

Research article

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

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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 currently lacks a unifying theoretical framework. We present a novel conceptual model for dispersal in migrants that builds upon existing 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 of a solo-migrant population with a genetically encoded migratory programme 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, distribution change, Mantel, migration, migratory connectivity, non-breeding, range dynamics, range shift

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, Reed 2004, Kendrick et al. 2012). Dispersal is particularly important in the context of anthropogenic change, as it influences whether populations can track shifting zones of environmental suitability (Peterson et al. 2003, Thuiller 2004, Collins et al. 2013, IPCC 2014), as well as persist in fragmented landscapes (Chaine and Clobert 2012). While dispersal has been subject to intensive study, most theoretical and empirical work focusses on movements within and around breeding ranges (Ronce 2007, Le Galliard et al. 2012, Bocedi et al. 2014). 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

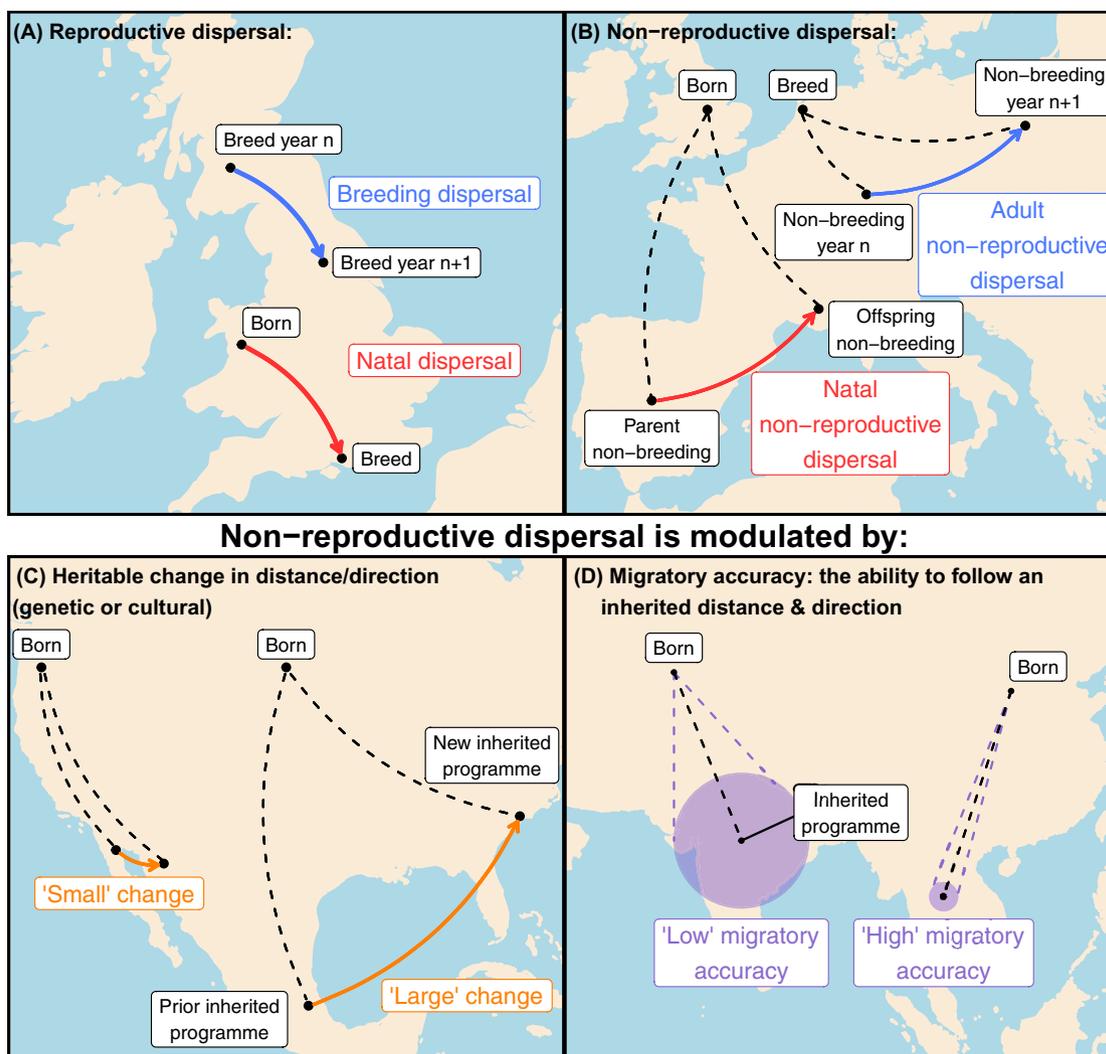


Figure 1. Conceptual dispersal framework for migratory species. Dispersal may be (A) reproductive dispersal or (B) non-reproductive dispersal. These dispersive movements can be either breeding (blue) or natal (red), describing the life stage in which these movements occur. Non-breeding dispersal can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

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 and 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).

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 and 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). Unless this new wind-drifted migratory destination can be transferred to the subsequent generation (either through cultural learning or genetic inheritance), offspring are likely to follow 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 (Riveros and Srygley 2010, Broms et al. 2012, Berdahl et al. 2014, Bingman and Ewry 2020, 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 programmes.

Migratory heritability influences dispersal outcomes

The transfer of migratory programmes between generations can occur through genetic or cultural mechanisms (Harrison et al. 2010, Liedvogel et al. 2011), with significant variation across taxa – although our understanding of this remains limited. Migration is known to have a strong genetic

basis in many organisms (Berthold 2003, Liedvogel et al. 2011, Zhan et al. 2014, Gu et al. 2021), 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 (Mouritsen 1998, Froy et al. 2003, Helm and Muheim 2021). This is likely to involve polygenic complexes spanning an organism’s sensory and circadian apparatus, morphology and neurophysiology (Merlin et al. 2020, Gu et al. 2021). Mutations in this genetic basis (or plasticity in migratory programme of adults in culturally learned systems) have the potential to generate significant heritable changes in migration (Fig. 1C), and thus the intergenerational colonisation of new non-breeding ranges. While there is evidence for rapid evolution of migratory programmes (Fiedler 2003, Bearhop et al. 2005, Sutherland 1998), 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 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, particularly in species that rely heavily upon genetically encoded migratory programmes. In such species, 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. This effect may be diminished in systems where cultural learning takes place, as offspring may be able to follow their parents back to the wind-drifted non-breeding location in subsequent years.

In organisms that migrate alone, where genetic control of migratory programmes may be commonplace, we might expect migratory accuracy to be generally low, particularly among immature individuals that are more vulnerable to weather-related drift or compass errors, or which 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 (Marra et al. 2019) – 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 or learned migratory programmes between individuals.

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 (Korner-Nievergelt et al. 2017, Cohen et al. 2018, DeSaix et al. 2019, Marra et al. 2019), with stronger connectivity often being taken to imply greater population sensitivity to perturbations like habitat loss (Dolman and Sutherland 1994, Taylor and Norris 2010, Taylor and Stutchbury 2016, Taylor 2019). However, because measurements of connectivity describe emergent spatial or temporal patterns within and across populations, 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 and Sutherland 1994, Taylor and Norris 2010, Taylor and Stutchbury 2016, Taylor 2019). Given our hypothesis that low migratory accuracy (non-heritable) has the potential to contribute significantly to realised migratory connectivity patterns, we predict that connectivity metrics may be relatively uninformative about the capacities of some species to respond to rapid spatial change.

To test these hypotheses about migratory dispersal and connectivity, we developed an individual-based simulation model of a solo-migrant population with genetically encoded migratory programmes, to examine how non-reproductive dispersal influences both realised migratory connectivity patterns and population responses to environmental change. For the latter, we focussed 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 (see Supporting information for full details). 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; Mouritsen 1998, Åkesson et al. 2017, Muheim et al. 2018, Helm and Muheim 2021). 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 parents’ migratory programmes. Empirical studies suggest that pairings of individuals with differing migration orientations often produce intermediate orientations in offspring (Helbig 1991, Berthold and Helbig 1992, Albert et al. 2006), suggesting that this assumption is likely to be reasonable for many real-world systems (but see Delmore and 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 $2 \times b$ 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 (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). A Gamma distribution was used as it produces zero-bounded continuous values which are highly flexible and allow for left-skewed heavy-tailed distributions that are often utilised in dispersal kernel literature (Nathan et al. 2012).

We incorporate non-reproductive dispersal via two mechanisms. First, 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; Supporting information) 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%, 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; Supporting information).

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 (Pärt et al. 2011, Ciaglo et al. 2021).

We ran each model for a 500-year burn-in, within which stable population and range dynamics were always achieved. To ensure model variation was 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 was identical to that of the breeding range (i.e. perfect connectivity; Supporting information). Variation in migratory destinations then emerged 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 (Supporting information).

Range shift scenarios

After the initial 500-year burn-in period, we exposed each simulated population to gradual shifts in the habitable zones for the breeding and non-breeding seasons. Shifts persisted 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); and

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 zone's 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 and Dufour 2007). Mantel correlations represent a correlation between two distance matrices that can be used to measure the strength of migratory 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 (www.r-project.org). Scripts for the completed analysis are available in Supporting information.

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 by 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).

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

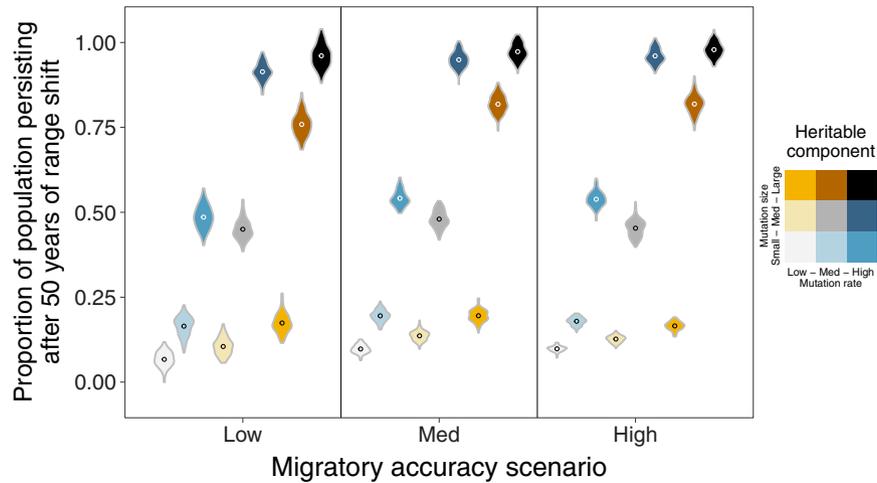


Figure 2. Persistence of simulated populations following uncoupled shifts in seasonal habitat zones, where breeding habitable zones shift more rapidly than non-breeding. Violin plots represent density distributions of individual model runs, spanning scenarios that vary in the levels of three drivers of non-reproductive dispersal (migratory accuracy, migratory programme mutation rate and mutation size). Mutation rate and size represent heritable components as their outcomes are passed on to the next generation under a genetically inherited migratory programme system. White or black outlined points indicate mean values for each given scenario.

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 and E). This

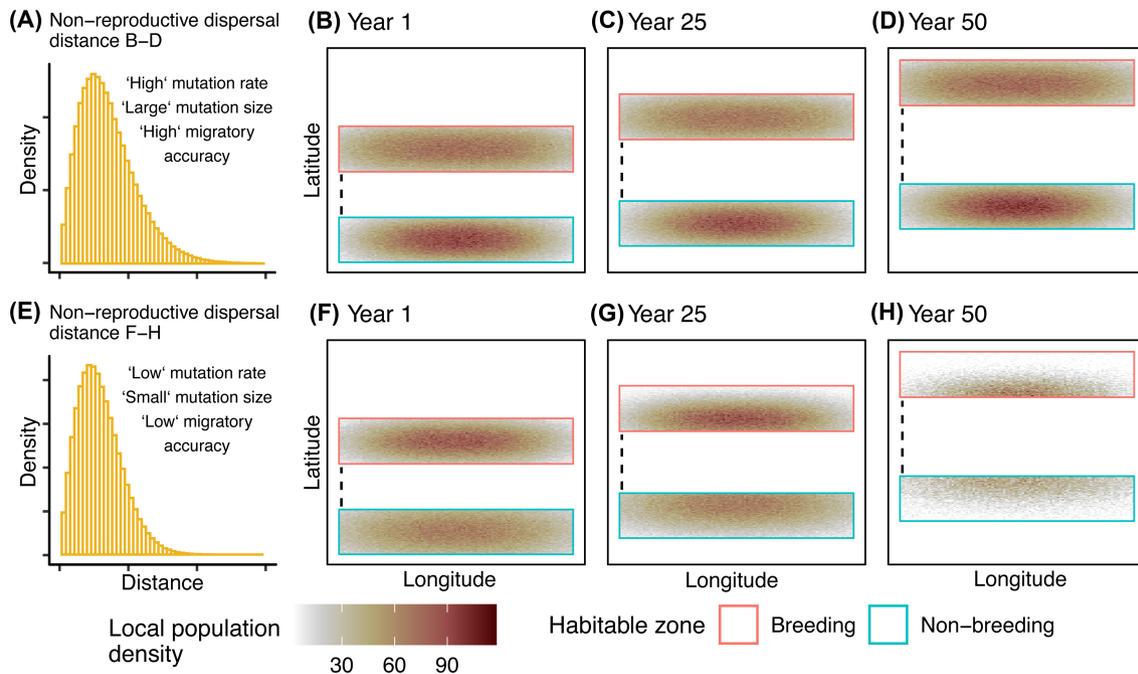


Figure 3. Realised non-reproductive dispersal distances in two example simulated populations, one with high mutation rate, large mutation size and high migratory accuracy (A–D) and another with low mutation rate, small mutation size and low migratory accuracy (E–H). Plots B–D and F–H illustrate the composite 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.

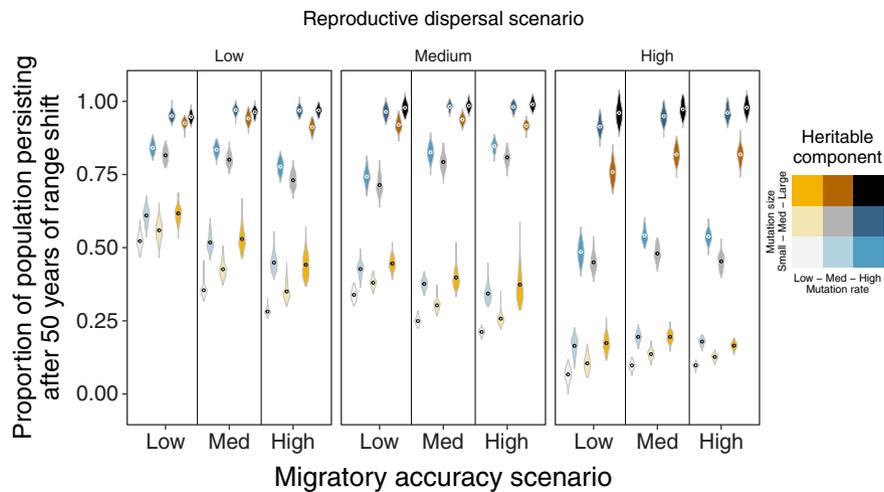


Figure 4. Interactive effects of non-reproductive and reproductive dispersal on population persistence in response to uncoupled shifts in seasonal habitable zones (breeding zone shifting more rapidly than non-breeding zone). Violin plots represent density distributions of replicate model runs for scenarios that vary in four drivers of dispersal (reproductive dispersal, migratory accuracy, migratory programme mutation rate and mutation size). Mutation rate and size represent heritable components as their outcomes are passed on to the next generation under a genetically inherited migratory programme system. White or black outlined points indicate mean values for a given scenario.

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).

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.

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

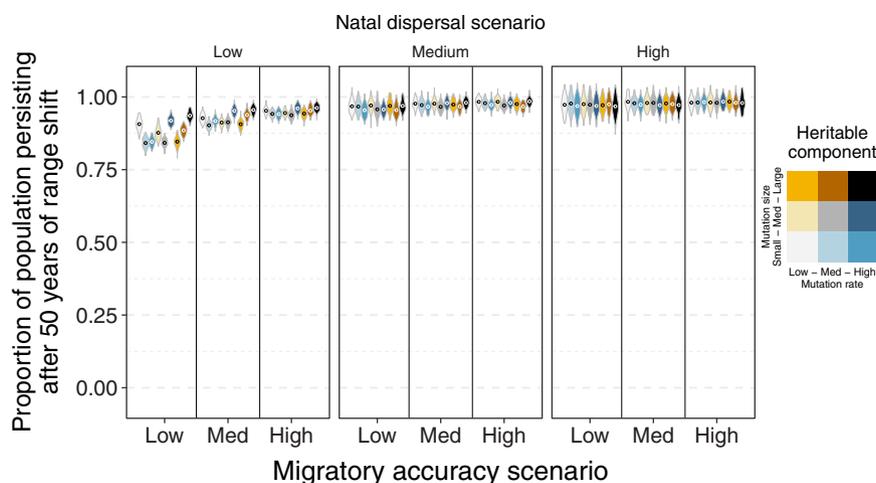


Figure 5. Population persistence under coupled range-shift scenarios where breeding and non-breeding habitable zones shift northwards at the same rate. Violin plots represent density distributions of replicate model runs for scenarios that vary in four drivers of dispersal (reproductive dispersal, migratory accuracy, migratory programme mutation rate and mutation size). Mutation rate and size represent heritable components as their outcomes are passed on to the next generation under a genetically inherited migratory programme system. White or black outlined points indicate mean values for a given scenario.

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.

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).

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 (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). While some populations can adapt in situ to changing climates, range shifting has been vital to many species' responses (Visser and Both 2005, Singer 2017, Hällfors et al. 2021). Our models demonstrate that non-reproductive dispersal is a critically important driver of range shifts in the non-breeding phase of the annual cycle, but the capacity for spatial change depends the extent to which these processes generate heritable outcomes. The complex balance between heritable and non-heritable drivers of non-reproductive dispersal also means that 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

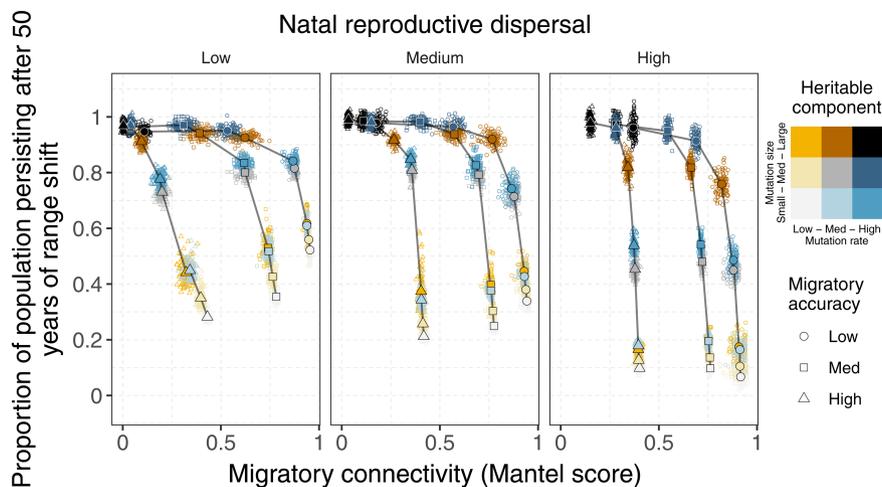


Figure 6. Relationship between realised migratory connectivity and the persistence of populations under uncoupled shifts in seasonal habitat zones. Connectivity is measured as the Mantel correlation at the end of a 500-year burn-in period, prior to range-shift exposure. Points represent model runs for a given combination of the four drivers of dispersal (reproductive dispersal, migratory accuracy, migratory programme mutation and size). Mutation rate and size represent heritable components as their outcomes are passed on to the next generation under a genetically inherited migratory programme system. White or black outlined points indicate mean values for a given scenario.

common seasonally coupled shifts are in reality, though some lines of evidence suggest that uncoupled shifts may be more frequent (Potvin et al. 2016, Howard et al. 2018, Zurell et al. 2018a, Curley et al. 2020). 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 and Leberg 2007, La Sorte and Thompson 2007, Zuckerman et al. 2009), but more complex multidirectional range shifts comprising both latitudinal and longitudinal shifts are also commonplace (Potvin et al. 2016, Fei et al. 2017, Huang et al. 2017, Curley et al. 2020), as well as rapid changes in migratory patterns (Sutherland 1998, Dufour et al. 2021). 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 (Sutherland 1998, Elmberg et al. 2014, 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 learning (Gill et al. 2019). Culturally learned 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 learning, 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 learning 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. 1B), 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. However, this may be complicated by spatiotemporal 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. 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). While this may be true for scenarios of habitat loss (Dolman and Sutherland 1994, Taylor and Norris 2010, Taylor and Stutchbury 2016, Taylor 2019), our models suggest this may not 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 capture–mark–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 (Williams et al. 2016, Zurell et al. 2018b). Centroid distances between seasonal home ranges could thus be used to directly measure non-reproductive dispersal distances (Sweaner and 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. 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. While reproductive dispersal *sensu stricto* is supported by a comprehensive theoretical literature, the existing framework does not capture the distinct set of dispersal processes that operates 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. While dramatic changes in migratory ranges are known to have occurred in many species (Sutherland 1998, Ruegg and Smith 2002), 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.

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Author contributions

Stephen H. Vickers: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Software (lead); Visualization (lead); Writing – original draft (lead). **Aldina M. A. Franco:** Conceptualization (supporting); Funding acquisition (supporting); Writing – review and editing (supporting). **James J. Gilroy:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (supporting); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.51c59zwh> (Vickers et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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