RESEARCH ARTICLE

Modelling the responses of partially migratory metapopulations to changing seasonal migration rates: From theory to data

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Abstract

1. Among-individual and within-individual variation in expression of seasonal migration versus residence is widespread in nature and could substantially affect the dynamics of partially migratory metapopulations inhabiting seasonally and spatially structured environments. However, such variation has rarely been explicitly incorporated into metapopulation dynamic models for partially migratory systems. We, therefore, lack general frameworks that can identify how variable seasonal movements, and associated season- and location-specific vital rates, can control system persistence.

2. We constructed a novel conceptual framework that captures full-annual-cycle dynamics and key dimensions of metapopulation structure for partially migratory species inhabiting seasonal environments. We conceptualize among-individual variation in seasonal migration as two variable vital rates: seasonal movement probability and associated movement survival probability. We conceptualize three levels of within-individual variation (i.e. plasticity), representing seasonal or annual variation in seasonal migration or lifelong fixed strategies. We formulate these concepts as a general matrix model, which is customizable for diverse life-histories and seasonal landscapes.

3. To illustrate how variable seasonal migration can affect metapopulation growth rate, demographic structure and vital rate elasticities, we parameterize our general models for hypothetical short- and longer-lived species. Analyses illustrate that elasticities of seasonal movement probability and associated survival probability can sometimes equal or exceed those of vital rates typically understood to substantially influence metapopulation dynamics (i.e. seasonal survival probability or fecundity), that elasticities can vary non-linearly, and that metapopulation outcomes depend on the level of within-individual plasticity.

4. We illustrate how our general framework can be applied to evaluate the consequences of variable and changing seasonal movement probability by parameterizing our models for a real partially migratory metapopulation of European shags *Gulosus aristotelis* assuming lifelong fixed strategies. Given observed conditions, metapopulation growth rate was most elastic to breeding season adult survival of the resident fraction in the dominant population. However, given doubled seasonal movement probability, variation in survival during movement would become the primary driver of metapopulation dynamics.

5. Our general conceptual and matrix model frameworks, and illustrative analyses, thereby highlight complex ways in which structured variation in seasonal migration can influence dynamics of partially migratory metapopulations, and pave the way for diverse future theoretical and empirical advances.

1 | INTRODUCTION

Identifying which life-history traits, and resulting population-wide vital rates, show environmentally induced variation and substantially affect population growth rate (λ) can facilitate prediction of population responses to environmental change and inform population management (Caswell, 2001; Heppell et al., 2000; Saether & Bakke, 2000). As effects of environmental variation on λ can depend on population demographic structure (Coulson et al., 2001; Hansen et al., 2019), efforts to explain and predict λ should aim to capture multiple dimensions of structure that can apply in wild populations (Tujlapurkar & Caswell, 1997).

To date, most theoretical and empirical studies have incorporated structure by considering variation in vital rates among ages or stages across locations and/or years (Gaillard & Yoccoz, 2003; Koons et al., 2016; Revilla & Wiegand, 2008). However, many populations also experience seasonal (i.e. within-year) environmental variation, which often exceeds the magnitude of among-year environmental variation (Gauthier et al., 2001; Paniw et al., 2019; Sendor & Simon, 2003). Such seasonal environmental variation can drive seasonal movements among locations that could both cause additional demographic structure, and interact with that structure to shape λ.

Specifically, individuals can respond to seasonal environmental variation by reversibly moving between discrete breeding and non-breeding locations across seasons (hereafter 'seasonal migration'), alongside permanent or semi-permanent movements between discrete breeding locations (hereafter 'dispersal'). Even though seasonal migration and dispersal are different processes with distinct implications, the words are often used interchangeably, generating widespread confusion (e.g. Inchausti & Weimerskirch, 2002). Considerable work has focused on understanding how variation in dispersal affects metapopulation structure and persistence, including in seasonal landscapes (Akçakaya, 2000; Bocedi et al., 2014; Hokit et al., 2001; Lecomte et al., 2020; Shima et al., 2010; Travis

et al., 2012). However, metapopulation dynamic consequences of variation in seasonal migration remain scarcely examined (de Castro et al., 2006; Hanski et al., 2000; Lee & Bolger, 2017). Indeed the need to build and analyse 'full-annual-cycle' metapopulation models for mobile populations has been repeatedly emphasized, but still not fully enacted (Hostetler et al., 2015; Sample et al., 2018; Small-Lorenz et al., 2013). Such models could identify key locations in spatio-seasonally heterogeneous landscapes, and season-specific vital rates including migration rates, that constrain λ.

Explicitly considering metapopulation consequences of changing seasonal migration is relevant because expression of migration (versus residence) commonly varies among individuals and years within populations, generating variable 'partial migration' (Chapman et al., 2011; Grist et al., 2017; White et al., 2007). Given multiple breeding locations, 'partially migratory metapopulations' can then arise (Reid et al., 2018). Here, different sets of individuals from single the same breeding populations can experience different non-breeding season environmental conditions and associated vital rates. Meanwhile, seasonally sympatric individuals from different breeding populations can experience similar seasonal conditions. Moreover, migrants might experience additional movement mortality on top of mortality attributable to conditions at their destinations (Mora Alvarez et al., 2019). Seasonal movement probability is therefore a key variable vital rate that can affect λ both by exposing individuals to movement-induced mortality risk, and by creating substantial within-population structure in other key vital rates through both direct and carry-over environmental effects.

Further structure could then result from the temporal scale of within-individual variation in seasonal migration versus residence, and associated plasticity (i.e. the potential of a single genotype or individual to express differing phenotypes, (Dingemanse et al., 2010; Scheiner, 1993). Here, individuals could make independent decisions to move or not after each breeding and non-breeding season (hereafter 'seasonally plastic' movement, Figure 1). This generates
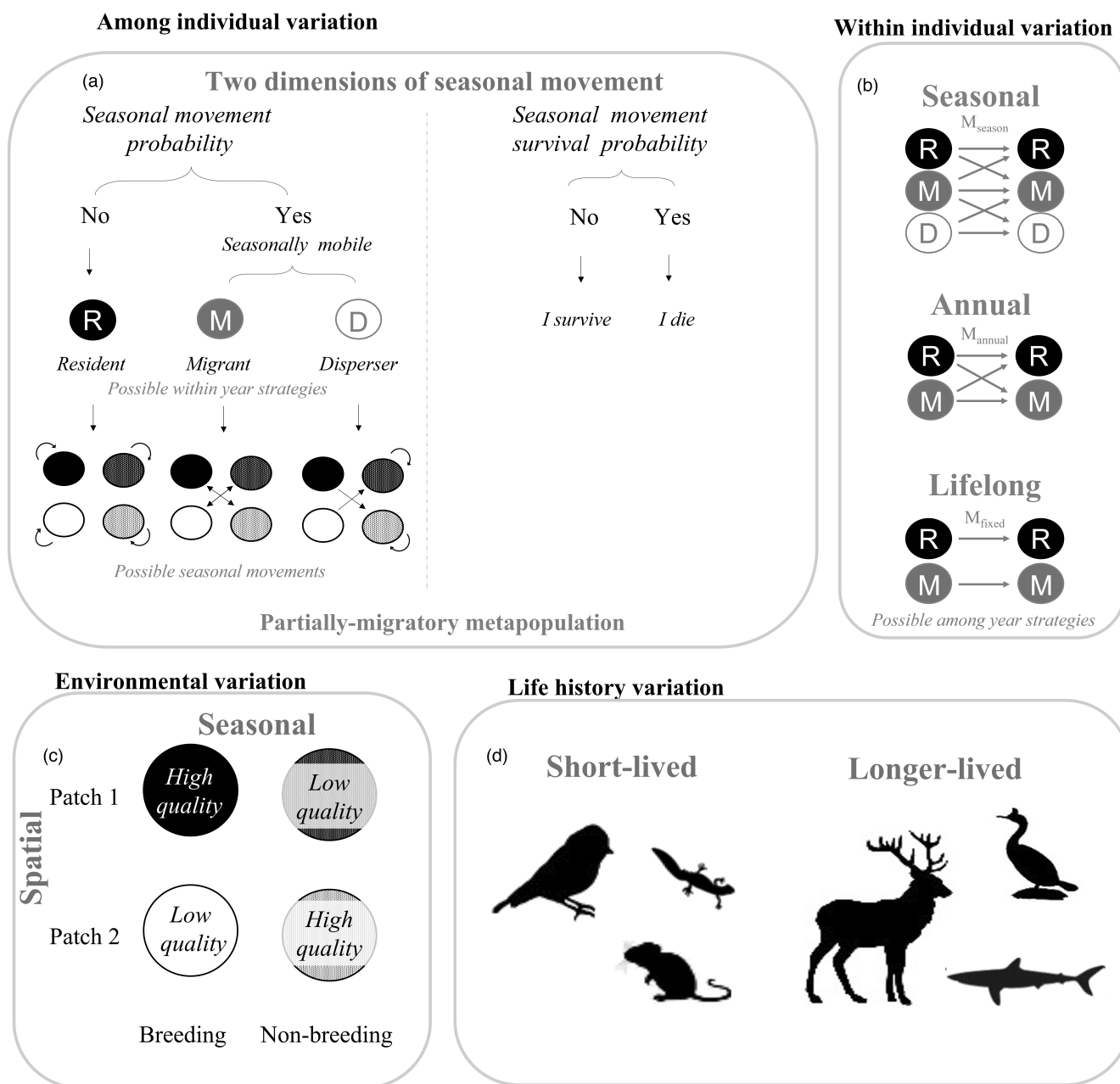
Sources of demographic structure

FIGURE 1 Conceptual framework highlighting considered sources of demographic structure in partially migratory metapopulations: (a) among individual variation, (b) within individual variation, (c) environmental variation illustrated for a landscape with two patches (black and white) and two seasons (dark and light grey) and (d) life history variation illustrated for short- and longer-lived species. Possible seasonal movements (a) result in three within-year strategies: residents (R), seasonal migrants (M) and dispersers (d). Possible among-year strategies (b) result in three distinct models, with seasonally plastic movement (M_{season}), annually plastic seasonal migration (M_{year}) or lifelong fixed seasonal migration (M_{life}). Arrows represent different potential individual paths among years.

three possible annual outcomes: residence, seasonal migration and dispersal. Alternatively, individuals could make such decisions annually after each breeding season, with all moving individuals returning after the non-breeding season (hereafter 'annually plastic' migration, Figure 1). Both seasonally and annually plastic movements generate partial migration at the population level with within-individual

variation in movement between years. Such outcomes have been observed in diverse species including North Atlantic right whales *Eubalaena glacialis* and red-spotted newts *Notophthalmus viridescens* (Gowan et al., 2019; Grayson et al., 2011). Finally, individuals could develop fixed migrant or resident strategies at or soon after birth, with little or no subsequent within-individual plasticity. Surviving

individuals then consistently enact seasonal migration or residence each year throughout their lifetime (hereafter 'lifelong fixed' migration, Figure 1). Indeed, high individual migratory repeatability occurs in diverse species including European shag *Gulosus aristotelis*, elk *Cervus elaphus* and white perch *Morone americana* (Eggeman et al., 2016; Grist et al., 2014; Kerr et al., 2009). Then, if residents and migrants experience different survival probabilities, the proportion of each cohort that is seasonally migrant will change across years due to within-generation phenotypic selection. Resulting deviations from the seasonal movement probability manifested at birth could further alter metapopulation structure and responses to spatially structured environmental perturbations.

Considering within-individual variation occuring across the three levels of seasons, years and lifetimes provides a useful conceptual framework to evaluate the consequences of structured variation in seasonal migration for the dynamics of partially migratory metapopulations inhabiting seasonally and spatially structured environments (Figure 1). Such capabilities are valuable because numerous species are partially migratory and rely on multiple seasonally occupied locations, which could make them particularly vulnerable to environmental change (Both et al., 2006; Chapman et al., 2011). Yet, we still lack general theory and models that identify fundamental demographic and (meta-)population properties of such systems and predict potential responses to changes in seasonality, as are expected under climate change (IPCC, 2022; Reid et al., 2018).

One approach to understanding impacts of changing migration is to utilize well-established principles of matrix population models to project λ (e.g. Caswell, 2001). This approach could identify parameter spaces where partially migratory metapopulations are expected to grow, remain stable or decrease given differing probabilities of seasonal migration and associated vital rates. 'Elasticities' can then be computed to predict relative impacts of perturbations (e.g. Caswell, 2001). Moreover, such models can facilitate generalization along the 'fast-slow' life-history continuum (i.e. short-lived vs longer-lived, Figure 1, Sæther & Bakke, 2000), project demographic structure, and identify links between vital rate variation and life-history evolution (Benton & Grant, 1999; Caswell, 2001; van Tienderen, 1995). Seasonal matrix models have previously been formulated, for instance considering seasonal demography in European ticks *Ixodes ricinus* (Dobson et al., 2011) and Caribbean Red-tailed Hawks *Buteo jamaicensis jamaicensis* (Gallardo et al., 2019). However, general models that jointly and explicitly consider variation in seasonal migration probability, plasticity and associated survival have not previously been formulated or analysed.

Accordingly, we construct a general full-annual-cycle matrix model framework that considers seasonal and spatial variation in vital rates in partially migratory metapopulations. Our framework is novel in conceptualizing multiple levels of among-individual and within-individual variation in seasonal migration, as could arise given any life-history pace and spatio-seasonal landscape. Specifically, we conceptualize seasonal migration as the outcome of two vital rates: seasonal movement probability and seasonal movement survival probability. We formulate within-individual variation by allowing seasonal or annual plasticity, or lifelong fixed strategies. We evaluate how variation in migration, and associated survival, can affect persistence, demographic structure and associated elasticitie. To illustrate how our framework can quantify properties of such systems, we parameterize and analyse models first for hypothetical short-lived and longer-lived partially migratory species, and second using empirical data from a partially migratory metapopulation of European shags. We thereby demonstrate how vital rates that constrain λ for partially migratory metapopulations can be identified both theoretically and empirically, and highlight parameters that now need to be widely estimated in natural systems.

PART 1. GENERAL FRAMEWORK FOR PARTIALLY MIGRATORY METAPOPULATIONS

2 | MATERIALS AND METHODS

2.1 | Seasonal matrix modelling approach and demographic formulation

We construct a general stage-structured full-annual-cycle matrix model with explicit seasonal and spatial variation in vital rates (Figures 1 and 2). The model considers females within a sexually reproducing population, and an annual projection interval based on a pre-breeding census. Each year comprises two consecutive seasons (*b*): a breeding season (hereafter, $b = 1$) and a non-breeding season (hereafter, $b = 2$). The landscape consists of two patches (hereafter $k = 1$ and $k = 2$) with one population breeding in each patch. This is the simplest structure that allows spatial and seasonal variation in vital rates following the concept of a partially migratory metapopulation (Reid et al., 2018). The annual projection matrix characterizes a full-annual-cycle comprising reproduction, breeding season survival, post-breeding seasonal movement (and associated survival) or residence, non-breeding season survival, and post non-breeding seasonal movement (and associated survival) or residence. Specifically, we model metapopulation dynamics from time *t* to $t + 1$ as $N_{t+1} = AN_t$, where N_t and N_{t+1} are vectors of metapopulation size in each age or stage at time *t* and $t + 1$ respectively, and *A* is the full-annual-cycle metapopulation projection matrix. *A* is the product of non-breeding (B_2) and breeding (B_1) season metapopulation projection matrices (i.e. $A = B_2 B_1$), thereby conceptually allowing movement between patches and demographic strata between seasons (Caswell, 2001). Each seasonal matrix (B_b) has sub-matrices B_{bdo}, where d refers to the destination (to) patch and o refers to the original (from) patch. For example, B_{b12} is the projection matrix for the population that was in patch 2 at the beginning of season b and moved to patch 1, while B_{b22} is the projection matrix for the population that was in patch 2 and remained there. Overall, B_b is defined as:
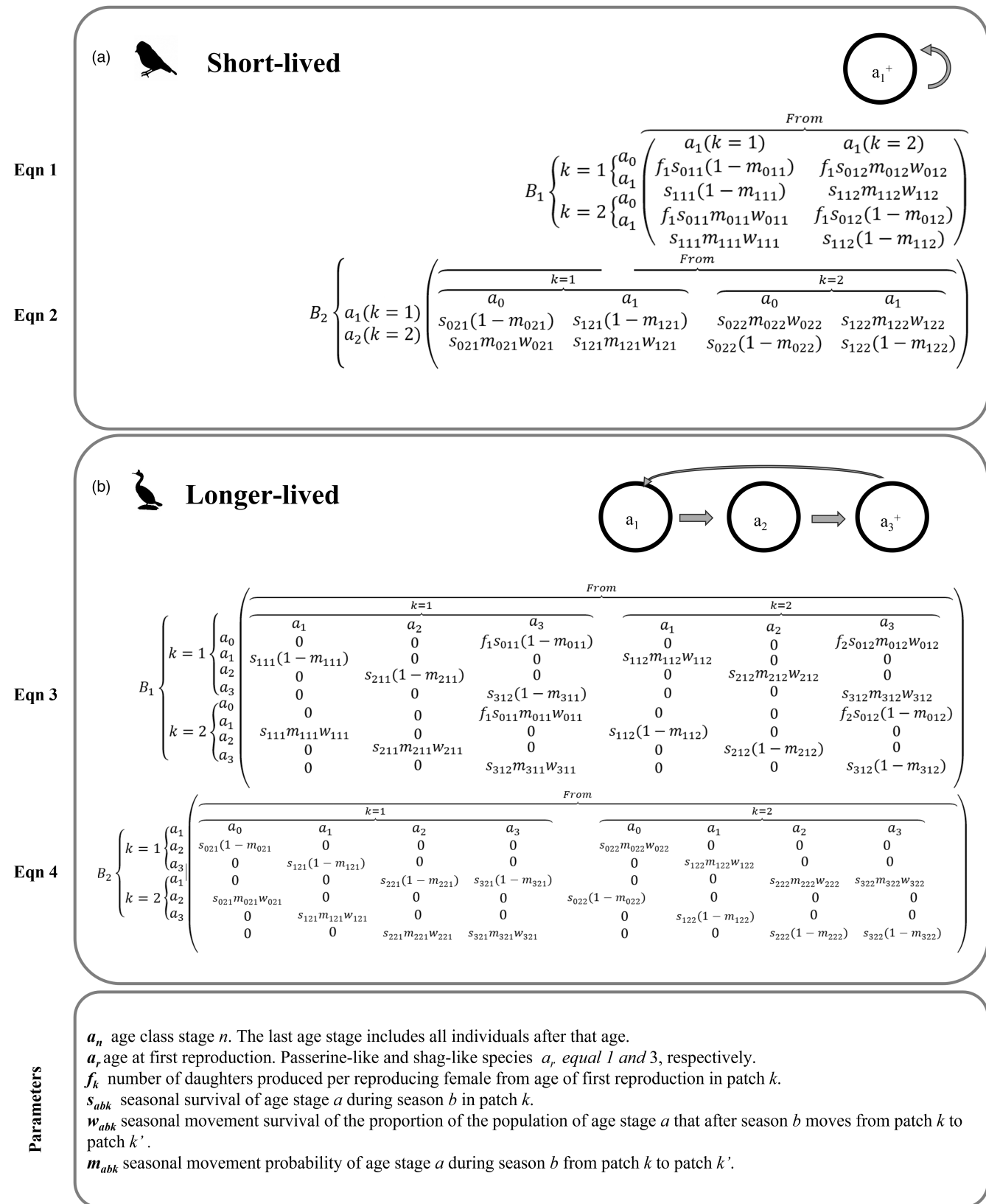
FIGURE 2 Annual life cycles and $M_{season} B_b$ sub-matrices for hypothetical (a) short-lived and (b) longer-lived species for a landscape with two patches ($k = 1$ and $k = 2$) and two seasons ($b = 1$ and $b = 2$). Life-histories are defined by setting parameters for age-, season- and location-dependent survival (s_{abk}), for age-, season- and location-dependent seasonal movement (m_{abk}) and seasonal movement survival (w_{abk}), age at first reproduction (a_r) and location-dependent fecundity (f_k). Short-lived and longer lived species consider age at first reproduction (a_r) equal 1 and 3 respectively. Age classes are noted as a_n. For further illustration see Appendix S1.

$$B_b = \begin{pmatrix} B_{b11} & B_{b12} \\ B_{b21} & B_{b22} \end{pmatrix}.$$

As the full life-cycles and A and B_b matrices are cumbersome, they are presented in Appendix S2. However, illustrative sub-matrices of B_b for the general movement model are shown in Figure 2. Within each B_b sub-matrix we define life-histories by setting parameters for age-, season- and location-dependent survival (s_{abk}), age at first reproduction (a_r) and location-dependent fecundity (f_k, daughters produced per female from age of first reproduction, assuming a 1:1 sex ratio). To allow age-specific survival, we define seasonal adult survival as a baseline and define seasonal newborn survival as a proportion (i.e. $s_{01k} = \alpha_a s_{a1k}$).

2.2 | Conceptualizing environmental variation

We capture demographic structure resulting from varying spatial and seasonal environmental quality by implementing spatio-seasonal variation in survival and fecundity. To achieve this, we define baseline parameters in patch 1 ($k = 1$) during the breeding season ($b = 1$), then define other parameters as proportions. For example, we set patch 1 breeding season adult survival probability to s_{a11}. Non-breeding season survival probability in patch 1 is a proportion α_s of s_{a11} (i.e. $s_{a2k} = \alpha_s s_{a1k}$), while breeding season survival probability in patch 2 is a proportion α_g of that in patch 1 (i.e. $s_{a12} = \alpha_g s_{a11}$). To create a biologically relevant seasonal landscape in which a population breeding in patch 1 can escape deteriorating conditions by seasonal movement, we set non-breeding season survival probability in patch 1 to be α_R of that in patch 2 (i.e. $s_{a21} = \alpha_R s_{ak2}$). Spatial differences in fecundity follow the same pattern as differences in survival. Therefore, fecundity in patch 2 is α_g of that in patch 1 (i.e. $f_2 = \alpha_s f_1$). However, our general model framework allows for any desired parameterisation.

2.3 | Conceptualizing among-individual variation in seasonal migration

We capture structure resulting from among-individual variation in seasonal migration (Figures 1 and 2) by formulating seasonal movement as the product of two variable vital rates: seasonal movement probability (m_{abk}) and seasonal movement survival probability (w_{abk}). Specifically, a proportion m_{abk} of each age stage class a at the end of season b moves from their current patch ($k = 1$ or $k = 2$) towards the other patch. The proportion m_{abk} of the population that moves has probability w_{abk} of surviving the movement. This general formulation allows any desired form of symmetry or asymmetry in seasonal movement probability and seasonal movement survival probability across ages, seasons and patches. Appropriate parameterizations can generate diverse forms of

movement, including seasonal migration, temporary and permanent dispersal, or skipping breeding (e.g. Alderman et al., 2010; Shaw & Levin, 2011, Appendix S1).

2.4 | Conceptualizing within-individual variation in seasonal migration

We capture structure resulting from within-individual variation in seasonal migration by defining a general model, which we constrain to consider seasonal or, annual plasticity, or lifelong fixed strategies (Figure 1, Appendix S1). First, we consider a general 'seasonal movement model' (hereafter M_{season}, Figure 1) where movement between patches after each season occurs with probability m_{abk} that is independent of previous seasonal movement or residency (i.e. seasonal plasticity). Hence, at the start of each annual projection cycle, patch 1 contains a mixture of individuals that are susceptible to be year-round residents, migrants and dispersers in proportions that depend on the values of m_{a11} and m_{a21}.

Second, we constrain M_{season} by forcing the surviving population fraction that had moved between patches after the breeding season to return to their original patch after the non-breeding season and preventing any new movement at this time (hereafter M_{year}, Figure 1). This generates seasonal migration sensu stricto with no dispersal due to seasonal movement. This is achieved by specifying $m_{a21} = 0$ in B_2 for fractions of the patch 1 population that were already in patch 1 in season 1, and $m_{a21} = 1$ for fractions of the patch 1 population that were previously in patch 2 in season 1 (with identical constraints on m_{a22} for patch 2). These transitions occur repeatedly across successive years. At the start of each annual projection cycle, both patches can contain resident and migrant fractions, where the population proportions that will undertake seasonal migration equal m_{a11} and m_{a12} for patches 1 and 2 respectively. M_{year} does not allow dispersal due to seasonal movement, but allows random switching between year-round residence and seasonal migration between years (i.e. annual plasticity).

Third, we further constrain M_{year} by forcing population fractions to retain the migrant or resident strategy acquired at birth (i.e. no plasticity, hereafter M_{life}, Figure 1). At the start of each annual cycle, each patch can contain individuals that are lifelong residents and migrants. To achieve this, we explicitly define discrete resident and migrant stages for each patch population, with no between-stage transitions allowed. Consequently, M_{life} has twice as many stages as M_{year} and M_{season}. During the breeding season, migrant and resident offspring are produced in proportions m_{01k} and $1 - m_{01k}$ by both residents and migrants. For each patch k we set $m_{a1k} = 0$ for residents, and $m_{a1k} = 1$ for migrants (highlighted in Appendix S2) for juvenile or older. This generates seasonal migration sensu stricto with no dispersal due to seasonal movement. Full details of implementation of models M_{season}, M_{year} and M_{life} are in Appendix S2.

2.5 | Model analyses

All three models can be parameterized and analysed to quantify how metapopulation persistence ($\lambda \geq 1$), underlying demographic structure, and asymptotic elasticity (e_θ) of λ to each vital rate (Θ) vary across the potential range of values of seasonal movement probability (m_{abk}) and seasonal movement survival probability (w_{abk}) considering any given level of plasticity and life-history. λ is the dominant eigenvalue of the annual projection matrix A. Characterizing demographic structure helps illuminate the mechanisms underlying variation in λ, by showing the population proportion that moves and is consequently susceptible to movement costs. Specifically, metapopulation mobile fraction (Ω) is the proportion of individuals that start each annual projection cycle that is susceptible to moving at any given time during the focal year. Ω can be further decomposed into migrant (ω) and disperser (δ) fractions which respectively correspond to individuals susceptible for seasonal migration and for dispersal. These individuals experience a cost of movement twice or once a year, respectively. If we assume equal movement probabilities (m) among patches, ages and seasons, then for M_{season} $\omega = m^2$ and $\delta = 2(1 - m)m$, and for M_{year} $\omega = m$ and $\delta = 0$. For M_{life}, which explicitly includes separate resident and migrant stages, ω is the sum of the elements of the right eigenvector of M_{life} matrix that corresponds with the migrant stages and $\delta = 0$. For M_{season} and M_{life}, Ω will deviate from the specified value of m. This deviation results from the presence of both dispersers and seasonal migrants in M_{season}, and from phenotypic selection arising from any survival differences between residents and migrants in M_{life}. Values of asymptotic elasticity e_θ, which quantify the proportional change in λ given a proportional change in a vital rate θ, can be calculated as scaled partial derivatives using the chain rule (Caswell, 2001), facilitating comparison across vital rates and life-histories. In M_{year} and M_{life}, the two breeding populations are reproductively isolated as there is no dispersal. The size of the population with the lower λ is consequently asymptotically negligible. Accordingly, the metapopulation λ, Ω and e_θ correspond to those of the population with the higher λ. However, dispersal among patches can be explicitly implemented to connect populations (see the empirical case study and Appendix S6).

PART 2. THEORETICAL EXAMPLES: PROPERTIES OF PARTIALLY MIGRATORY METAPOPULATIONS

3 | MATERIALS AND METHODS

3.1 | Illustrative parameterizations

Our general model allows formulation of any life-history representing any partially migratory taxa by implementing an appropriate age or stage structure, and allows parameterizations for any desired two-patch landscape (Appendices C and F). However, to illustrate

how our framework can quantify key properties of partially migratory metapopulations and highlight roles of migratory plasticity, here we focus on two illustrative parameterizations representing seasonal landscapes supporting stereotypical relatively short-lived and longer-lived species.

We define a landscape where a population breeding in a high-quality patch ($k = 1$, i.e. higher breeding season vital rates) can escape locally deteriorating conditions during the non-breeding season by moving to another patch ($k = 2$, Figure 2). Meanwhile, a population breeding in patch 2 can remain resident or move to patch 1, which is of lower non-breeding season quality.

We then parameterize models M_{season}, M_{year} and M_{life} for a hypothetical short-lived species with relatively low annual survival and high reproductive rate, and a hypothetical longer-lived species with higher annual survival and lower reproductive rate (Figures 2 and 3). For current illustrative purposes, parameters were set to broadly resemble a partially migratory passerine bird and a European shag. The latter was chosen to facilitate subsequent parameterization with available empirical data, thereby facilitating direct transition from theory to data (see Empirical case study). We define baseline conditions by setting breeding season adult survival in patch 1 as $s_{111} = 0.73$ and $s_{111} = 0.99$, and age at first reproduction of $a_r = 1$ and $a_r = 3$, for the short- and longer-lived species respectively. To ensure a parameter space where populations persist, we set fecundity to give $\lambda = 1.3$ for a population resident in patch 1, giving $f_1 = 4.5$ and $f_2 = 2$ for the short-lived and longer-lived species, respectively. Environmental differences between patches and seasons were implemented as proportions of baseline vital rates (Figure 3; Appendix S3).

To understand how variation in seasonal migration and associated survival costs affect metapopulation dynamics we consider discrete values along the full parameter space that is possible for any species (i.e. m and $w \in [0, 0.1, 0.2, ..., 1]$). This captures the conceptual point that species with any relatively fast or slow baseline life-history can potentially occupy any position on the continuum of year-round residence to full seasonal migration, which can potentially be perturbed. Our general model readily allows m_{abk} and w_{abk} to vary among seasons, patches and/or ages. However, to maintain a tractable number of dimensions of variationfor current illustrative analyses, we set m_{abk} constant across these dimensions and allowed w_{abk} to vary among ages. Movement survival probability of young from the current breeding season (w_{0bk}, hereafter 'newborn') is defined as a proportion of adult movement survival probability (w_{arbk}, where a_r is age at first reproduction; Appendix S3). For simplicity, presented results refer to m and w, with no subscripts.

We quantify metapopulation growth rate (λ), mobile fraction (Ω) and vital rate elasticities (e_θ) for each model and hypothetical species across the full possible ranges of m and w ($\in [0, 1]$). Mobile fraction (Ω) is a composite of the fraction susceptible to migrate (ω) and the fraction susceptible to disperse (δ), and δ is necessarily 0 for M_{year} and M_{life}. We present these results as heat maps across axes of m and w structured by level of plasticity, life-history and θ, thereby summarizing up to six dimensions (further explained in Appendix S4).
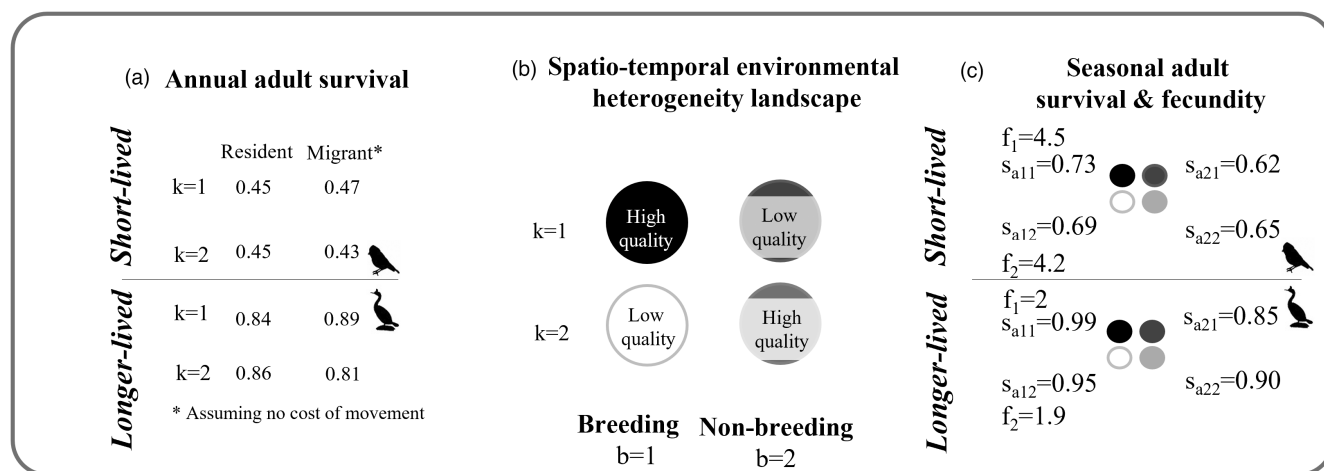
FIGURE 3 Summary of survival and fecundity values in a hypothetical landscape with seasonal and spatial variation for short-lived and longer-lived species. (a) Realized annual adult survival probabilities and fecundities for residents and migrants from patches $k = 1$ and $k = 2$. (b) Spatio-temporal landscape given a two-patch and two-season model. (c) Seasonal adult survival probabilities s_{1bk}, b is season and k is patch, and fecundities are f_k.

We ran all analyses in R 3.5.2 (R Core Team, 2013). General code that is customizable for any desired life-history is in Appendix S8. These theoretical explorations did not require ethical approval.

4 | RESULTS

4.1 | Results from illustrative parameterizations: Growth rate (λ), mobile fraction (Ω) and elasticity of λ to vital rates (e_θ)

As expected, λ is high when movement survival probability (w) is high irrespective of seasonal movement probability (m, Figure 4ai–iii vs. bi–iii). Decreasing w decreases λ unless m is small (Figure 4ai–iii vs. bi–iii). These patterns of variation in λ are qualitatively consistent across the two illustrative life-histories (Figure 4ai–iii vs. 4bi–iii) and levels of seasonal movement plasticity (Figure 4 columns). However, the parameter space that allows metapopulation persistence ($\lambda > 1$) differs between life-histories. In general, persistence occurs in a wider range of $m - w$ parameter space for the longer-lived species (Figure 4aiii vs. biii). Further, within each life-history, metapopulation persistence occurs in a more restricted part of the $m - w$ parameter space when seasonal movement is seasonally plastic (M_{season}) or annually plastic (M_{year}), than when it is fixed (M_{life}, Figure 4a,b i and ii vs. iii).

Differences between λ given seasonal and annual plasticity result from differing underlying metapopulation mobile fractions and resulting survival costs experienced. Given seasonal plasticity, the population fractions susceptible to migrate (ω) and disperse (δ) at the beginning of each year are m^2 and $2(1 - m)m$ respectively. Given annual plasticity, these fractions are m and 0 respectively. As migrants experience the direct cost of movement twice a year while dispersers experience it once, seasonal plasticity results in a slightly

lower annual survival probability (Figures 4a,b iv vs v). Finally, differences between M_{year} and M_{life}, for which disperser fraction is 0, arise because in M_{life} within-generation phenotypic selection can decrease Ω and thereby reduce exposure to lower survival probability (Figure 4a,b v vs vi). In our illustrative parameterization, migrants are the less fit strategy. For instance, for migrants originating in patch 1, the direct cost of moving after the breeding season exceeds the benefit of moving to a patch with higher non-breeding season survival probability (Figure 3). Consequently, in M_{life}, migrants experience the cost of migration twice a year and are selected out, leaving an increasing proportion of residents (the fitter strategy, Figure 4, panel b ix). This is particularly evident for the longer-lived species, where the mobile fraction Ω can decrease well below the specified seasonal movement probability m, and hence 'rescues' λ by exposing fewer individuals to seasonal movement mortality ($1 - w$). This is less evident for the short-lived species, because a high proportion of the metapopulation alive at any time is newborn and life expectancy is much shorter, which limits the impact of within-generation selection on Ω and hence λ.

As expected, elasticities of λ to fecundity (f_k) and newborn survival (s_{0bk}) are positive and higher for the short-lived species, while elasticities of λ to adult seasonal survival (s_{1bk}) are higher for the longer-lived species (Figure 5). Meanwhile, elasticities of λ to the seasonal movement vital rates m and w show substantial variation across the full $m - w$ parameter space (Figure 5). The elasticity of λ to w is always positive, but the elasticity of λ to m is widely negative. This occurs because increasing w can only increase λ, while increasing m can increase or decrease λ depending on the overall costs versus benefits of increasing the proportion of the metapopulation that moves. When m is moderately high, the seasonal movement parameters can have elasticities comparable to, or even higher than, the fecundity and survival rates that are typically considered to drive metapopulation dynamics (Figure 5). Additionally, when m
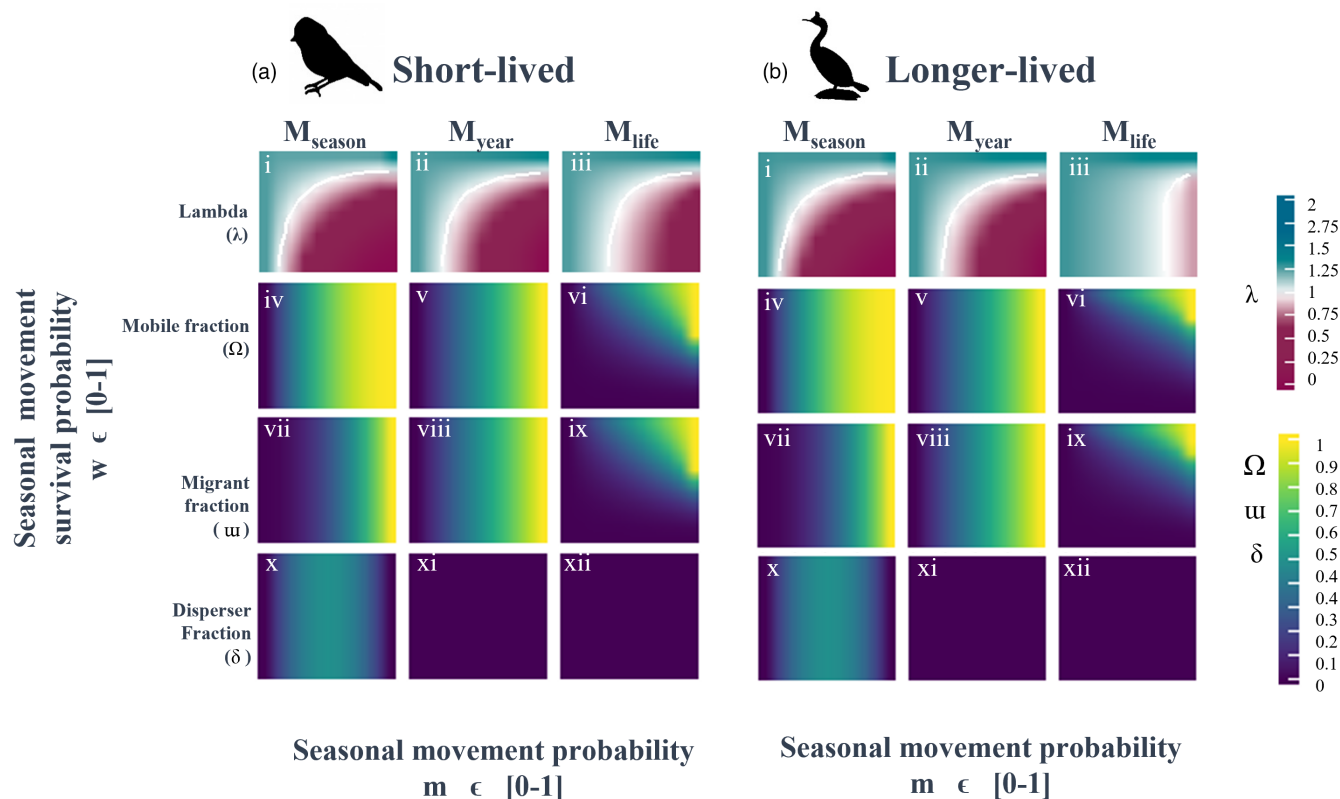
FIGURE 4 Projected asymptotic metapopulation growth rate (λ), mobile fraction (Ω), migrant fraction (ω) and disperser fraction (δ) for (a) short-lived and (b) longer-lived species. Columns depict the level of movement plasticity: seasonal (M_{season}), annual (M_{year}) and lifelong fixed (M_{life}). Each square depicts values across the full possible range of values of the seasonal movement probability ($m\epsilon[0-1]$) and the seasonal movement survival probability ($w\epsilon[0-1)$). The white contour line represents $\lambda = 1$. The heat map representation is further explained in Appendix S4.

is very high and w is very low, elasticities to seasonal movement parameters become several orders of magnitude higher than the other parameters' elasticities, especially when $\lambda < 1$ (Figure 5).

Given our illustrative parameterizations, λ is generally slightly more elastic to breeding season vital rates ($b = 1$) than to non-breeding season vital rates ($b = 2$, Figure 5). Also, λ is slightly more elastic to vital rates in the high-quality breeding patch ($k = 1$) than in the patch with worse breeding season vital rates ($k = 2$, Figure 5). These differences are more evident for the parameters to which λ is more elastic for each life-history; namely fecundity (f_k) and newborn survival (s_{0bk}) for the short-lived species, and adult survival (s_{abk}) for the longer-lived species (Figure 5). Most of these overarching patterns are less pronounced given seasonal plasticity (M_{season}) in movement than given annual (M_{year}) or no plasticity (M_{life}, Figure 5). This is because the intrinsic emergence of dispersal in M_{season} reduces the effect of seasonal and spatial differences in vital rates on λ and allows individuals to contribute to λ in a different patch from their origin (Figure 5). Beyond these summary patterns, our illustrative parameterizations also demonstrate that elasticities can vary in complex, non-linear ways along the full axes of variation in m and w, depending on the level of plasticity (examples in Appendix S5).

PART 3. FROM THEORY TO APPLICATION: AN EMPIRICAL CASE STUDY

5 | MATERIALS AND METHODS

5.1 | Empirical parameterization

Applying our conceptual framework to real systems requires estimating seasonal vital rates, including movement probabilities, in partially migratory systems. This is challenging (Marra et al., 2015; Sample et al., 2018), but will become increasingly feasible as individual tracking technologies, large-scale monitoring programs and associated statistical tools reach maturity (Eggeman et al., 2016; Grist et al., 2017; Reid et al., 2018). For instance, combinations of breeding and non-breeding season monitoring data can allow estimation of season and location specific vital rates (Acker, Daunt, et al., 2021; Grayson et al., 2011), carry-over effects (Gillanders et al., 2015; Grist et al., 2017), and forms of within-individual repeatability (or plasticity) in non-breeding location (Eggeman et al., 2016; Grist et al., 2014). Given such estimates, our models allow quantitative evaluation of the impact of changing seasonal
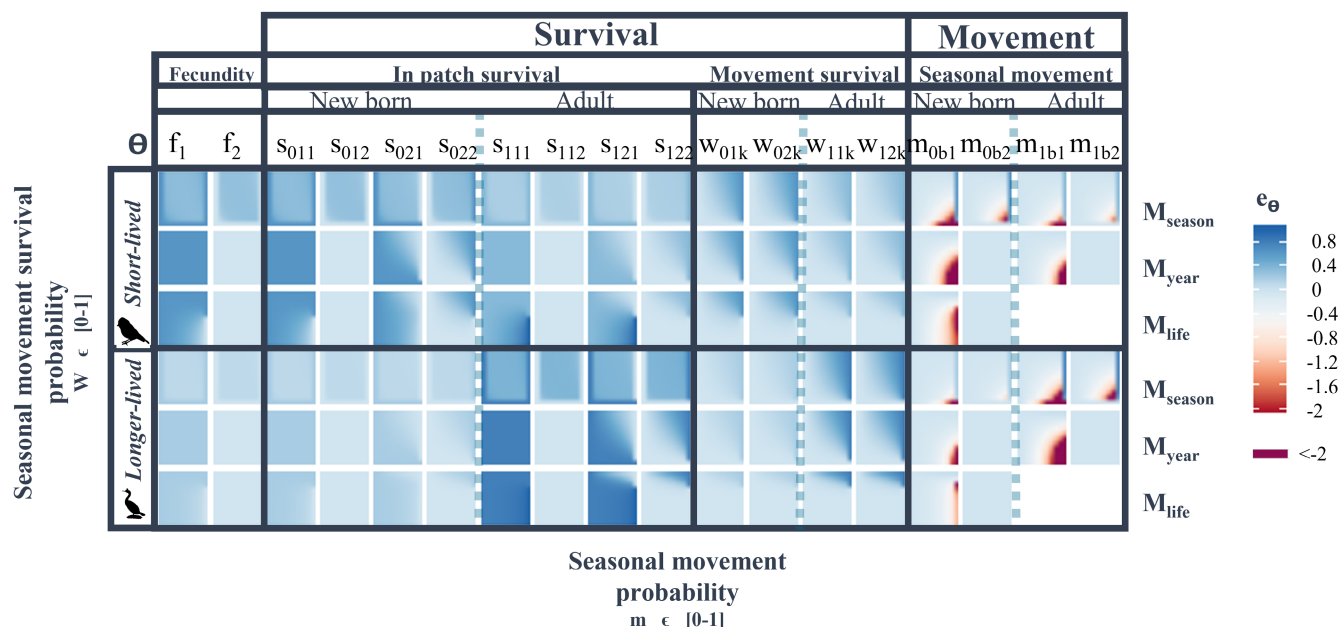
FIGURE 5 Elasticity (e_θ) of metapopulation growth rate (λ) to vital rates (θ) for the short-lived and longer-lived species (top and bottom blocks) and three levels of plasticity: seasonal (M_{season}), annual (M_{year}) and lifelong fixed (M_{life}). Parameter notation: f_k, fecundity in patch k; s_{abk}, seasonal survival at age a during season b in patch k; w_{abk} and m_{abk}, seasonal movement survival probabilities and seasonal movement probabilities at age a during season b in patch k; $a = 0$, newborns and $a = 1$, adults. Each square depicts values of e_θ across the full possible range of values of seasonal movement probability ($m\epsilon[0-1]$) and seasonal movement survival probability ($w\epsilon[0-1]$), as explained in Appendix S4. The deep red represents $e_\theta < -2$ and white panels correspond to parameters absent in M_{year} and M_{life}. Dashed lines separate newborn from adult vital rates.

migration probability, and associated survival probability, on metapopulation dynamics.

As a proof of concept, we consider a partially migratory metapopulation of European shags for which seasonal vital rates have recently been estimated. We consider shags breeding across two colonies in north-east Scotland: Isle of May (hereafter 'IoM') and Bullers of Buchan (hereafter 'BoB', Figure 6). From 2009, shags hatched or breeding at IoM and BoB have been individually marked with alphanumeric metal rings and field-readable color rings (Acker, Daunt, et al., 2021; Grist et al., 2014, 2017; Reid et al., 2020). From 2009, extensive year-round resightings have been undertaken to identify individuals' breeding and non-breeding season locations (Acker, Daunt, et al., 2021). These resightings reveal that shags breeding at both colonies can remain resident there through the non-breeding season or migrate elsewhere, and that seasonal vital rates can differ between residents and seasonal migrants (Acker, Daunt, et al., 2021; Grist et al., 2017; Reid et al., 2020). Moreover, shags show high within-individual repeatability in non-breeding location across years (~0.8, Grist et al., 2014). We therefore considered metapopulation dynamics by directly parameterizing model M_{life}, as set up for our theoretical example for the longer-lived species.

As shags typically first breed aged 3 years (Aebischer et al., 1995), we formulate M_{life} considering three stages (Figure 3): yearlings ($a = 1$, 1–2 years), sub-adults ($a = 2$, 2–3 years) and breeding adults ($a = 3$, ≥ 3 years). We take previously estimated values of local breeding success for residents and migrants (f_k) and seasonal

survival probabilities (s_{abk}; Acker, Burthe, et al., 2021; Acker, Daunt, et al., 2021; Grist et al., 2017; Reid et al., 2020). As seasonal movement survival probabilities (w_{abk}) have not previously been explicitly estimated, we derive an estimate from the maximum observed difference in annual survival between residents and migrants (Appendix S7) and assume that w is season- and site-independent but age-dependent (w_a). We use proportional age-specific survival rates estimated by Frederiksen et al. (2008) (Appendix S7). We take seasonal movement probability m_k as the realized migratory fraction estimated following (Acker, Daunt, et al., 2021) averaged across years and assume that m is age independent ($m_1 = 0.441$, $m_2 = 0.306$). As the IoM and BoB breeding populations are connected through occasional dispersal (Barlow et al., 2013), we extend M_{life} to allow age-independent dispersal probability $\delta = 0.1$, assuming that demography and dispersal occur sequentially within the annual projection interval (Appendix S6). All resulting parameter values are shown in Figure 6 (further details in Appendix S7).

We calculate metapopulation growth rate (λ), mobile fraction (Ω) and associated elasticities of λ to vital rates (e_θ) at the asymptotic equilibrium. Our assumption that m_k equals the realized (observed) mobile fraction will likely underestimate the true value of m_k, because some individuals will die before achieving movement. Further, previous studies suggested that movement probability can increase with increased environmental stochasticity (Kokko & Lundberg, 2001). Therefore, we explore potential metapopulation consequences of higher m_k by doubling the initial values (i.e. $2m_k$).
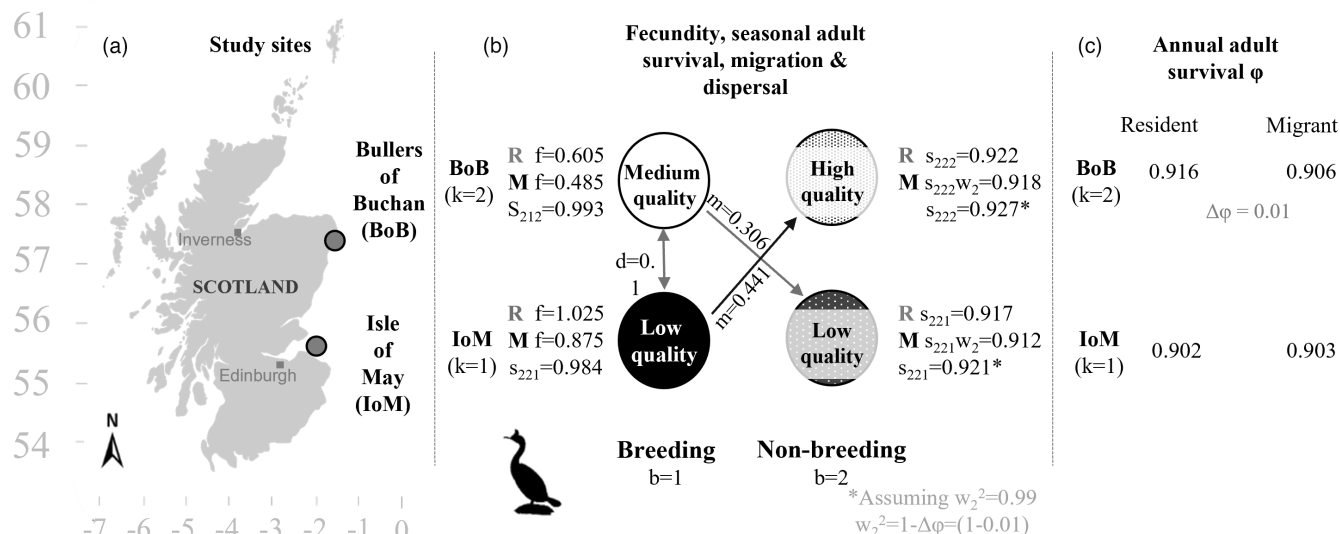
FIGURE 6 Summary of vital rates estimated for a European shag *Gulosus aristotelis* partially migratory metapopulation in Scotland to illustrate a landscape with seasonal and spatial variation in survival and fecundity. (a) Location of Isle of May (IoM) and Bullers of Buchan (BoB) colonies. (b) Spatio-temporal vital rates: f_k, fecundity; s_{2bk}, seasonal adult survival probabilities (i.e. $y \geq 2$) during each season ($b = 1$, breeding, solid fill and $b = 2$, non-breeding, dotted fill) at IoM ($k = 1$; dark fill) and BoB ($k = 2$; light fill) for resident (R) and migrant (M) population fractions; w and w^2, seasonal and annual movement survival probabilities; m, seasonal movement/migration probability and d, dispersal probability. (c) Realized annual survival probabilities for residents and migrants breeding at IoM and BoB.

We used data from previously published studies therefore we did not require ethical approval.

6 | RESULTS

6.1 | Results from empirical case study: Growth rate (λ), mobile fraction (Ω) and elasticity of λ to vital rates (e_θ)

Estimated λs were 1.11 and 1.05 given m_k and $2m_k$ respectively. Both scenarios therefore allow metapopulation growth and persistence. Migrants are the less fit strategy and are selected out, leaving increasing proportions of residents. Accordingly, in both scenarios, Ω is lower than the imposed value of m_k. Specifically, Ω is only 0.14 at IoM and 0.09 at BoB given m_k, and 0.37 at IoM and 0.26 at BoB given $2m_k$.

The elasticities of λ to adult seasonal survival probability (s_{2bk}) and adult movement survival probability (w_2) are higher than those to fecundity (f_k) and newborn and sub-adult local survival probability (s_{0bk}, s_{1bk}) and movement survival probability (w_0, w_1, Figure 7). While elasticities to fecundity (f) and survival rates are of course positive, elasticities to seasonal migration (m_k) and dispersal (δ) probabilities are negative (Figure 7). The elasticity to m_k is comparable to that of seasonal survival (s_{abk}) given the observed m_k values, but approximately doubles given $2m_k$. For both m_k and $2m_k$ the elasticity to dispersal is negative and negligible compared to the elasticities of other vital rates ($e_\delta = -0.002$).

Elasticities also differ between the two focal populations breeding on IoM and BoB, and between residents and seasonal migrants.

Elasticities of λ to breeding season vital rates are greater at IoM, while elasticities of non-breeding season vital rates are greater at BoB. The pattern of differences in elasticities of λ to breeding and non-breeding season vital rates is consistent given m_k and $2m_k$, but the magnitude is greater for doubled m_k (Figure 7). With m_k, λ is more elastic to changes in f_k and s_{abk} than in w_a, m_k and δ (Figure 7a). Moreover, λ is most elastic to the vital rates of the population fraction breeding at IoM (i.e. f_1 and $s_{ab1}s_{ab1}$ Figure 7a). Likewise, λ is most elastic to vital rates of the resident fraction of the population (Figure 7a). However, with doubled m_k, λ is most elastic to w_2 (Figure 7b). Overall, elasticities of λ to w_a approximately doubled. Still, λ is more elastic to changes in vital rates of the resident fraction than the migrant fraction (Figure 7c). However, the overall relative contribution of the resident fraction decreases. With doubled m_k, the effect of seasonality becomes more obvious with notable increase in the differences between the elasticities of λ to the breeding and non-breeding season vital rates.

7 | DISCUSSION

Increasingly important aims in fundamental and applied ecology are to identify which seasonal vital rates, life-history stages and locations regulate the size and persistence of partially migratory metapopulations, and thereby forecast likely impacts of deteriorating seasonally occupied habitats (Reid et al., 2018; Small-Lorenz et al., 2013). In such systems, individuals can potentially respond to seasonal environmental variation by migrating between discrete locations. Yet, while the metapopulation dynamic consequences of variable dispersal rates have been widely studied (Akçakaya, 2000;
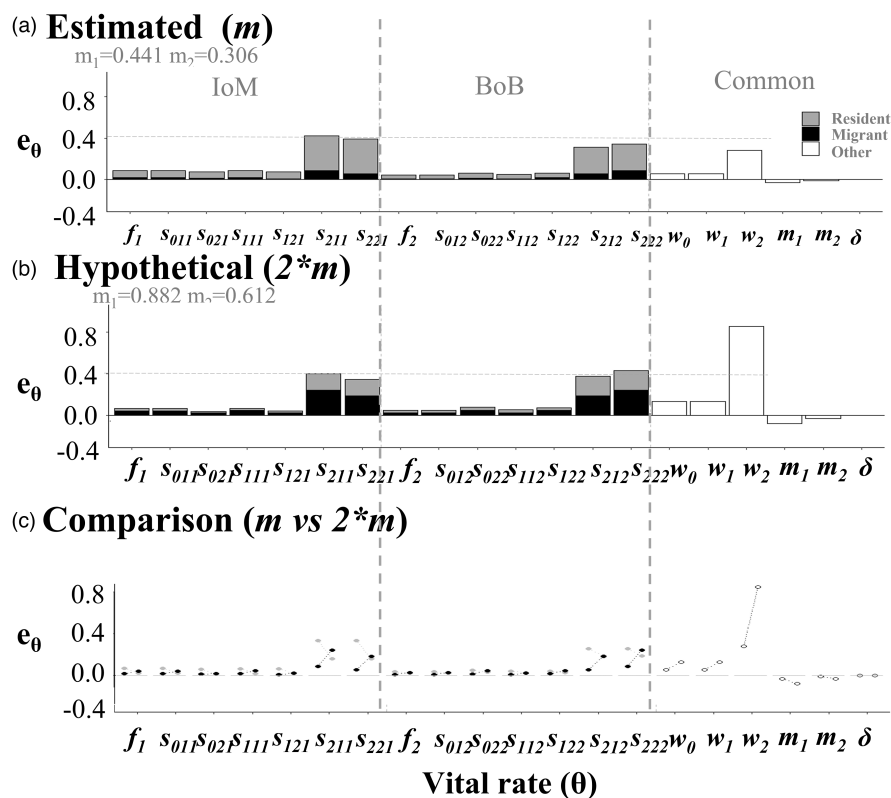
FIGURE 7 Elasticity of metapopulation growth rate (λ) to vital rates (θ) for estimated value of seasonal movement probability (a) m, (b) $2m$, and (c) their comparison. Parameter notation: f_k, fecundity in patch k; s_{abk}, age a, season b and patch k survival; w_a, age a movement survival; m_k, seasonal migration probability from patch k and δ dispersal probability; $a = 0$, newborns; $a = 1$, sub-adults; $a = 2$, adults. Parameters from Isle of May (IoM) and Bullers of Buchan (BoB) or both are separated by dashed lines and noted in grey, black and white, respectively. In c dashed lines between the two scenarios are used as reference in the change of value but they do not denote trends as these are often non-linear (see Appendix S6).

Hokit et al., 2001; Lecomte et al., 2020; Travis et al., 2012), effects of structured variation in seasonal migration on dynamics of partially migratory metapopulations remain largely unexplored. We provide a general conceptual framework that explicitly incorporates seasonal movement probability (m), and movement survival probability (w), as population-level vital rates, and conceptualizes several forms of within-individual variation (i.e. 'plasticity') in seasonal movement. Our example theoretical and empirical example parameterizations illustrate how movement vital rates and plasticity can interact to shape the dynamics and persistence of partially migratory metapopulations across different life-histories.

7.1 | Implications of variation in seasonal migration for metapopulation dynamics

Our illustrative theoretical parameterizations provide proof of concept of how our framework can identify regions of movement parameter space where partially migratory metapopulations can persist ($\lambda > 1$), and identify what values of m are sustainable for any given values of w. The point that when m is high, persistence is only possible when w is also high (Figure 4), is qualitatively intuitive. However, our analyses quantitatively evaluate such relationships, and show how they can vary with life-history. For example, our hypothetical longer-lived species persisted in a wider range of the explored movement parameter space. Additionally, our parameterizations show how such outcomes

can depend on the level of individual plasticity. Persistence occurred across wider movement parameter space when seasonal migration or residence are lifelong fixed strategies than given seasonal or annual plasticity, especially in the longer-lived species. With fixed strategies, the less fit phenotype (migrants in our examples) is selected out, causing the mobile fraction Ω to be lower than m. Effects of such within-generation selection are smaller in the short-lived species, leaving a higher proportion of the metapopulation susceptible to movement costs.

Our results highlight the potentially key contributions of variable seasonal migration rates to metapopulation dynamics. Specifically, elasticities highlight those perturbations in m and associated w can have comparable (or even larger) effects on λ than perturbations in the vital rates that are typically taken to have the greatest impacts (i.e. fecundity for short-lived species; adult survival for longer-lived species). As vital rates are location- and season-specific, our framework can identify critical locations and seasons that could underlie system dynamics (Erickson et al., 2018; Sample et al., 2020). Such understanding could aid effective conservation or management of vulnerable seasonally mobile species (Møller et al., 2008; White et al., 2018), including eradication of pest or invasive species (Stuart et al., 2006). However, as elasticities of λ to vital rates varied non-linearly with seasonal movement rates, and interacted with plasticity levels (Appendix S5), simple overarching generalizations cannot be readily drawn. To make progress towards identifying general principles of constraints on partially migratory metapopulations, we now need empirical estimates of key vital rates comprising stage-,

season- and location-specific seasonal movement probability and associated survival and plasticity, alongside seasonal survival and reproduction (see also Norris & Taylor, 2006; Reid et al., 2018; Runge & Marra, 2005; Small-Lorenz et al., 2013).

Accordingly, our empirical case study illustrates how year-round demographic monitoring can allow initial parameterization of required models. We characterized the relevant $m - w$ parameter space, and other vital rates, for a shag metapopulation where individuals are consistently resident or migrant across years (Figure 6). By parameterizing the model M_{life}, we show that λ would be most elastic to perturbations of adult survival probability for the resident fraction of the metapopulation breeding at the Isle of May colony. However, under a hypothetical scenario with higher m, adult survival during seasonal movement would become the vital rate to which λ is most elastic. Thus, our framework can be used to consider the relative value of managing the breeding colony versus the larger-scale coastal environment. As technologies develop, the required estimates of key seasonal movement vital rates such as m and m will soon become available for diverse seasonally mobile species (Eggeman et al., 2016; Grayson et al., 2011; Grist et al., 2017). Future ambitions should be to systematically include such estimates within comparative demography databases (e.g. Salguero-Gómez et al., 2017). This would also facilitate further exploration of how matrix dimensions can affect calculated elasticities of λ to vital rates, and hence affect demographic inferences (Reid et al., 2004; Salguero-Gómez & Plotkin, 2010). Meanwhile our current analyses illustrate how, when explicit vital rate estimates are not yet available, reasonable assumptions can allow exploration of biologically plausible or postulated scenarios.

7.2 | Extensions and open questions

Our conceptual framework is implemented as a flexible and customizable matrix model, enabling future implementation of multiple scenarios and extensions. It allows formulating particular baseline life-history structures (i.e. modifying age or stage structure) and specifying specific vital rates associated with any postulated seasonal and spatial landscape. It allows including variation in m and w among age, locations and seasons, such as widely occurs in nature (Chapman et al., 2011; Lundberg, 1988; Mysterud et al., 2011). This could allow for instance evaluating whether further imbalance in patch quality may result more substantial differences in resident and moving fractions. Further, it allows consideration of 'carry-over effects', wherein conditions experienced in one season affect vital rates expressed subsequently (e.g. persistent effects of seasonal location on body condition or territory maintenance, Grist et al., 2017; Kokko, 2011; Norris & Taylor, 2006). Carry-over effects can be implemented within M_{life} by allowing vital rates to differ between resident and seasonally mobile subpopulations that are seasonally sympatric. This would also be readily achievable for M_{season} and M_{year}, by explicitly modelling two stages for previous migrants and previous residents. The magnitude of the carry-over effects could be defined as a parameter itself that could vary among age, locations

or seasons. The elasticity of λ to the magnitude of carry-over effects could then be evaluated.

Systems where resident versus migrant strategies are acquired at a given life stage (e.g. fish, Chapman et al., 2012) could be implemented by applying appropriate constraints on stage structure. For instance, specific combinations of pre-migratory and post-migratory stages could be formulated, with m defined as the transition rate. Systems where movements occur more than twice per year could be considered by defining additional seasonal matrices (e.g. representing stop-over locations, Bauer et al., 2008). More patches could be included; incorporating greater spatial complexity has illuminated the causes and consequences of dispersal (Bocedi et al., 2014), and might be similarly influential for systems involving seasonal migration.

In practice, expanding our current framework to more than three patches would be cumbersome, due to the need to explicitly formulate all possible seasonal and spatial transitions through nonsymmetric matrices. However, our current analyses highlight that, in the absence of environmental stochasticity and when populations are not connected through dispersal, key aspects of system dynamics and specifically λ could be captured by solely considering the dominant population. But, considering the full system will still be necessary if density- or frequency-dependence in vital rates occurs in seasonally shared locations. Moreover, variation in seasonal migration and/or environmental stochasticity can modify which is the dominant population at any given time.

Indeed, our current models could be extended to explicitly consider density-dependence, environmental and demographic stochasticity and resulting transient dynamics, as previously done for matrix models that do not consider variable seasonal migration (Caswell, 2007; Haridas & Tuljapurkar, 2007). Yet, such extensions would yield additional interesting challenges, due to the implied demographic, spatial and seasonal structure. Environmental stochasticity and extreme climatic events might differentially affect vital rates of seasonally mobile versus resident subpopulations rather than have system-wide effects (Acker, Daunt, et al., 2021). Further, environmental changes could potentially directly affect movement probabilities and associated survival probabilities; indeed it has been previously suggested that increasing environmental stochasticity can increase movement propensity (Kokko & Lundberg, 2001).

Seasonal movement probabilities could also be density-dependent (Grayson et al., 2011; Mysterud et al., 2011), and will certainly alter local seasonal densities and thereby affect other density-dependent vital rates. Indeed, intrinsic relationships between the frequency of seasonal migration and local density have been suggested to cause frequency-dependent selection on seasonal migration, and thereby maintain partial migration (Kokko & Lundberg, 2001; Runge & Marra, 2005). However, such tight relationships between migration probability and density only arise when migratory subpopulations move to otherwise unoccupied patches. Much more complicated relationships could potentially arise in partially migratory metapopulations inhabiting weakly seasonal landscapes where different locations can hold residents

alongside incoming and outgoing migrants, as envisaged by our current models (Reid et al., 2018). Such effects may ultimately be best considered by placing our concepts within a spatially explicit individual-based model framework, which could track local density and effects of differing spatio-temporal regimes of environmental perturbations. Individual-based models would also facilitate eco-evolutionary extensions to examine evolutionary dynamics of partial migration and associated plasticity or canalization. This approach will ultimately facilitate integration of holistic understanding of metapopulation dynamic consequences of variation in seasonal migration into forecasting and management tools (e.g. Bocedi et al., 2014).

AUTHORS' CONTRIBUTIONS

A.P.-P. conceived the ideas, undertook the analyses and drafted the manuscript, assisted by J.M.R. and P.A.; J.M.R. and P.A. provided empirical estimates; F.D., S.W., S.B., M.N., M.P.H. and J.M.R. collected the data used in previous manuscripts to generate used empirical estimates. All authors contributed to conceptual, technical and manuscript development and gave the final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

There are no primary data associated with this manuscript.

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REFERENCES

Acker, P., Burthe, S., Newell, M., Grist, H., Gunn, C., Harris, M., Payo-Payo, A., Swann, R., Wanless, S., Daunt, F., & Reid, J. (2021). Episodes of opposing survival and reproductive selection cause strong fluctuating selection on seasonal migration versus residence. *Proceedings of the Royal Society B: Biological Sciences*, 288(20210404), 1–10.

Acker, P., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., Grist, H., Sturgeon, J., Swann, R. L., Gunn, C., Payo-Payo, A., & Reid, J. M. (2021). Strong survival selection on seasonal migration versus residence induced by extreme climatic events. *Journal of Animal Ecology*, 90(4), 796–808. https://doi.org/10.1111/1365-2656.13410

Aebischer, N. J., Potts, G. R., & Coulson, J. C. (1995). Site and mate fidelity of Shags *Phalacrocorax aristotelis* at two British colonies. *Ibis*, 137(1), 19–28. https://doi.org/10.1111/j.1474-919X.1995.tb03215.x

Akçakaya, H. R. (2000). Viability analyses with habitat-based metapopulation models. *Population Ecology*, 42(1), 45–53. https://doi.org/10.1007/s101440050043

Alderman, R., Gales, R., Hobday, A., & Candy, S. (2010). Post-fledging survival and dispersal of shy albatross from three breeding colonies in Tasmania. *Marine Ecology Progress Series*, 405, 271–285. https://doi.org/10.3354/meps08590

Barlow, E. J., Daunt, F., Wanless, S., & Reid, J. M. (2013). Estimating dispersal distributions at multiple scales: Within-colony and among-colony dispersal rates, distances and directions in European Shags *Phalacrocorax aristotelis*. *Ibis*, 155(4), 762–778. https://doi.org/10.1111/ibi.12060

Bauer, S., Dinther, M. V., Høgda, K.-A., Klaassen, M., & Madsen, J. (2008). The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. *Journal of Animal Ecology*, 77(4), 654–660. https://doi.org/10.1111/j.1365-2656.2008.01381.x

Benton, T. G., & Grant, A. (1999). Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution*, 14(12), 467–471. https://doi.org/10.1016/S0169-5347(99)01724-3

Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K., & Travis, J. M. J. (2014). RangeShifter: A platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology and Evolution*, 5(4), 388–396. https://doi.org/10.1111/2041-210X.12162

Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(7089), 81–83. https://doi.org/10.1038/nature04539

Caswell, H. (2007). Sensitivity analysis of transient population dynamics. *Ecology Letters*, 10, 1–15.

Caswell, H. (2001). *Matrix population models: Construction, analysis and interpretation*. Sinauer.

Chapman, B. B., Brönmark, C., Nilsson, J.-Å., & Hansson, L.-A. (2011). The ecology and evolution of partial migration. *Oikos*, 120(12), 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Chapman, B. B., Hulthén, K., Brodersen, J., Nilsson, P. A., Skov, C., Hansson, L.-A., & Brönmark, C. (2012). Partial migration in fishes: Causes and consequences. *Journal of Fish Biology*, 81(2), 456–478. https://doi.org/10.1111/j.1095-8649.2012.03342.x

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J., & Grenfell, B. T. (2001). Age, sex, density, winter weather, and population crashes in Soay Sheep. *Science*, 292(5521), 1528–1531. https://doi.org/10.1126/science.292.5521.1528

de Castro, M. L., Silva, J. A. L., & Justo, D. A. R. (2006). Stability in an age-structured metapopulation model. *Journal of Mathematical Biology*, 52(2), 183–208. https://doi.org/10.1007/s00285-005-0352-4

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Dobson, A. D. M., Finnie, T. J. R., & Randolph, S. E. (2011). A modified matrix model to describe the seasonal population ecology of the European tick *Ixodes ricinus*. *Journal of Applied Ecology*, 48, 1017–1028.

Eggeman, S. L., Hebblewhite, M., Bohm, H., Whittington, J., & Merrill, E. H. (2016). Behavioural flexibility in migratory behaviour in a

long-lived large herbivore. *The Journal of Animal Ecology*, *85*(3), 785–797. https://doi.org/10.1111/1365-2656.12495

Erickson, R. A., Diffendorfer, J. E., Norris, D. R., Bieri, J. A., Earl, J. E., Federico, P., Fryxell, J. M., Long, K. R., Mattsson, B. J., Sample, C., Wiederholt, R., & Thogmartin, W. E. (2018). Defining and classifying migratory habitats as sources and sinks: The migratory pathway approach. *Journal of Applied Ecology*, *55*(1), 108–117. https://doi.org/10.1111/1365-2664.12952

Frederiksen, M., Daunt, F., Harris, M. P., & Wanless, S. (2008). The demographic impact of extreme events: Stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, *77*(5), 1020–1029. https://doi.org/10.1111/j.1365-2656.2008.01422.x

Gaillard, J.-M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, *84*(12), 3294–3306. https://doi.org/10.1890/02-0409

Gallardo, J. C., Vilella, F. J., & Colvin, M. E. (2019). A seasonal population matrix model of the Caribbean Red-tailed Hawk *Buteo jamaicensis jamaicensis* in eastern Puerto Rico. *Ibis*, *161*(2), 459–466. https://doi.org/10.1111/ibi.12703

Gauthier, G., Pradel, R., Menu, S., & Lebreton, J.-D. (2001). Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. *Ecology*, *82*(11), 3105–3119. https://doi.org/10.1890/0012-9658(2001)082[3105:SSOGSG]2.0.CO;2

Gillanders, B. M., Izzo, C., Doubleday, Z. A., & Ye, Q. (2015). Partial migration: Growth varies between resident and migratory fish. *Biology Letters*, *11*(3), 20140850. https://doi.org/10.1098/rsbl.2014.0850

Gowan, T. A., Ortega-Ortiz, J. G., Hostetler, J. A., Hamilton, P. K., Knowlton, A. R., Jackson, K. A., George, R. C., Taylor, C. R., & Naessig, P. J. (2019). Temporal and demographic variation in partial migration of the North Atlantic right whale. *Scientific Reports*, *9*(1), 353. https://doi.org/10.1038/s41598-018-36723-3

Grayson, K. L., Bailey, L. L., & Wilbur, H. M. (2011). Life history benefits of residency in a partially migrating pond-breeding amphibian. *Ecology*, *92*(6), 1236–1246. https://doi.org/10.1890/11-0133.1

Grist, H., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., & Reid, J. M. (2017). Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. *The Journal of Animal Ecology*, *86*(5), 1010–1021. https://doi.org/10.1111/1365-2656.12691

Grist, H., Daunt, F., Wanless, S., Nelson, E. J., Harris, M. P., Newell, M., Burthe, S., & Reid, J. M. (2014). Site fidelity and individual variation in winter location in partially migratory european shags. *PLoS One*, *9*(6), e98562. https://doi.org/10.1371/journal.pone.0098562

Hansen, B. B., Gamelon, M., Albon, S. D., Lee, A. M., Stien, A., Irvine, R. J., Sæther, B.-E., Loe, L. E., Ropstad, E., Veiberg, V., & Grøtan, V. (2019). More frequent extreme climate events stabilize reindeer population dynamics. *Nature Communications*, *10*(1), 1616. https://doi.org/10.1038/s41467-019-09332-5

Hanski, I., Alho, J., & Moilanen, A. (2000). Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, *81*(1), 239–251. https://doi.org/10.1890/0012-9658(2000)081[0239:ETPOSA]2.0.CO;2

Haridas, C. V., & Tuljapurkar, S. (2007). Time, transients and elasticity. *Ecology Letters*, *10*(12), 1143–1153. https://doi.org/10.1111/j.1461-0248.2007.01108.x

Heppell, S., Caswell, H., & Crowder, L. (2000). Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology*, *81*(3), 654–665. https://doi.org/10.2307/177367

Hokit, D. G., Stith, B. M., & Branch, L. C. (2001). Comparison of two types of metapopulation models in real and artificial landscapes. *Conservation Biology*, *15*(4), 1102–1113.

Hostetler, J. A., Sillett, T. S., & Marra, P. P. (2015). Full-annual-cycle population models for migratory birds. *The Auk*, *132*(2), 433–449. https://doi.org/10.1642/AUK-14-211.1

Inchausti, P., & Weimerskirch, H. (2002). Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology*, *71*(5), 765–770. https://doi.org/10.1046/j.1365-2656.2002.00638.x

IPCC. (2022). *Climate change 2022: Impacts, adaptation, and vulnerability. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change*. H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.). Cambridge University Press. In Press.

Kerr, L. A., Secor, D. H., & Piccoli, P. M. (2009). Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries*, *34*(3), 114–123. https://doi.org/10.1577/1548-8446-34.3.114

Kokko, H. (2011). Directions in modelling partial migration: How adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos*, *120*(12), 1826–1837. https://doi.org/10.1111/j.1600-0706.2011.19438.x

Kokko, H., & Lundberg, P. (2001). Dispersal, migration, and offspring retention in saturated habitats. *The American Naturalist*, *157*(2), 188–202. https://doi.org/10.1086/318632

Koons, D. N., Iles, D. T., Schaub, M., & Caswell, H. (2016). A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecology Letters*, *19*(9), 1023–1031. https://doi.org/10.1111/ele.12628

Lecomte, J.-B., Le Pape, O., Baillif, H., Nevoux, M., Vermard, Y., Savina, M., Veron, M., Lehuta, S., Hunter, E., & Rivot, E. (2020). State-space modeling of multidecadal mark–recapture data reveals low adult dispersal in a nursery-dependent fish metapopulation. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(2), 342–354. https://doi.org/10.1139/cjfas-2019-0037

Lee, D. E., & Bolger, D. T. (2017). Movements and source–sink dynamics of a Masai giraffe metapopulation. *Population Ecology*, *59*(2), 157–168. https://doi.org/10.1007/s10144-017-0580-7

Lundberg, P. (1988). The evolution of partial migration in Birds. *Trends in Ecology & Evolution*, *3*(7), 172–175. https://doi.org/10.1016/0169-5347(88)90035-3

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, *11*(8), 20150552. https://doi.org/10.1098/rsbl.2015.0552

Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(42), 16195–16200. https://doi.org/10.1073/pnas.0803825105

Mora Alvarez, B. X., Carrera-Treviño, R., & Hobson, K. A. (2019). Mortality of monarch butterflies (*Danaus plexippus*) at two highway crossing 'hotspots' during autumn migration in Northeast Mexico. *Frontiers in Ecology and Evolution*, *7*, 1–7. https://doi.org/10.3389/fevo.2019.00273

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., & Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes – A role for density dependence? *Oikos*, *120*(12), 1817–1825. https://doi.org/10.1111/j.1600-0706.2011.19439.x

Norris, D. R., & Taylor, C. M. (2006). Predicting the consequences of carry-over effects for migratory populations. *Biology Letters*, *2*(1), 148–151. https://doi.org/10.1098/rsbl.2005.0397

Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T. H., & Ozgul, A. (2019). Life history responses of meerkats to seasonal changes in extreme environments. *Science*, *363*(6427), 631–635.

R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., & Monaghan, P. (2004). Identifying the demographic determinants of population growth rate: A case study of red-billed choughs *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, *73*(4), 777–788. https://doi.org/10.1111/j.0021-8790.2004.00854.x

Reid, J. M., Souter, M., Fenn, S. R., Acker, P., Payo-Payo, A., Burthe, S. J., Wanless, S., & Daunt, F. (2020). Among-individual and within-individual variation in seasonal migration covaries with subsequent reproductive success in a partially migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1931), 20200928. https://doi.org/10.1098/rspb.2020.0928

Reid, J. M., Travis, J. M. J., Daunt, F., Burthe, S. J., Wanless, S., & Dytham, C. (2018). Population and evolutionary dynamics in spatially structured seasonally varying environments. *Biological Reviews*, *3*, 1578–1603. https://doi.org/10.1111/brv.12409

Revilla, E., & Wiegand, T. (2008). Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19120–19125. https://doi.org/10.1073/pnas.0801725105

Runge, M. C., & Marra, P. P. (2005). Modeling seasonal interactions in the population dynamics of migratory birds. In R. Greenberg & P. P. Marra (Eds.), *Birds of two worlds: The ecology and evolution of migration* (pp. 375–389). The John Hopkins University Press.

Saether, B.-E., & Bakke, O. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, *81*(3), 642–653. https://doi.org/10.2307/177366

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Bein, C., Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y. M., Che-Castaldo, J., ... Vaupel, J. W. (2016). COMADRE: A global data base of animal demography. *Journal of Animal Ecology*, *85*(2), 371–384. https://doi.org/10.1111/1365-2656.12482

Salguero-Gómez, R., & Plotkin, J. B. (2010). Matrix dimensions bias demographic inferences: Implications for comparative plant demography. *The American Naturalist*, *176*(6), 710–722. https://doi.org/10.1086/657044

Sample, C., Bieri, J. A., Allen, B., Dementieva, Y., Carson, A., Higgins, C., Piatt, S., Qiu, S., Stafford, S., Mattsson, B. J., Semmens, D. J., Diffendorfer, J. E., & Thogmartin, W. E. (2020). Quantifying the contribution of habitats and pathways to a spatially structured population facing environmental change. *The American Naturalist*, *196*(2), 157–168. https://doi.org/10.1086/709009

Sample, C., Fryxell, J. M., Bieri, J. A., Federico, P., Earl, J. E., Wiederholt, R., Mattsson, B. J., Flockhart, D. T. T., Nicol, S., Diffendorfer, J. E., Thogmartin, W. E., Erickson, R. A., & Norris, D. R. (2018). A general modeling framework for describing spatially structured population dynamics. *Ecology and Evolution*, *8*(1), 493–508. https://doi.org/10.1002/ece3.3685

Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, *24*(1), 35–68. https://doi.org/10.1146/annurev.es.24.110193.000343

Sendor, T., & Simon, M. (2003). Population dynamics of the pipistrelle bat: Effects of sex, age and winter weather on seasonal survival. *Journal of Animal Ecology*, *72*(2), 308–320. https://doi.org/10.1046/j.1365-2656.2003.00702.x

Shaw, A. K., & Levin, S. A. (2011). To breed or not to breed: A model of partial migration. *Oikos*, *120*(12), 1871–1879. https://doi.org/10.1111/j.1600-0706.2011.19443.x

Shima, J. S., Noonburg, E. G., & Phillips, N. E. (2010). Life history and matrix heterogeneity interact to shape metapopulation connectivity in spatially structured environments. *Ecology*, *91*(4), 1215–1224. https://doi.org/10.1890/08-2058.1

Small-Lorenz, S. L., Culp, L. A., Ryder, T. B., Will, T. C., & Marra, P. P. (2013). A blind spot in climate change vulnerability assessments. *Nature Climate Change*, *3*, 91–93. https://doi.org/10.1038/nclimate1810

Stuart, I. G., Williams, A., McKenzie, J., & Holt, T. (2006). Managing a migratory pest species: A selective trap for common carp. *North American Journal of Fisheries Management*, *26*(4), 888–893. https://doi.org/10.1577/M05-205.1

Travis, J. M. J., Mustin, K., Bartoń, K. A., Benton, T. G., Clobert, J., Delgado, M. M., Dytham, C., Hovestadt, T., Palmer, S. C. F., Dyck, H. V., & Bonte, D. (2012). Modelling dispersal: An eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution*, *3*(4), 628–641. https://doi.org/10.1111/j.2041-210X.2012.00193.x

Tujlapurkar, S., & Caswell, H. (1997). *Structured-population models in marine, terrestrial, and freshwater systems* (Vol. *18*). Chapman & Hall.

van Tienderen, P. H. (1995). Life cycle trade-offs in matrix population models. *Ecology*, *76*(8), 2482–2489. https://doi.org/10.2307/2265822

White, D., David, T. L., Barnowe-Meyer, K. K., Carbtree, R. L. C., & Garrott, R. A. (2007). Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation*, *135*(4), 502–510. https://doi.org/10.1016/j.biocon.2006.10.041

White, K. S., Gregovich, D. P., & Levi, T. (2018). Projecting the future of an alpine ungulate under climate change scenarios. *Global Change Biology*, *24*(3), 1136–1149. https://doi.org/10.1111/gcb.13919

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