Calcarius ornatus*	Mourning Warbler	*Geothlypis philadelphia*	Worm-eating Warbler	*Helmitheros vermivorum*
Chestnut-sided Warbler	*Setophaga pensylvanica*	Mute Swan	*Cygnus olor*	Wrentit	*Chamaea fasciata*
Chimney Swift	*Chaetura pelagica*	Northern Bobwhite	*Colinus virginianus*	Yellow-billed Cuckoo	*Coccyzus americanus*

Chukar	*Alectoris chukar*	Northern Cardinal	*Cardinalis cardinalis*	Yellow-breasted Chat	*Icteria virens*
Clay-colored Sparrow	*Spizella pallida*	Northern Mockingbird	*Mimus polyglottos*	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
Common Grackle	*Quiscalus quiscula*	Northern Parula	*Setophaga americana*	Yellow-throated Vireo	*Vireo flavifrons*
Common Yellowthroat	*Geothlypis trichas*	Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	Yellow-throated Warbler	*Setophaga dominica*

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6

General discussion and future directions

Amongst a backdrop of widespread biodiversity declines (McCarthy 2002), extinctions (Barnosky et al. 2011), and the potential for ecosystem collapse (MacDougall et al. 2013), migratory species are experiencing outsized impacts (Rosenberg et al. 2019, Sanderson et al. 2006). The reliance on multiple ranges, stopover sites, and migratory flyways not only elevates the risk of being exposed to disparate region-specific pressures, but also makes targeted conservation efforts harder to implement (Faaborg et al. 2010, Horns & Şekercioğlu 2018). To ensure efficient use of limited conservation resources and evaluate the impacts of current trajectories of environmental change, conservationists increasingly rely upon predictive modelling, as well as trait-based inferences about species vulnerability (Elith and Leathwick 2009).

In this thesis I have worked to expand our current understanding of the specific challenges that migratory species face under a changing environment. This has included developing underlying theory on spatial population dynamics unique to migratory species, considering best-use practices for an existing proxy of population vulnerability, and assessments of real-world impacts that have been observed over the past 50 years of significant environmental change.

In **Chapter 2**, I demonstrated that migratory connectivity metrics (Mantel correlations) that are often touted as a good proxy for species vulnerability to environmental change may often give unreliable inferences due to sampling bias. These metrics demonstrate spatial scale-dependency, and I provided general guidance for how these metrics can be best applied. In **Chapter 3**, I explored the mechanisms underpinning spatial dynamics in migrant birds, and evaluated the efficacy of migratory connectivity metrics in predicting propensity for range-shifts under environmental change. Using models, I demonstrated that connectivity metrics are unlikely to be informative in these circumstances. This stems from the potential for connectivity patterns to be driven by non-heritable components of dispersal that are unlikely to promote inter-generational change. Improved understanding of the role of heritable dispersal components was a key outcome of the development of dispersal models in **Chapter 3**. I developed a novel theoretical framework for 'non-reproductive dispersal', analogous to traditional dispersal within the breeding range, that can be used to make more robust predictions about non-breeding range dynamics. In **Chapter 4**, I developed upon themes set out within **Chapter 3**, focussing on the prediction that spatially-uncoupled seasonal range shifts require heritable changes in migratory programmes, and that such heritability might be promoted by flocking behaviour during migration. I demonstrated that North American migratory birds travelling in flocks, particularly with experienced migrants, have experienced elevated rates of non-breeding range shifts over the last 50 years relative to those migrating solo. This conforms to the theory that cultural inheritance pathways can facilitate faster adaptation of the migratory programme. Finally in **Chapter 5**, I went on to assess direct impacts of climate on inter-annual population growth rates of North-American migratory birds, and the extent to which populations are sensitive to conditions experienced in breeding versus non-breeding seasons. Overall, this thesis has contributed towards an improved understanding of spatial dynamics for migrants under a changing environment, and will hopefully act as a foundation for future empirical study.

Implications for migratory connectivity

The concept of migratory connectivity (i.e. the extent to which spatial aggregations of individuals are maintained between consecutive phases of the migratory cycle, Marra et al. 2019) has and continues to receive significant interest among ecologists and conservationists. Several international research projects explicitly focus on ascertaining patterns of connectivity, with particular focus within birds (e.g., The Eurasian African Bird Migration Atlas 2022, The Migratory Connectivity Project 2022) and ocean-dwelling species (Migratory Connectivity in the Ocean 2022). In some instances, migratory connectivity is framed primarily through visual representation of emergent spatial patterns, but many researchers also rely upon statistical methods to quantify the relative strength between species and populations (Marra et al. 2019). A wide variety of statistical methods have been utilised to do so

(DeSaix et al. 2019, Korner-Nievergelt et al. 2017, Marra et al. 2018), with Mantel correlations (Sokal & Rohlf 1995) probably the most popular method, in part thanks to their relative simplicity. However, as demonstrated in **Chapter 2**, Mantel correlations display clear scale-dependence (Chapter 2 Figure 2) and are thus strongly influenced by the spatial arrangement of sampling effort. Practitioners must therefore take care in how spatial occurrence data are collected in order to avoid bias. Much of the existing migratory connectivity literature likely suffers from inherent sampling biases, although the specific nature and importance of this bias is likely to be study- and method-dependent. Broadly, studies are often biased towards sampling individuals marked within a single season in migratory species (often the breeding season), driven by factors such as disparities in regional funding availability or season-specific species detectability/catchability (Tonra et al. 2019). Developments in measuring the strength of connectivity by Cohen et al. (2018) have resolved some of the potential sampling-based sources of bias such as abundance among regions, spatial arrangement of regions, and sample sizes, but require range-wide demographic data that are lacking for many species. Furthermore, issues of scale-dependence are not fully resolved with this method, and Cohen et al. (2018) suggest that practitioners seek to measure migratory connectivity over as much of the species' range as logistically possible – a recommendation that is echoed in our work.

Fundamentally, as demonstrated in **Chapter 2** and further developed in **Chapter 3**, patterns of migratory connectivity are an emergent property of underlying mechanistic processes. Connectivity patterns are developed and maintained across generations by dispersal – both reproductive and non-reproductive. Whilst dispersal kernels can be shaped by extrinsic and intrinsic factors and are not necessarily uniform across populations of a species (Nathan et al. 2012), the dispersal ability of a population is ultimately a scale-independent process. Whether we assess species at the regional or continental scale, underlying absolute dispersal distances for individuals remain constant, but their role in determining patterns like connectivity vary strongly relative to the spatial scale of inference. Therefore, any attempt to quantify strength of migratory connectivity will always depend upon the spatial scale at which it is being assessed.

This does not necessarily imply that migratory connectivity metrics cannot represent useful conservation tools, but rather that their use and implications must be fully thought through. There is strong simulation modelling evidence for the importance of migratory connectivity in determining the impacts of habitat loss, where populations with weak connectivity are less impacted (Dolman & Sutherland 1994, Taylor & Norris 2010, Taylor & Stutchbury 2016, Taylor 2019). Furthermore, visual representations of migratory connectivity can provide invaluable evidence for population-specific targeted conservation efforts to link protected areas across the annual cycle. However, there has been a tendency across the migratory connectivity literature to focus on emergent spatial patterns rather than their underlying mechanisms. These are vital to understand how spatial patterns may be maintained across generations, rather than just as a snapshot in time. Currently there has been very little work on the temporal stability of migratory connectivity, particularly in the case of range shifts (Gómez et al. 2021).

Metrics of migratory connectivity are widely cited as a general tool for assessing vulnerability to environmental change in migratory species (Cohen et al. 2018, DeSaix et al. 2019, Korner-Nievergelt et al. 2017, Marra et al. 2019). Colonising new ranges is one of the key responses to environmental change that we are observing (Burrows et al. 2014, Chen et al. 2011, Couet et al. 2022, Gillings et al. 2015, Lehikoinen and Virkkala 2016, Parmesan and Yohe 2003, Stephens et al. 2016), and it was therefore important to assess whether connectivity metrics can be used to predict range-shift capacity. In **Chapter 3**, I showed that the strength of migratory connectivity can be a poor predictor of range shift propensity in simulations. Empirical studies are now required to fully assess the performance of connectivity metrics as predictors of spatial range dynamics. This would require population-specific or species-wide metrics of migratory connectivity, combined with quantification of range shift rates – such data are currently available for very few species, notwithstanding the additional issues of scale-dependence, but future advances may allow general assessments to be made.

Non-reproductive dispersal

Underlying the poor performance of migratory connectivity metrics in predicting propensity for range shifts (**Chapter 3**) was a novel theoretical framework describing the fundamental mechanisms that drive spatial change across migratory ranges. Previous work has demonstrated the key role of dispersal as a facilitator of range shifts (Årevall et al. 2018, Huang et al. 2020), but has failed to address the analogous movement processes that govern range dynamics in the non-breeding ranges of migrants. As set out in **Chapter 3**, these movements can be termed 'non-reproductive dispersal' and describe the distance between non-breeding locations occupied between years or generations. Non-reproductive dispersal is effectively an inverse measurement of non-breeding site fidelity (just as reproductive dispersal is to natal and breeding philopatry; Pearce 2007), which has received some attention (e.g. Blackburn and Cresswell 2020, Fullman et al 2021). Previous work has on occasion used the term *dispersal* to describe both reproductive and non-reproductive dispersal without distinction (Blackburn and Cresswell 2016). However, these non-reproductive dispersal movements do not fit any widely-used definition of dispersal, and the use of this general term does not accurately reflect the extent to which these types of dispersal differ. Unlike traditional 'reproductive dispersal' where novel locations can be automatically transferred to subsequent generations as they are born there, 'successful' non-reproductive dispersal may not always result in heritable colonisation events. This subtle difference means the two forms of dispersal should be distinguished as they have significantly different implications for population dynamics.

To reduce complexity, I tested the theoretical framework in a simple simulated population containing a single breeding range migrating to a single non-breeding range. In the real world, spatial patterns of migrations can also be highly complex (**Appendix 1**), and for multi-stop migrants that utilise several distinct ranges throughout the non-breeding period, there may be several distinct non-reproductive dispersal movements within each annual cycle that have the potential for interacting effects. Despite this, the underlying dispersal mechanisms and their implications are expected to remain consistent. Where genetic inheritance of the migratory programme is present, realised migratory routes are a result of an individual's ability to accurately follow its inherited programme. In **Chapter 3**, I modelled the stochastic nature of ability to follow the inherited programme as non-directional and without spatial auto-correlation. Currently, our understanding of what these stochastic forces are and how they influence resultant migratory programmes is relatively limited, but it is possible that 'migratory accuracy' could vary in consistent ways across a species' range. Environmental conditions such as wind drift have the potential to alter realised migratory routes (Acácio et al. 2022, McLaren et al. 2014) and their impacts across a populations may be spatially auto-correlated (provided migratory timing also shows spatial auto-correlation). However, there is also suggestion that clock and compass style inherited programmes lack the ability for precision navigation at the small (< 100 km) or medium (100–1000 km) scale for many species (Cresswell 2014), which if true is unlikely to be spatially auto-correlated. Other factors such as magnetic anomalies, geographical barriers, range limits, and anthropogenic developments (e.g., wind farms and urban sprawl) may also play a role in determining variation in realised migration routes, and all merit consideration in future work.

Chapter 3 indicated the need to empirically disentangle non-heritable drivers of variation in realised migratory programmes from heritable adaptations in order to better evaluate species capacities for rapid distributional change. Achieving this in the real world is challenging, requiring significant advances in our understanding of the genetic control of migration, and its variability within and between populations. Currently, although candidate genes associated with migration have been identified (Mueller et al. 2011; Saino et al. 2015; Johnston et al. 2016; Lugo Ramos et al. 2017, Gu et al. 2021), their effects on migratory programmes appear to be species-specific, and our understanding is limited in scope to describing general patterns across complex migratory programmes (Lugo Ramos et al. 2017). One approach to elucidating the role of patterns of heritable vs. non-heritable factors in determining migratory variability may be through increased tracking efforts. For example, comparisons of within-brood similarity of migratory programmes, relative to a wider population, could yield valuable insights. Here, the greater the relative similarity of realised migratory programmes within-broods may indicate a greater role of heritable drivers. Whilst existing tracking studies have made assessments of inter- and intra-individual consistency of migratory programmes (Franklin et al. 2022, Stanley et al. 2012, Tedeschi et al. 2020), there seems to be a lack of studies focussing on within-brood consistency or associating migratory outcomes with genetic relatedness.

Cultural inheritance of migratory programmes

Where cultural inheritance of migratory programmes takes place, the potential for non-heritable drivers of non-reproductive dispersal remain, but may be diminished in some cases. For species that form flocks on migration with naïve first-time migrants joining experienced individuals, stochastic forces that give rise to novel migration routes may be passed to subsequent generations in the absence of any heritable genetic novelty. This is because naïve juveniles following mature individuals can inherit an end-point destination through direct experience, rather than just genetically-encoded 'clock and compass' navigation instructions. We hypothesised that this has the potential to facilitate rapid migratory change across generations, being less dependent on mutation rates within underlying gene complexes that encode the clock-and-compass components of an inherited migratory programme. Culturally-inherited migratory change might still require some degree of plasticity in migratory programmes among experienced individuals (i.e. 'adult' non-reproductive dispersal), which current evidence indicates may be relatively limited (e.g. Blackburn and Cresswell 2016, Lourenço et al. 2016, Paruk et al. 2015). However, as with reproductive dispersal it can be expected to follow a 'fat-tailed' distribution with long-distance dispersive individuals having outsized impacts on population dynamics (Nathan 2001).

Changes in migratory programmes across generations may be essential in order for migratory populations to keep pace with seasonally-uncoupled shifts in their discrete ranges (**Chapter 3**), and current evidence indicates that uncoupled shifts are commonplace (Curley et al. 2020, Potvin et al. 2016). Previous work has illustrated how migratory programmes can adapt in large step changes, presumably through chance mutations followed by selection (Berthold et al. 1992). How migratory programmes have adapted and evolved over millennial timespans has also received attention (Gu et al. 2021). It is less clear how frequently populations have the capacity to alter migration programmes across decadal timespans, as potentially required under rates of current environmental change. Detection of observed seasonally-independent range shifts does however indicate that at least some species are changing their migratory programmes in the short-term. For example, approximate migratory distances have been demonstrated to be changing by up to 15km per annum in some North American and European birds (Curley et al. 2020, Gómez et al. 2021, Potvin et al. 2016). However, little attention has been given to whether the relative rates of uncoupled shifts are limited by traits that influence the heritability of migratory programmes.

In **Chapter 4**, I demonstrated that non-breeding range shift rates are significantly higher in species that migrate in mixed-age flocks. Whilst this is only correlative evidence, it supports the hypothesis that cultural inheritance may facilitate greater rates of heritable non-reproductive dispersal, and thus promote faster non-breeding range shifts. The reason we do not see the same effect in breeding ranges could be attributed to changes in the migratory programme being less significant in influencing reproductive dispersal. However, further work is required to better refine our understanding of how season-specific ranges are shifting throughout the annual cycle. Comparisons of range shift rates between seasons are hampered by differences in sampling effort and survey methodologies for collecting species occurrence data that can be difficult to account for statistically. Furthermore, quantification of range shifts themselves is difficult to achieve due to the challenges of defining range boundaries, stochastic species occurrence, and changes in abundance centres unrelated to range shifts (Yalcin and Leroux 2017). There also remains significant gaps in our understanding of migratory behaviour for many species, particularly pertaining to how individuals interact during migratory flights (Birds of the World 2022).

Drivers of population change

Chapters 3 and **4** highlighted the potential for the mechanisms determining species' demographic responses to environmental change to differ between seasonal ranges. In addition to differing spatial dynamics, we might expect species to show different levels of sensitivity to environmental changes between seasonal stages of the annual cycle. My comparative analyses in **Chapter 5** indicated that direct relationships between annual climate anomalies and inter-annual population growth rates were of a broadly similar magnitude across species for both breeding and non-breeding seasons in

North-American migratory birds. This was in contrast to results from Europe that found long-term trends were more strongly associated with breeding range climate change (Howard et al. 2020). This may however reflect key differences in the nature of inter-annual climate impacts versus long-term trends. We found that short-term effects of climate anomalies on population growth had low explanatory power for most species (**Chapter 5**), a surprising result considering the growing body of evidence for the impacts of climate change on population growth rates (Stephens et al. 2016, Howard et al. 2020) and evidence of strong season-specific climate sensitivity in some model species (Robinson et al. 2007; Schaub et al. 2011; Woodworth et al. 2017). However, even small short-term impacts may compound across longer time-spans to produce significant impacts on long-term trends. Furthermore, fine-scale spatial heterogeneity in climate anomalies and species population dynamics (including density-dependent processes) may make general impacts difficult to detect at the broad spatial scales studied in **Chapter 5**.

Currently, our capacity to study the effects of climate change on population growth rates for migratory birds across the full annual cycle are limited by the low spatial resolution of climate and population abundance data. We are also particularly limited in our ability to track population-scale movement patterns (i.e. migratory connectivity) in order to examine the role of seasonal carry-over effects in determining local population trends in most species. Whilst the rise of citizen science initiatives such as eBird (Sullivan et al. 2009) are expanding our ability to map spatiotemporal changes in species abundance at high resolution, there remain large areas with poor sampling coverage (particularly in developing and sparsely populated regions), and trends are still limited in their temporal scope to the 21st century (Horns et al. 2018). Advances combining these large-scale datasets with insights from individual tracking data may enable us to model the movement patterns of entire populations (Meehan et al. 2022), offering a promising means of improving our understanding of key season-specific sensitivities to environmental change.

General Conclusions

Without a sound understanding of underlying mechanisms that drive spatial population dynamics, we will remain limited in our capacity to forecast likely responses of migratory species to environmental change. The dependence of migrants on several distinct ranges through the annual cycle, and the act of migration itself, add various layers of complexity to many of the processes underpinning species responses to their environment. Dispersal is one of the most important ecological processes within population ecology, but in migratory species it operates in several unique ways that have previously been largely overlooked from a theoretical perspective. This thesis has explored how dispersal drives realised patterns of migratory connectivity, revealing key mechanistic differences between the processes involved in dispersal around breeding and non-breeding ranges. Within the non-breeding range, 'non-reproductive dispersal' is largely a result of changing migratory programmes between years or generations, but we lack in-depth knowledge of how change in migratory programmes arise and the heritability of these changes. These concepts have important implications for understanding the spatial dynamics of migratory populations, as well as how these populations respond to season-specific environmental change. Initial evidence points towards the importance of cultural inheritance mechanisms for migratory programmes, but further research into the complex mechanisms driving migratory programme development and heritability are needed. A better understanding of the drivers of demographic trends in migratory populations, accounting for the proximate and cumulative impacts of conditions experienced across the annual cycle, will also help in enabling researchers to inform effective and targeted conservation strategies.

7

Appendix

Appendix 1. A typology of spatial patterns of migration

Effectively assessing and predicting the effects of climate and land-use change is complex, and more so for migratory species that rely upon multiple distinct ranges. This is particularly the case when we consider the vast complexity of migratory programmes that occur across taxa. Surprisingly, researchers lack a clear unifying set of definitions of these different forms of migration, as well as a framework for understanding their commonalities and differences. Diverse spatial patterns of migration have been described across many taxa, but variations in definitions and descriptions often unique to a single species have led to obfuscating or confounding terminology in some circumstances. What’s more, many specific patterns have been left undefined and thus lack appropriate terminology. Here I set out 7 descriptive assessments that can be applied to a migratory species based on current understanding in order to classify them into ecologically distinct and clearly-defined spatial migratory patterns.

Assessment 1. Trans- vs. Cis-equatorial migration

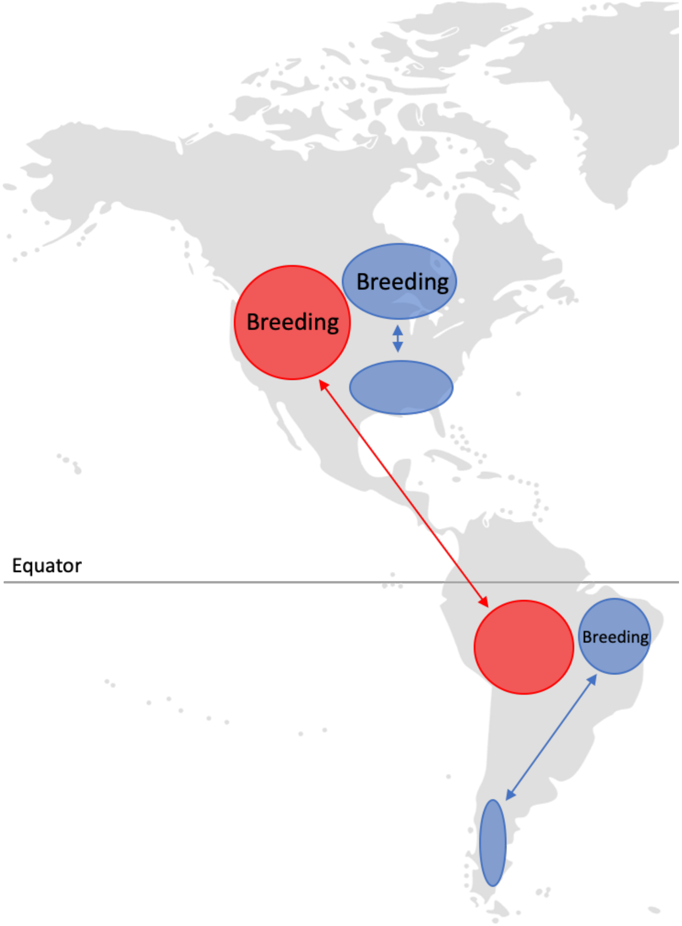

Figure 1. Simplified schematic illustrating seasonal ranges of a trans-equatorial migrant (red) and two cis-equatorial migrants (blue). Breeding range is labelled 'breeding' and the unlabelled ranges are the non-breeding ranges. Arrows depict seasonal migration.

Trans- and cis- equatorial migration (Figure 1) describes whether the migratory journey crosses the equator. Whilst at first this may seem an arbitrary distinction, this can be an important distinction when discussing the future impacts of climate change or species range shifts where independent ranges are predictive to shift poleward (Howard et al. 2018). Under such circumstances, trans-equatorial migrants would likely experience greater increases in required migratory distance than comparative cis-equatorial migrants.

Due to geographical, morphological, and energetic constraints most migrations are cis-equatorial. Of those species that are trans-equatorial migrants, most tend to be avian (Mellone et al. 2013). The primary exceptions to this are species that reside close to the equator, or marine based species where energetic costs of travel are lower.

Assessment 2. Directional vs. Dispersive migration

Figure 2. Simplified schematic illustrating a dispersive migrant. Breeding range (dark-orange) is labelled ‘breeding’ and the unlabelled wider range is the non-breeding range. Arrows depict seasonal migration.

Whilst most migratory programmes are directional (such as those depicted in Figure 1), and is sometimes a feature used to define migration, dispersive migration (Figure 2) describes a migration that lacks bias in direction at the population scale, but is cyclic (i.e. involves a return stage) and is thus distinct from nomadism. Dispersive migration is relatively uncommon in studied cases of migration, particularly in longer distance migrants (Newton 2008). Those documented examples that do exist are predominantly avian (Spruce Grouse: Herzog and Keppie 1980, Atlantic Puffin: Guilford et al. 2011, Common Guillemot: Wernham et al. 2002, Black-legged Kittiwake: Flegg 2004, Wandering albatross: Weimerskirch and Wilson 2000, Red Kite: Evans et al. 1999), however whether this is a sign of a wider trend or simply a result of vastly more migration research taking place for birds, is not known. Many examples of dispersive migrations involve relatively short migratory movements, in species sometimes thought of as residents (Wernham et al. 2002).

Assessment 3. Multi-stop migration

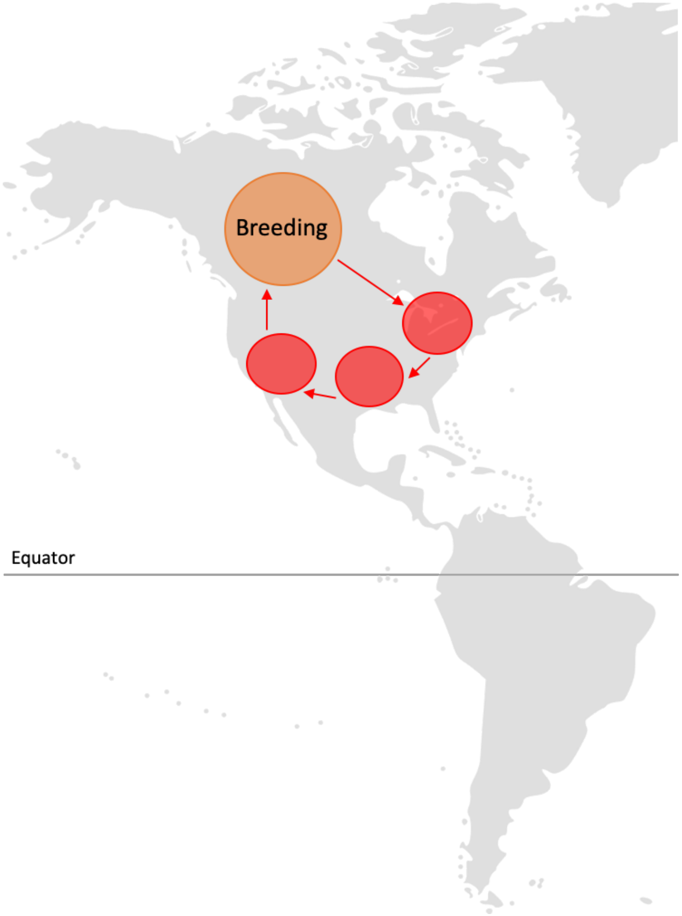

Figure 3. Simplified schematic illustrating a multi-stop migrant. Breeding range (dark-orange) is labelled 'breeding' and the three unlabelled ranges (red) are the distinct non-breeding range 'stops'. Arrows depict seasonal migration route.

Many simplistic migration schematics (e.g. Figure 1) show migratory journeys as arrows depicting flight lines, but this potentially fails to address the necessary stops that many species make on migration (Figure 3). Across taxa, there are many examples of species that undertake 'stopovers' at 'stopover sites' or 'staging sites' on their migration, but the definition of such sites are ill-defined and it is not clear at what point a stopover site become a wintering site. We argue that all species can be placed upon a bivariate scale describing the number of stops made during migration and the evenness of these stops (Figure 4). Some species may begin their migratory journey and only stop upon arrival at the non-breeding grounds, these are usually referred to as ‘non-stop migrants’ (Great Snipe: Klaassen et al. 2011). Others may make many stops with many stopover sites but at only one of these stops, their non-breeding site, do they spend an extended period (European Roller: Rodríguez-Ruiz et al. 2014). Whilst some species are not restricted to a single non-breeding site within a year and will make multiple stops across different non-breeding sites, as well as what would traditionally be determined as stopovers (Red-backed shrike: Pedersen et al. 2018).

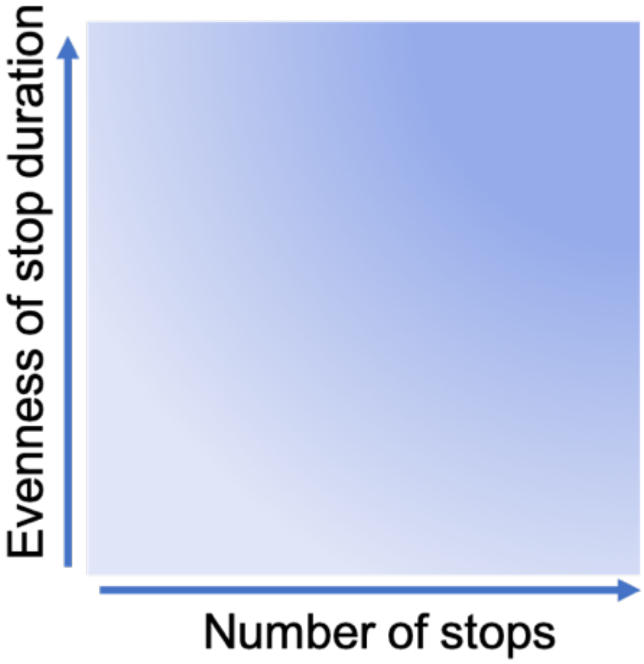

Figure 4. A bivariate scale could be used to measure migratory species based on their evenness of stop duration and the number of stops undertaken.

Assessment 4. Pattern consistency within/between populations

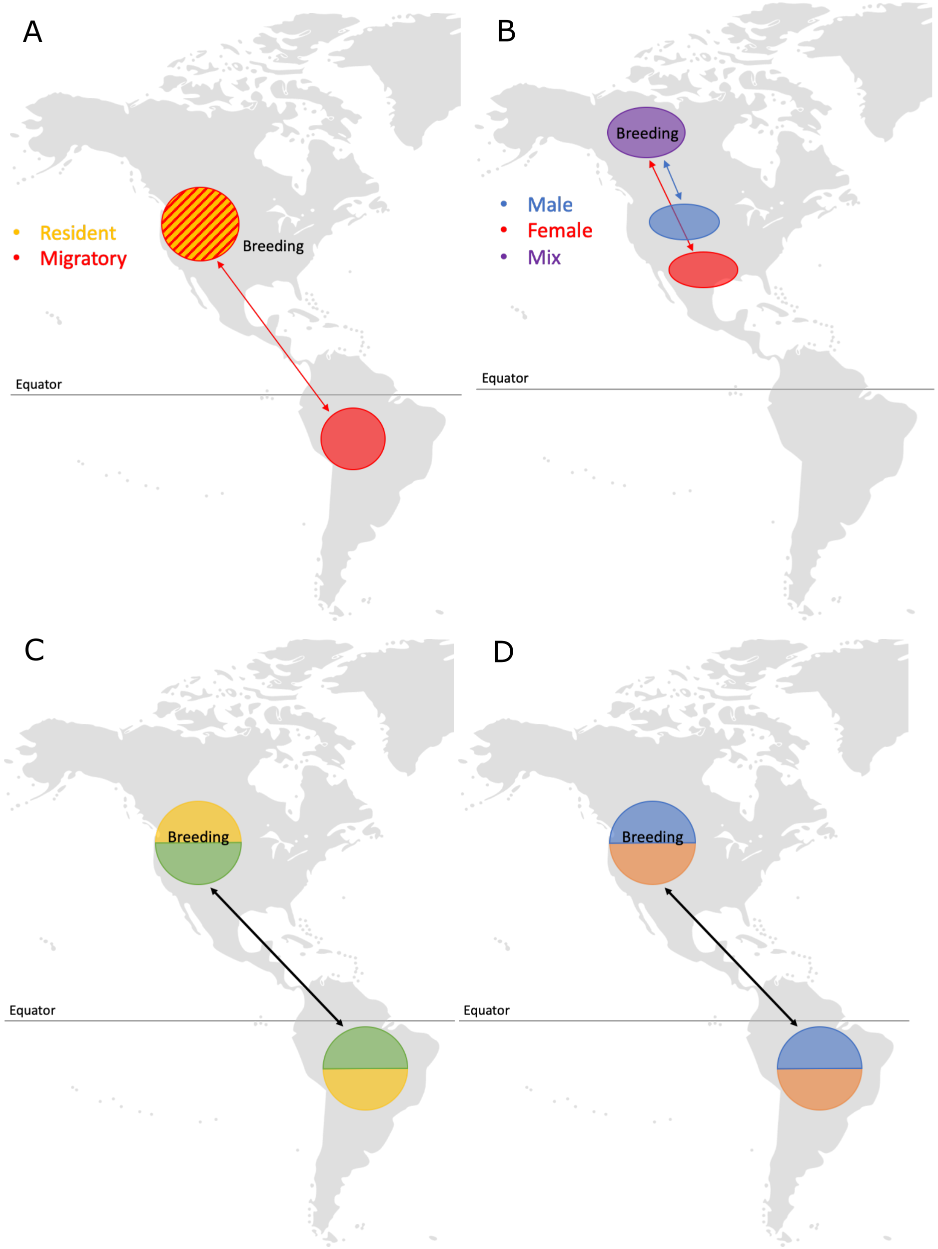

Figure 5. Simplified schematics illustrating variations in pattern consistency within and between populations. **A)** A partial migratory system where some individuals are resident and do not undertake migration. **B)** A differential migratory system, in this example differentiated by sex where females (red) migrate further than males (blue). **C)** Leap-frog migration – more northern breeding individuals (yellow) leap-frog more southern breeding individuals (green) on migration and the non-breeding region is thus further south. **D)** Chain migration – latitudinal sorting of individuals is maintained across the migration such that more northern breeding individuals (blue) have a non-breeding region further north than more southern breeding individuals (orange).

Certain spatial patterns of migration are described by the differences in distance travelled between individuals or populations of the same species. *Partial migration* (Figure 5A) for example refers to populations or species where only a proportion conduct a migratory journey at all, whilst the remaining individuals are resident year-round. Partial migration is widely documented across migratory taxa, occurring in all migratory groups including birds, mammals, fish, and invertebrates (Chapman et al. 2011). Variation in distance travelled within a species or population is also observed under *differential migration* (Figure 5B), where individuals migrate differing distances, directions, or timing based on either their sex (Blue Grouse: Cade and Hoffman 1993, Great Bustard: Morales et al. 2000), age (Spina et al. 2010, European Osprey: Bai and Schmidt 2012), or morph (Snow Goose: Cooke et al. 1975). *Leap-frog migration* (Figure 5C) occurs where higher latitude populations of a migratory species have non-breeding locations further south (or north in northerly migrating species) than populations at lower latitudes. Leap-frog migrations can be distinguished from differential migration in that the leap-frogging generally occurs between separate populations rather than within a single population. In some cases of leap-frog migration, such as in Fox Sparrows *Passerella iliaca,* the described leap-frog migration occurs between subspecies (Swarth 1920), but such leap-frogs have also been noted between populations of a single subspecies (Boland 1990). *Chain migration* (Figure 5D) on the other hand describes the opposing spatial pattern of migration to leap-frog migration, where latitudinal or longitudinal position is maintained across populations in both the breeding and wintering locations. Thereby the higher latitude breeders will winter at higher latitudes than the lower latitude breeders. Such migratory patterns are commonplace in migratory species (Fort et al. 2012, Goodrich et al. 2012).

Assessment 5. Pattern consistency between years

Figure 6. Simplified schematic illustrating a irruptive migrant. Typical seasonal ranges are shown in blue with the irruptive range shown in orange. Arrows depict seasonal migration.

In some species the timing, direction, and distance of migration can vary significantly between years. *Facultative migration* covers spatial patterns of migrations which can vary greatly depending on resource availability, and as such is characterised by being optional in whether the migration takes place and by being variable. Whilst this is superficially similar to partial migration, pattern consistency in facultative migrants is far less stable between years. Perhaps the most common type of facultative migration is *irruptive migration* (Figure 6) where certain species may migrate further or in far larger numbers in certain years. Food availability is often thought of as the primary driver of such irruptions (Newton 2006), where either a lack of food resources or an overabundance can both be a driver. Nomadism (non-seasonal, irregular movements) are sometimes also referred to as a form of facultative migration, however nomadic movements between breeding attempts are not strictly migratory movements as they are not cyclic and as such should be referred to as a form of sequential dispersal and not migration (Boyle 2018).

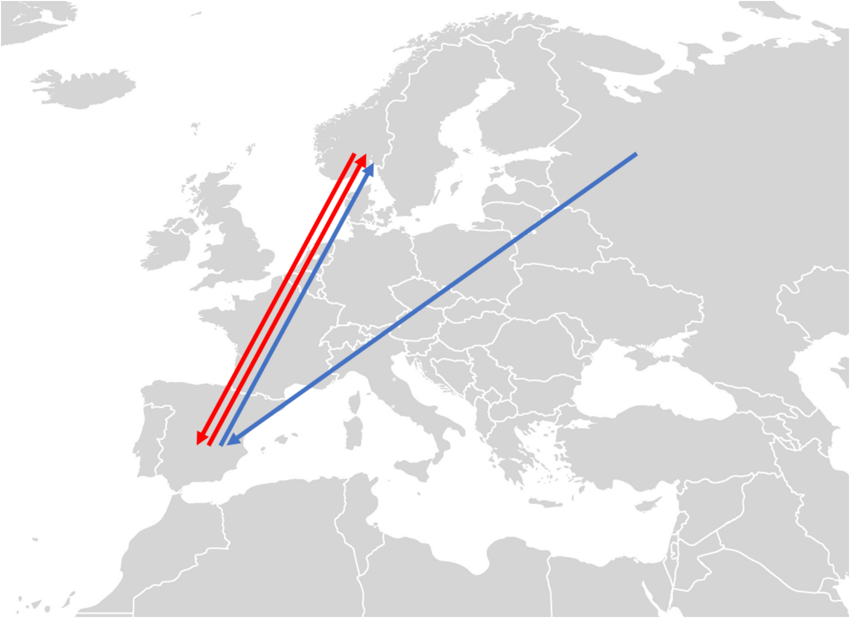

Figure 7. Simplified schematic illustrating abmigration. Arrows depict two individuals from different migratory flyways. The individual illustrated by blue arrows undergoes abmigration, switching to the red individuals migratory flyway.

Drastic changes in the specific migratory journey taken between years may also be described as *Abmigration* (Figure 7) and describes the spatial pattern of migration when there is a complete change in the migratory pathway. This change can take place within and between generations, acting at the individual or population scale but is not driven by resource availability like facultative migration. Guillemain et al. (2005) provided evidence of abmigration in Euarisan Teal *Anas crecca* shifting between an eastern and western European flyway, but recording evidence of abmigration such as this remains difficult due to the rarity of occurrence and inconspicuous nature of these changes. A possible more well-known example of abmigration may be certain cases of vagrancy. However, for vagrancy to truly be a form of abmigration it would require the vagrant to successfully return to the breeding range, for which there is limited evidence in most cases.

Assessment 6. Broad- vs. Narrow-fronted

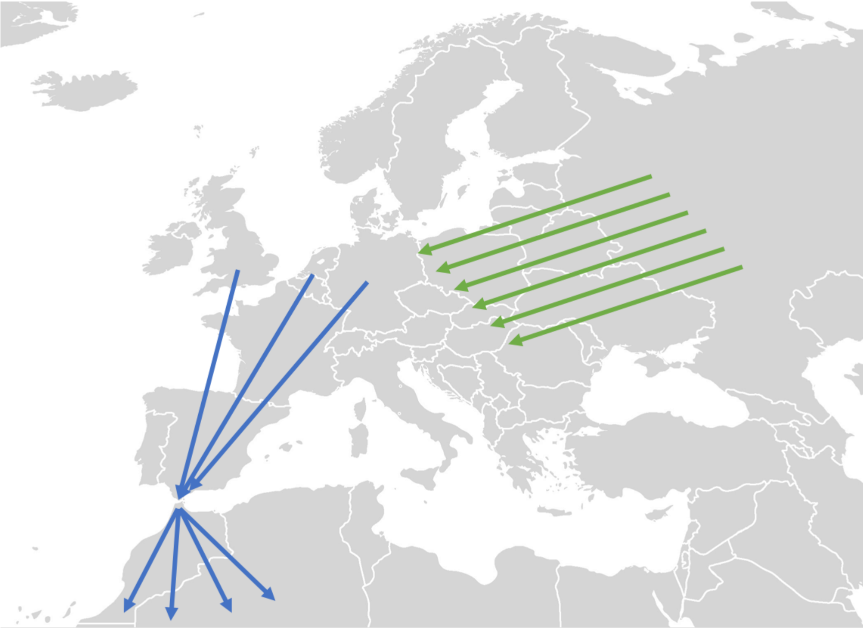

Figure 8. Simplified schematic illustrating broad-fronted (green arrows) and narrow-fronted (blue arrows) migration.

Migratory pathways can be assigned along a gradient between being *broad-* and *narrow-fronted* (Figure 8). Broad fronted migration describes movement in which the migrating population are spread across a wide geographic area, rarely confined by geographic features (Newton 2008, Bauer et al. 2018). Conversely, narrow fronted migration describes movement whereby the migrating population is confined to relatively narrow migratory pathways by geographic features such as mountain ranges, bodies of water, or habitat requirements (Newton 2008, Willemoes et al. 2014).

Assessment 7. Additional descriptors

In addition to the previous 6 assessment criteria, there is a non-exhaustive list of potential additional descriptors of spatial migratory patterns for which we outline those that are most commonly described across the literature.

Multi-generational migration

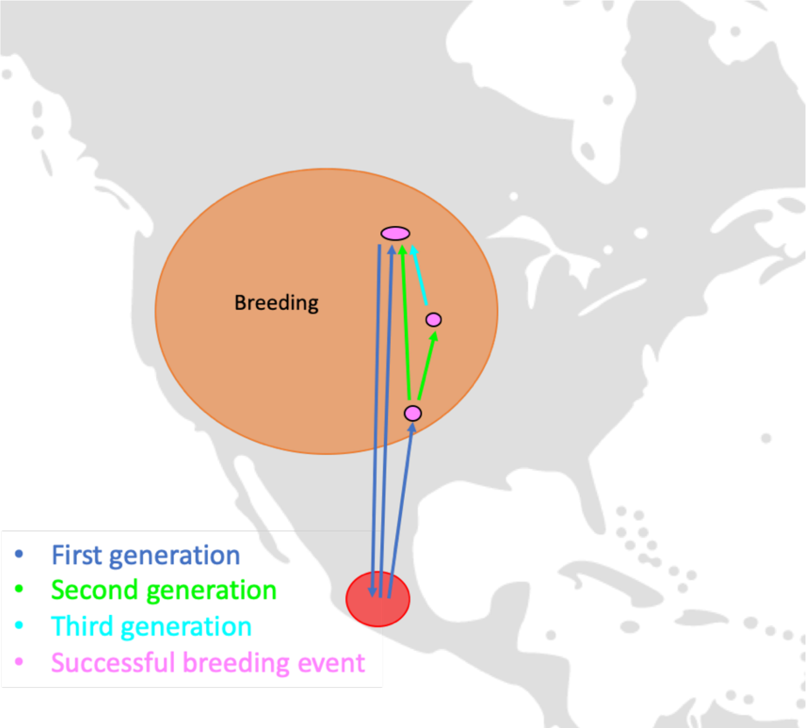

Figure 9. Simplified schematic illustrating multi-generational migration. Arrows depict the migration routes of three separate generations.

In shorter-lived species that undertake migratory journeys, multiple generations may be involved in a single cyclic migration (Figure 9). These multi-generational migrations are largely confined to invertebrates, with the most well-known examples coming from Lepidoptera (Stefanescu et al. 2012, Flockhart et al. 2013). Whilst these movements are widely considered migrations, they provide issues with defining migration itself. It can be argued that these movements are a form of sequential dispersal, in particular a cyclic sequential dispersal. Never-the-less, these movements predominantly behave as migrations at the population-scale and therefore remain important to consider when discussing spatial patterns of migration in some species.

Loop migration

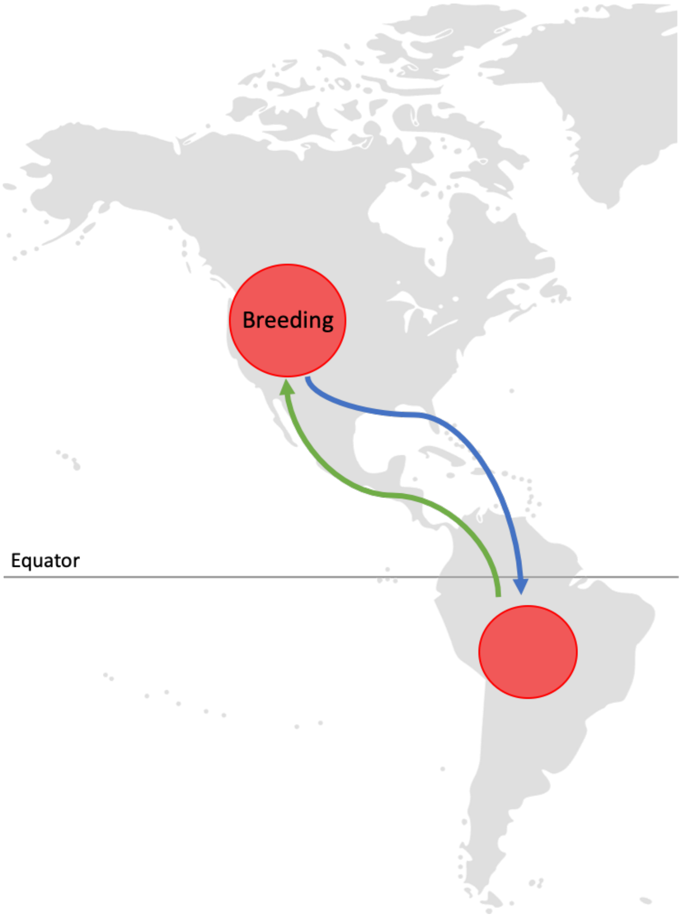

Figure 10. Simplified schematic illustrating loop migration. Arrows depict the migration routes, with the southern migration (blue) following a different route to the northern migration (green).

Although many species will use the same migratory flyway for their northern and southern migratory journeys, this is not always the case. *Loop migration* (Figure 10) is the spatial pattern of migration where the migratory route from the breeding range to the non-breeding range is different than the return migratory route back to the breeding range. Many species undergo loop migrations, and as is the case with much of the migration literature the bulk of examples are avian (Klaassen et al. 2010, Mellone et al. 2013, Willemoes et al. 2014). However, there are also well-known examples of non-avian species undergoing loop migrations such as the blue wildebeest *Connochaetes taurinus* of the Serengeti (Boone et al. 2006). These loop patterns of migration are often driven by differences in the spatial distribution of resource availability between seasons, but can also be driven by weather systems that aid migratory journeys in certain directions (Klaassen et al. 2010, Berdahl et al. 2016).

Altitudinal migration

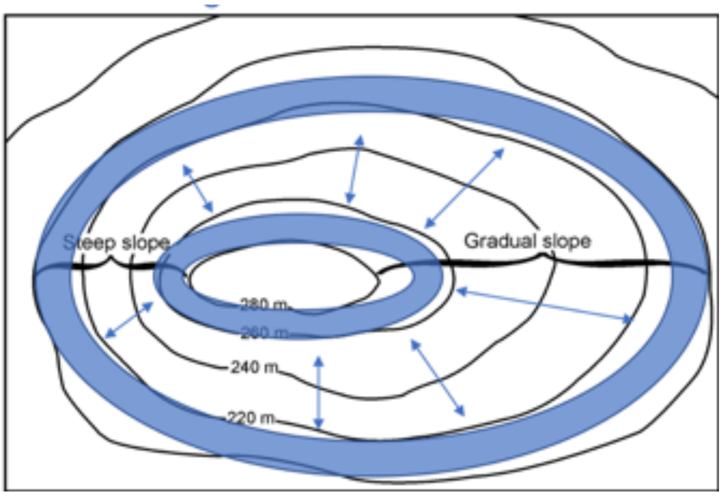

Figure 11. Simplified schematic illustrating altitudinal migration. Arrows depict the migration routes between two seasonal ranges at different altitudes.

Most spatial patterns of migrations are thought of as latitudinal and/or longitudinal movements, but migrations can also have an altitudinal element (Figure 11). Altitudinal migrants tend to breed at higher altitudes and migrate to lower altitudes during colder months, however the reverse is shown in some cases. As with many migratory journeys, altitudinal migrants appear to be driven by weather and resultant food availability (Hsiung et al. 2018). Whilst many of these migratory journeys are relatively short, drastic climatic changes can be achieved altitudinally with a much smaller journey than is required latitudinally. Altitudinal migration appears to be somewhat common in birds, but is also well documented in mammals, insects, and reptiles (Hsiung et al. 2018).

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