

1 Modelling the responses of partially-migratory metapopulations to changing seasonal
2 migration rates: from theory to data.

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22 **Abstract**

- 23 1. Among-individual and within-individual variation in expression of seasonal migration
24 versus residence is widespread in nature and could substantially affect the dynamics of
25 partially-migratory metapopulations inhabiting seasonally- and spatially-structured
26 environments. However, such variation has rarely been explicitly incorporated into
27 metapopulation dynamic models for partially migratory systems. We therefore lack
28 general frameworks that can identify how variable seasonal movements, and associated
29 season- and location-specific vital rates, can control system persistence.
- 30 2. We constructed a novel conceptual framework that captures full-annual-cycle dynamics
31 and key dimensions of metapopulation structure for partially-migratory species
32 inhabiting seasonal environments. We conceptualize among-individual variation in
33 seasonal migration as two variable vital rates: seasonal movement probability and
34 associated movement survival probability. We conceptualize three levels of within-
35 individual variation (i.e. plasticity), representing seasonal or annual variation in seasonal
36 migration or lifelong fixed strategies. We formulate these concepts as a general matrix
37 model, which is customizable for diverse life-histories and seasonal landscapes.
- 38 3. To illustrate how variable seasonal migration can affect metapopulation growth rate,
39 demographic structure and vital rate elasticities, we parameterize our general models for
40 hypothetical short- and longer-lived species. Analyses illustrate that elasticities of
41 seasonal movement probability and associated survival probability can sometimes equal
42 or exceed those of vital rates typically understood to substantially influence
43 metapopulation dynamics (i.e. seasonal survival probability or fecundity), that
44 elasticities can vary non-linearly, and that metapopulation outcomes depend on the level
45 of within-individual plasticity.

- 46 4. We illustrate how our general framework can be applied to evaluate the consequences
47 of variable and changing seasonal movement probability by parameterizing our models
48 for a real partially-migratory metapopulation of European shags (*Gulosus aristotelis*)
49 assuming lifelong fixed strategies. Given observed conditions, metapopulation growth
50 rate was most elastic to breeding season adult survival of the resident fraction in the
51 dominant population. However, given doubled seasonal movement probability,
52 variation in survival during movement would become the primary driver of
53 metapopulation dynamics.
- 54 5. Our general conceptual and matrix model frameworks, and illustrative analyses, thereby
55 highlight complex ways in which structured variation in seasonal migration can
56 influence dynamics of partially-migratory metapopulations, and pave the way for
57 diverse future theoretical and empirical advances.

58 **KEYWORDS** Demographic structure, elasticity, full-annual-cycle matrix model,
59 metapopulation, partial migration, persistence, seasonal movement, seasonality.

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69 **1 | INTRODUCTION**

70 Identifying which life-history traits, and resulting population-wide vital rates, show
71 environmentally-induced variation and substantially affect population growth rate (λ) can
72 facilitate prediction of population responses to environmental change and inform population
73 management (Caswell, 2001; Heppell et al., 2000; Saether & Bakke, 2000). As effects of
74 environmental variation on λ can depend on population demographic structure (Coulson et al.,
75 2001; Hansen et al., 2019), efforts to explain and predict λ should aim to capture multiple
76 dimensions of structure that can apply in wild populations (Tuljapurkar & Caswell, 1997).

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

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

93 al., 2001; Lecomte et al., 2020; Shima et al., 2010; Travis et al., 2012). However,
94 metapopulation dynamic consequences of variation in seasonal migration remain scarcely
95 examined (Castro et al., 2006; Hanski et al., 2000; Lee & Bolger, 2017). Indeed the need to
96 build and analyze ‘full-annual-cycle’ metapopulation models for mobile populations has been
97 repeatedly emphasized, but still not fully enacted (Hostetler et al., 2015; Sample et al., 2018;
98 Small-Lorenz et al., 2013). Such models could identify key locations in spatio-seasonally
99 heterogeneous landscapes, and season-specific vital rates including migration rates, that
100 constrain λ .

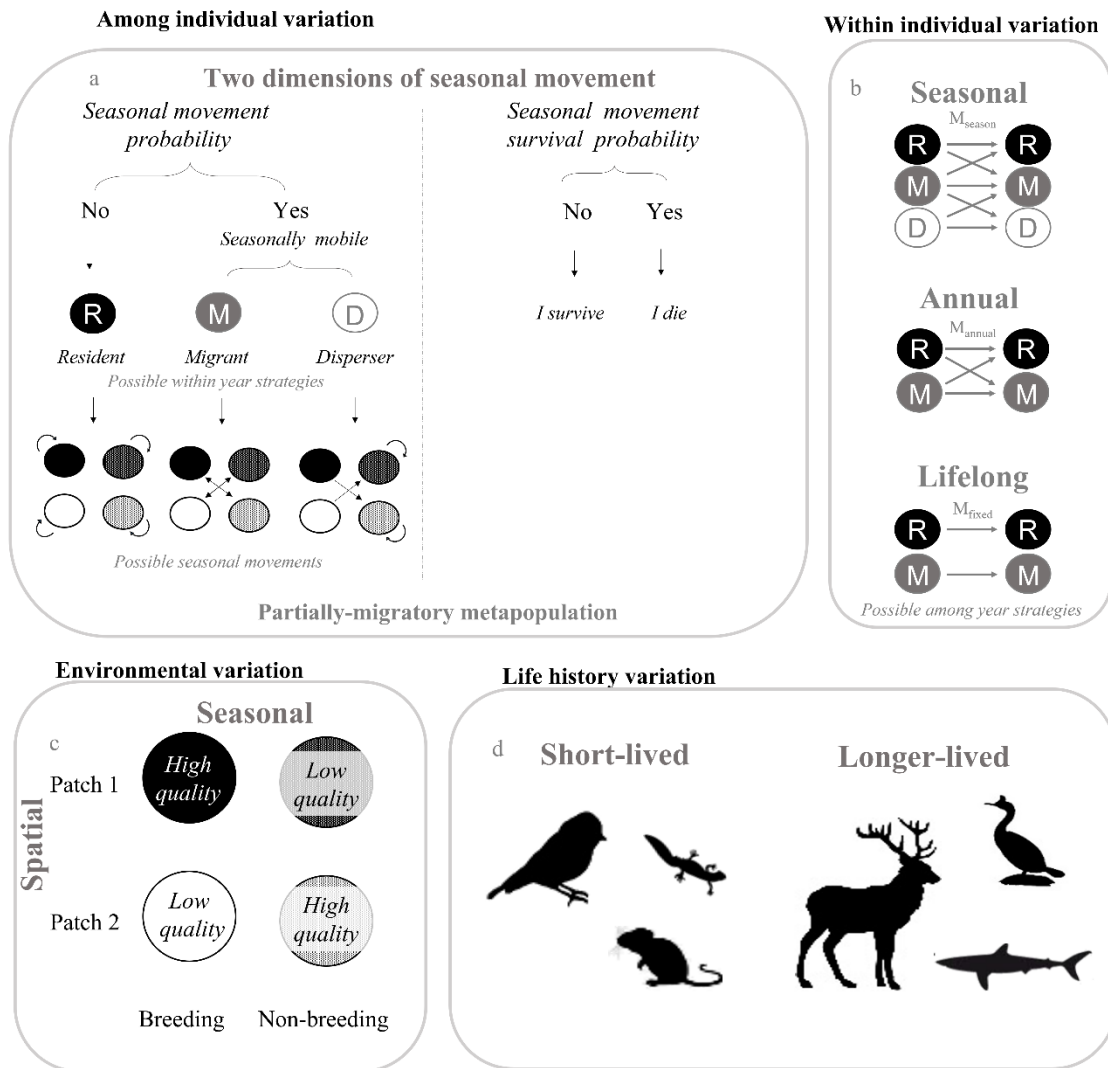
101 Explicitly considering metapopulation consequences of changing seasonal migration is
102 relevant because expression of migration (versus residence) commonly varies among
103 individuals and years within populations, generating variable ‘partial migration’ (Chapman et
104 al., 2011; Grist et al.,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

114 Further structure could then result from the temporal scale of within-individual
115 variation in seasonal migration versus residence, and associated plasticity(i.e. the potential of
116 a single genotype or individual to express differing phenotypes, (Dingemanse et al., 2010;
117 Scheiner, 1993). Here, individuals could make independent decisions to move or not after each

118 breeding and non-breeding season (hereafter ‘seasonally plastic’ movement, Fig. 1). This
119 generates three possible annual outcomes: residence, seasonal migration and dispersal.
120 Alternatively, individuals could make such decisions annually after each breeding season, with
121 all moving individuals returning after the non-breeding season (hereafter ‘annually plastic’
122 migration, Fig. 1). Both seasonally and annually plastic movements generate partial migration
123 at the population level with within-individual variation in movement between years. Such
124 outcomes have been observed in diverse species including North Atlantic right
125 whales (*Eubalaena glacialis*) and red-spotted newts (*Notophthalmus viridescens*) (Gowan et
126 al., 2019; Grayson et al., 2011). Finally, individuals could develop fixed migrant or resident
127 strategies at or soon after birth, with little or no subsequent within-individual plasticity.
128 Surviving individuals then consistently enact seasonal migration or residence each year
129 throughout their lifetime (hereafter ‘lifelong fixed’ migration, Fig. 1). Indeed, high individual
130 migratory repeatability occurs in diverse species including European shag (*Gulosus*
131 *aristotelis*), elk (*Cervus elaphus*) and white perch (*Morone americana*) (Eggeman et al., 2016;
132 Grist et al., 2014; Kerr et al., 2009). Then, if residents and migrants experience different
133 survival probabilities, the proportion of each cohort that is seasonally migrant will change
134 across years due to within-generation phenotypic selection. Resulting deviations from the
135 seasonal movement probability manifested at birth could further alter metapopulation structure
136 and responses to spatially-structured environmental perturbations.

137

Sources of demographic structure



138

139 **FIGURE 1** Conceptual framework highlighting considered sources of demographic structure
 140 in partially migratory metapopulations: (a) among individual variation, (b) within individual
 141 variation, (c) environmental variation illustrated for a landscape with two patches (black and
 142 white) and two seasons (dark and light grey) and (d) life history variation illustrated for short
 143 and longer lived species. Possible seasonal movements (a) result in three within year strategies:
 144 residents (R), seasonal migrants (M) and dispersers (D). Possible among year strategies (b)
 145 result in three distinct models, with seasonally plastic movement (M_{season}), annually plastic

146 seasonal migration (M_{year}) or lifelong fixed seasonal migration (M_{life}). Arrows represent
147 different potential individual paths among years.

148

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

159 One approach to understanding impacts of changing migration is to utilize well-
160 established principles of matrix population models to project λ (e.g. Caswell, 2001). This
161 approach could identify parameter spaces where partially-migratory metapopulations are
162 expected to grow, remain stable or decrease given differing probabilities of seasonal migration
163 and associated vital rates. ‘Elasticities’ can then be computed to predict relative impacts of
164 perturbations (e.g. Caswell, 2001). Moreover, such models can facilitate generalization along
165 the ‘fast-slow’ life-history continuum (i.e. short-lived vs longer-lived, Fig. 1, Sæther & Bakke,
166 2000), project demographic structure, and identify links between vital rate variation and life-
167 history evolution (Benton & Grant, 1999; Caswell, 2001; van Tienderen, 1995). Seasonal
168 matrix models have previously been formulated, for instance considering seasonal demography
169 in European ticks (*Ixodes ricinus*, Dobson et al., 2011) and Caribbean Red-tailed Hawks (*Buteo*
170 *jamaicensis jamaicensis*, Gallardo et al., 2019). However, general models that jointly and

171 explicitly consider variation in seasonal migration probability, plasticity and associated
172 survival have not previously been formulated or analyzed.

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

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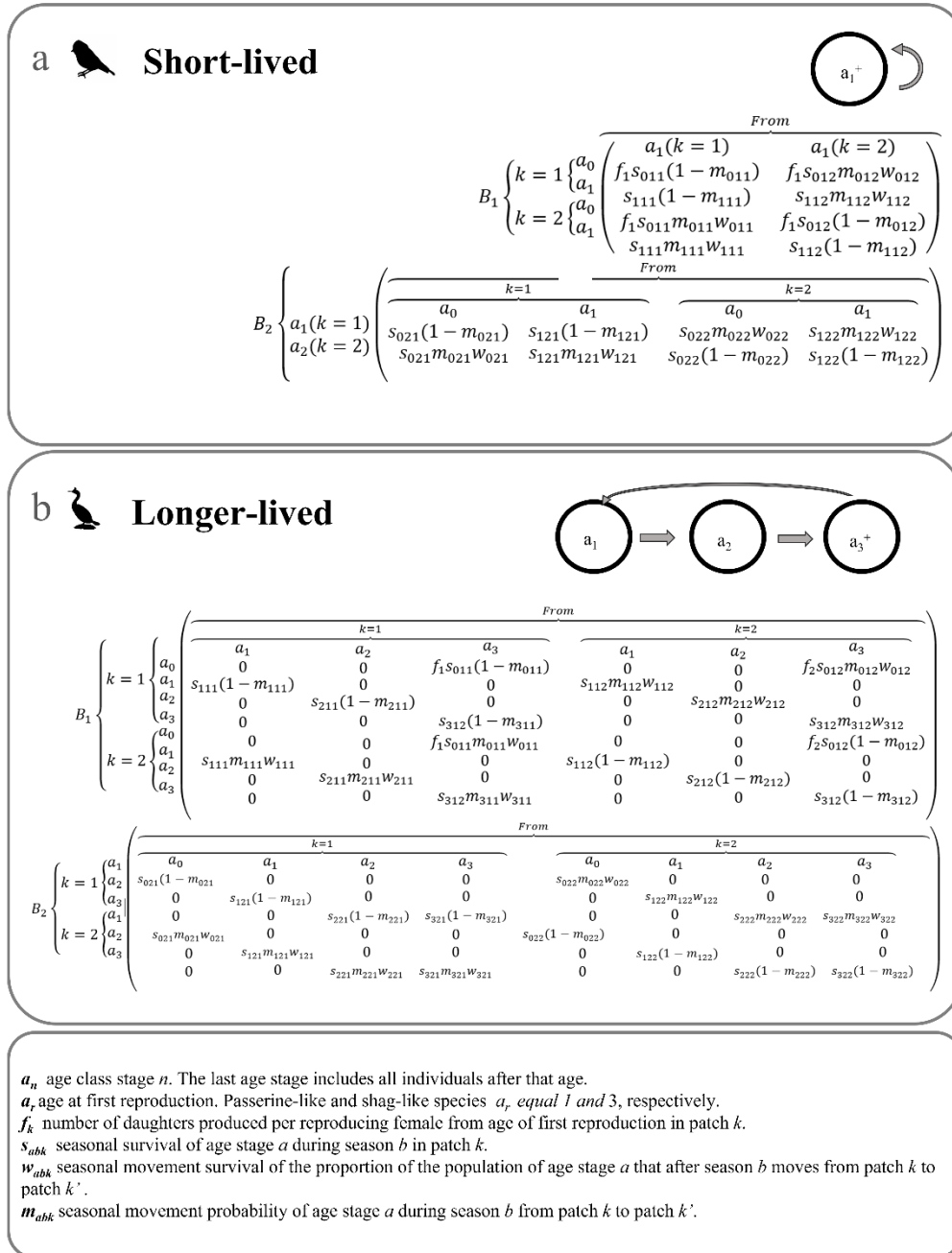
189 **2 | GENERAL FRAMEWORK FOR PARTIALLY MIGRATORY** 190 **METAPOPULATIONS**

191 **2.1 | Seasonal matrix modelling approach and demographic formulation**

192 We construct a general stage-structured full-annual-cycle matrix model with explicit seasonal
193 and spatial variation in vital rates (Figs.1 and 2). The model considers females within a sexually
194 reproducing population, and an annual projection interval based on a pre-breeding census. Each
195 year comprises two consecutive seasons (b): a breeding season (hereafter, $b = 1$) and a non-

196 breeding season (hereafter, $b = 2$). The landscape consists of two patches (hereafter $k = 1$ and
 197 $k = 2$) with one population breeding in each patch. This is the simplest structure that allows
 198 spatial and seasonal variation in vital rates following the concept of a partially-migratory
 199 metapopulation (Reid et al., 2018). The annual projection matrix characterizes a full-annual-
 200 cycle comprising reproduction, breeding season survival, post-breeding seasonal movement
 201 (and associated survival) or residence, non-breeding season survival, and post non-breeding
 202 seasonal movement (and associated survival) or residence. Specifically, we model
 203 metapopulation dynamics from time t to $t+1$ as $N_{t+1} = AN_t$, where N_t and N_{t+1} are vectors of
 204 metapopulation size in each age or stage at time t and $t+1$ respectively, and A is the full-annual-
 205 cycle metapopulation projection matrix. A is the product of non-breeding (B_2) and breeding
 206 (B_1) season metapopulation projection matrices (i.e. $A=B_2B_1$), thereby conceptually allowing
 207 movement between patches and demographic strata between seasons (Caswell 2001). Each
 208 seasonal matrix (B_b) has sub-matrices B_{bdo} , where d refers to the destination (to) patch and o
 209 refers to the original (from) patch. For example, B_{b12} is the projection matrix for the population
 210 that was in patch 2 at the beginning of season b and moved to patch 1, while B_{b22} is the
 211 projection matrix for the population that was in patch 2 and remained there. Overall, B_b is
 212 defined as: $B_b = \begin{pmatrix} B_{b11} & B_{b12} \\ B_{b21} & B_{b22} \end{pmatrix}$.

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



220

221 **FIGURE 2** Annual life cycles and $M_{\text{season}} B_b$ sub-matrices for hypothetical (a) short-lived and

222 (b) longer-lived species for a landscape with two patches ($k=1$ and $k=2$) and two seasons ($b=1$

223 and $b=2$). Life-histories are defined by setting parameters for age-, season- and location-

224 dependent survival (s_{abk}), for age-, season- and location-dependent seasonal movement

225 (m_{abk}) and seasonal movement survival (w_{abk}), age at first reproduction (a_r) and location-

226 dependent fecundity (f_k). Short-lived and longer lived species consider age at first reproduction
227 (a_r) equal 1 and 3 respectively. Age classes are noted as a_n . For further illustration see
228 Appendix S1.

229 **2.2 | Conceptualizing environmental variation**

230 We capture demographic structure resulting from varying spatial and seasonal environmental
231 quality by implementing spatio- seasonal variation in survival and fecundity. To achieve this,
232 we define baseline parameters in patch 1 ($k = 1$) during the breeding season ($b = 1$), then define
233 other parameters as proportions. For example, we set patch 1 breeding season adult survival
234 probability to s_{a11} . Non-breeding season survival probability in patch 1 is a proportion α_s of
235 s_{a11} (i.e. $s_{a2k} = \alpha_s s_{a1k}$), while breeding season survival probability in patch 2 is a proportion
236 α_g of that in patch 1 (i.e. $s_{a12} = \alpha_g s_{a11}$). To create a biologically relevant seasonal landscape
237 in which a population breeding in patch 1 can escape deteriorating conditions by seasonal
238 movement, we set non-breeding season survival probability in patch 1 to be α_R of that in patch
239 2 (i.e. $s_{a21} = \alpha_R s_{ak2}$). Spatial differences in fecundity follow the same pattern as differences
240 in survival. Therefore, fecundity in patch 2 is α_g of that in patch 1 (i.e. $f_2 = \alpha_s f_1$). However,
241 our general model framework allows for any desired parameterisation.

242

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244 **2.3 | Conceptualizing among-individual variation in seasonal migration**

245 We capture structure resulting from among-individual variation in seasonal migration (Figs.1
246 and 2) by formulating seasonal movement as the product of two variable vital rates: seasonal
247 movement probability (m_{abk}) and seasonal movement survival probability (w_{abk}).
248 Specifically, a proportion m_{abk} of each age stage class a at the end of season b moves from
249 their current patch ($k = 1$ or $k = 2$) towards the other patch. The proportion m_{abk} of the
250 population that moves has probability w_{abk} of surviving the movement. This general

251 formulation allows any desired form of symmetry or asymmetry in seasonal movement
252 probability and seasonal movement survival probability across ages, seasons and patches.
253 Appropriate parameterizations can generate diverse forms of movement, including seasonal
254 migration, temporary and permanent dispersal, or skipping breeding (e.g. Alderman et al.,
255 2010; Shaw & Levin, 2011, Appendix S1).

256

257 **2.4 | Conceptualizing within-individual variation in seasonal migration**

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

266 Second, we constrain M_{season} by forcing the surviving population fraction that had
267 moved between patches after the breeding season to return to their original patch after the non-
268 breeding season and preventing any new movement at this time (hereafter M_{year} , Fig.1). This
269 generates seasonal migration *sensu stricto* with no dispersal due to seasonal movement. This
270 is achieved by specifying $m_{a21} = 0$ in B_2 for fractions of the patch 1 population that were
271 already in patch 1 in season 1, and $m_{a21} = 1$ for fractions of the patch 1 population that were
272 previously in patch 2 in season 1 (with identical constraints on m_{a22} for patch 2). These
273 transitions occur repeatedly across successive years. At the start of each annual projection
274 cycle, both patches can contain resident and migrant fractions, where the population
275 proportions that will undertake seasonal migration equal m_{a11} and m_{a12} for patches 1 and 2

276 respectively. M_{year} does not allow dispersal due to seasonal movement, but allows random
277 switching between year-round residence and seasonal migration between years (i.e. annual
278 plasticity).

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

290

291 **2.5 | Model analyses**

292 All three models can be parameterized and analyzed to quantify how metapopulation
293 persistence ($\lambda \geq 1$), underlying demographic structure, and asymptotic elasticity (e_{θ}) of λ to
294 each vital rate (θ) vary across the potential range of values of seasonal movement probability
295 (m_{abk}) and seasonal movement survival probability (w_{abk}) considering any given level of
296 plasticity and life-history. λ is the dominant eigenvalue of the annual projection matrix A .
297 Characterizing demographic structure helps illuminate the mechanisms underlying variation in
298 λ , by showing the population proportion that moves and is consequently susceptible to
299 movement costs. Specifically, metapopulation mobile fraction (Ω) is the proportion of
300 individuals that start each annual projection cycle that is susceptible to moving at any given

301 time during the focal year. Ω can be further decomposed into migrant (u) and disperser (δ)
302 fractions which respectively correspond to individuals susceptible for seasonal migration and
303 for dispersal. These individuals experience a cost of movement twice or once a year,
304 respectively. If we assume equal movement probabilities (m) among patches, ages and seasons,
305 then for M_{season} $u = m^2$ and $\delta = 2(1 - m)m$, and for M_{year} $u = m$ and $\delta = 0$. For M_{life} , which
306 explicitly includes separate resident and migrant stages, u is the sum of the elements of the
307 right eigenvector of M_{life} matrix that corresponds with the migrant stages and $\delta = 0$. For M_{season}
308 and M_{life} , Ω will deviate from the specified value of m . This deviation results from the presence
309 of both dispersers and seasonal migrants in M_{season} , and from phenotypic selection arising from
310 any survival differences between residents and migrants in M_{life} . Values of asymptotic elasticity
311 e_{θ} , which quantify the proportional change in λ given a proportional change in a vital rate θ ,
312 can be calculated as scaled partial derivatives using the chain rule (Caswell 2001), facilitating
313 comparison across vital rates and life-histories. In M_{year} and M_{life} , the two breeding populations
314 are reproductively isolated as there is no dispersal. The size of the population with the lower λ
315 is consequently asymptotically negligible. Accordingly, the metapopulation λ , Ω and
316 e_{θ} correspond to those of the population with the higher λ . However, dispersal among patches
317 can be explicitly implemented to connect populations (see the empirical case study and
318 Appendix S6).

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3020 **3 | THEORETICAL EXAMPLES: PROPERTIES OF PARTIALLY MIGRATORY** 3021 **METAPOPOPULATIONS**

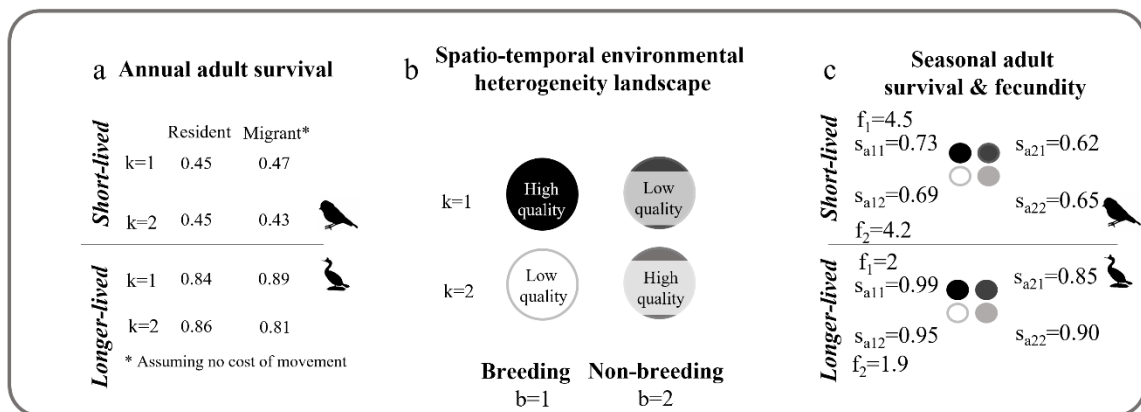
3022 **3.1 | Illustrative parameterizations**

3023 Our general model allows formulation of any life-history representing any partially-migratory
3024 taxa by implementing an appropriate age or stage structure, and allows parameterizations for
3025 any desired two-patch landscape (Appendices C and F). However, to illustrate how our

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

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

334



335

336 **FIGURE 3** Summary of survival and fecundity values in a hypothetical landscape with
 337 seasonal and spatial variation for short-lived and longer-lived species. (a) Realized annual adult
 338 survival probabilities and fecundities for residents and migrants from patches $k = 1$ and $k =$
 339 2. (b) Spatio-temporal landscape given a two-patch and two-season model. (c) Seasonal adult
 340 survival probabilities s_{1bk} , b is season and k is patch, and fecundities are f_k .

341 We then parameterize models M_{season} , M_{year} and M_{life} for a hypothetical short-lived
 342 species with relatively low annual survival and high reproductive rate, and a hypothetical
 343 longer-lived species with higher annual survival and lower reproductive rate (Figs. 2&3). For
 344 current illustrative purposes, parameters were set to broadly resemble a partially-migratory

345 passerine bird and a European shag. The latter was chosen to facilitate subsequent
346 parameterization with available empirical data, thereby facilitating direct transition from theory
347 to data (see Empirical case study). We define baseline conditions by setting breeding season
348 adult survival in patch 1 as $s_{111} = 0.73$ and $s_{111} = 0.99$, and age at first reproduction of $a_r =$
349 1 and $a_r = 3$, for the short- and longer-lived species respectively. To ensure a parameter space
350 where populations persist, we set fecundity to give $\lambda = 1.3$ for a population resident in patch
351 1, giving $f_1 = 4.5$ and $f_2 = 2$ for the short-lived and longer-lived species, respectively.
352 Environmental differences between patches and seasons were implemented as proportions of
353 baseline vital rates (Fig. 3, Appendix S3).

354

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

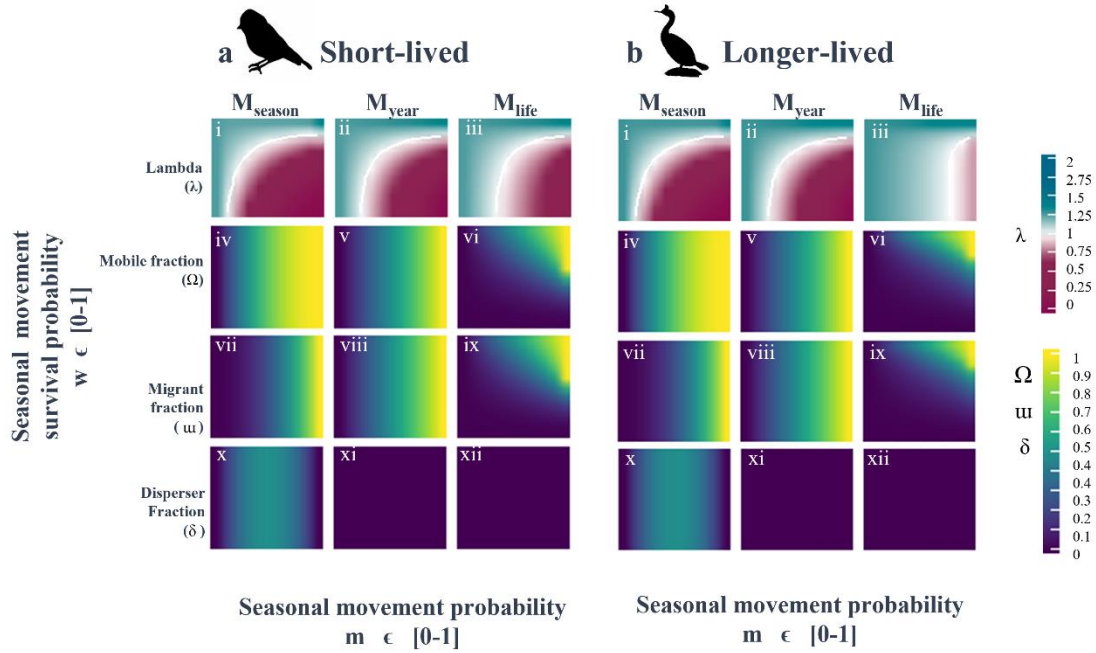
367 We quantify metapopulation growth rate (λ), mobile fraction (Ω) and vital rate
368 elasticities (e_θ) for each model and hypothetical species across the full possible ranges of m
369 and w ($\in [0,1]$). Mobile fraction (Ω) is a composite of the fraction susceptible to migrate (Ω)

370 and the fraction susceptible to disperse (δ), and δ is necessarily 0 for M_{year} and M_{life} . We
371 present these results as heat maps across axes of m and w structured by level of plasticity, life-
372 history and θ , thereby summarizing up to six dimensions (further explained in Appendix S4).
373 We ran all analyses in R 3.5.2 (R-Core Team, 2013). General code that is customizable for any
374 desired life-history is in Appendix S8.

375

376 **3.2 | Results from illustrative parameterizations: Growth rate (λ), mobile fraction (Ω) and** 377 **elasticity of λ to vital rates (e_θ).**

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



388

389 **FIGURE 4** Projected asymptotic metapopulation growth rate (λ), mobile fraction (Ω), migrant
 390 fraction (u) and disperser fraction (δ) for (a) short-lived and (b) longer-lived species. Columns
 391 depict the level of movement plasticity: seasonal (M_{season}), annual (M_{year}) and lifelong fixed
 392 (M_{life}). Each square depicts values across the full possible range of values of the seasonal
 393 movement probability ($m \in [0 - 1]$) and the seasonal movement survival probability ($w \in [0 -$
 394 $1]$). The white contour line represents $\lambda = 1$. The heat map representation is further explained
 395 in Appendix S4.

396

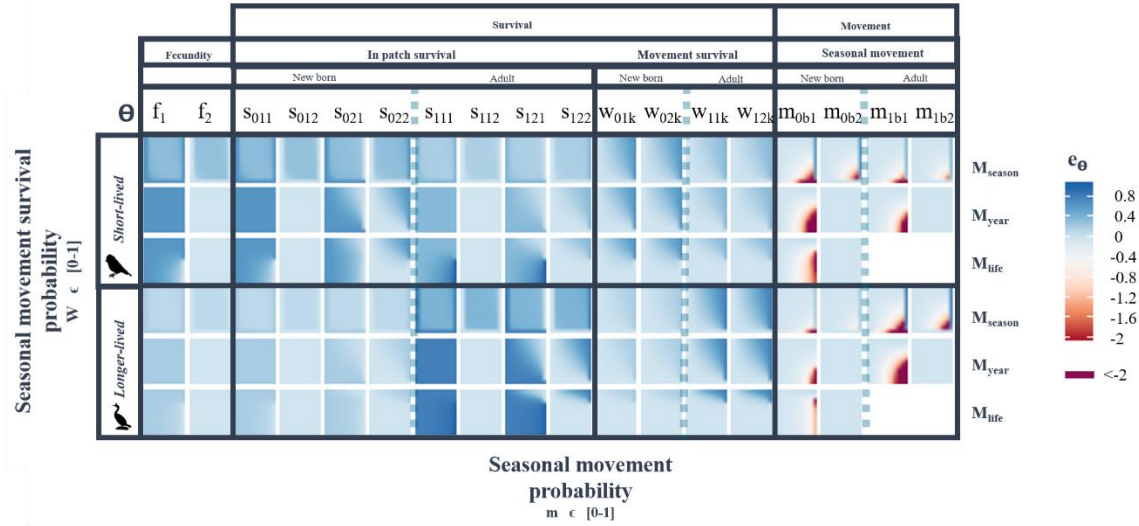
397 Differences between λ given seasonal and annual plasticity result from differing
 398 underlying metapopulation mobile fractions and resulting survival costs experienced. Given
 399 seasonal plasticity, the population fractions susceptible to migrate (u) and disperse (δ) at the
 400 beginning of each year are m^2 and $2(1 - m)m$ respectively. Given annual plasticity, these
 401 fractions are m and 0 respectively. As migrants experience the direct cost of movement twice
 402 a year while dispersers experience it once, seasonal plasticity results in a slightly lower annual
 403 survival probability (Figs 4a&b iv vs v). Finally, differences between M_{year} and M_{life} , for which

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

417 As expected, elasticities of λ to fecundity (f_k) and newborn survival (s_{0bk}) are positive
418 and higher for the short-lived species, while elasticities of λ to adult seasonal survival (s_{1bk})
419 are higher for the longer-lived species (Fig. 5). Meanwhile, elasticities of λ to the seasonal
420 movement vital rates m and w show substantial variation across the full $m - w$ parameter
421 space (Fig. 5). The elasticity of λ to w is always positive, but the elasticity of λ to m is widely
422 negative. This occurs because increasing w can only increase λ , while increasing m can
423 increase or decrease λ depending on the overall costs versus benefits of increasing the
424 proportion of the metapopulation that moves. When m is moderately high, the seasonal
425 movement parameters can have elasticities comparable to, or even higher than, the fecundity
426 and survival rates that are typically considered to drive metapopulation dynamics (Fig. 5).
427 Additionally, when m is very high and w is very low, elasticities to seasonal movement

428 parameters become several orders of magnitude higher than the other parameters' elasticities,
 429 especially when $\lambda < 1$ (Fig. 5).

430



431

432 **FIGURE 5** Elasticity (e_θ) of metapopulation growth rate (λ) to vital rates (θ) for the short-
 433 lived and longer-lived species (top and bottom blocks) and three levels of plasticity: seasonal
 434 (M_{season}), annual (M_{year}) and lifelong fixed (M_{life}). Parameter notation: f_k , fecundity in patch k ;
 435 s_{abk} , seasonal survival at age a during season b in patch k ; w_{abk} and m_{abk} , seasonal movement
 436 survival probabilities and seasonal movement probabilities at age a during season b in patch k ;
 437 $a = 0$, newborns and $a = 1$, adults. Each square depicts values of e_θ across the full possible
 438 range of values of seasonal movement probability ($m \in [0 - 1]$) and seasonal movement
 439 survival probability ($w \in [0 - 1]$), as explained in Appendix S4. The deep red represents $e_\theta <$
 440 -2 and white panels correspond to parameters absent in M_{year} and M_{life} . Dashed lines separate
 441 newborn from adult vital rates.

442

443 Given our illustrative parameterizations, λ is generally slightly more elastic to breeding
 444 season vital rates ($b = 1$) than to non-breeding season vital rates ($b = 2$, Fig. 5). Also, λ is
 445 slightly more elastic to vital rates in the high-quality breeding patch ($k = 1$) than in the patch

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

457

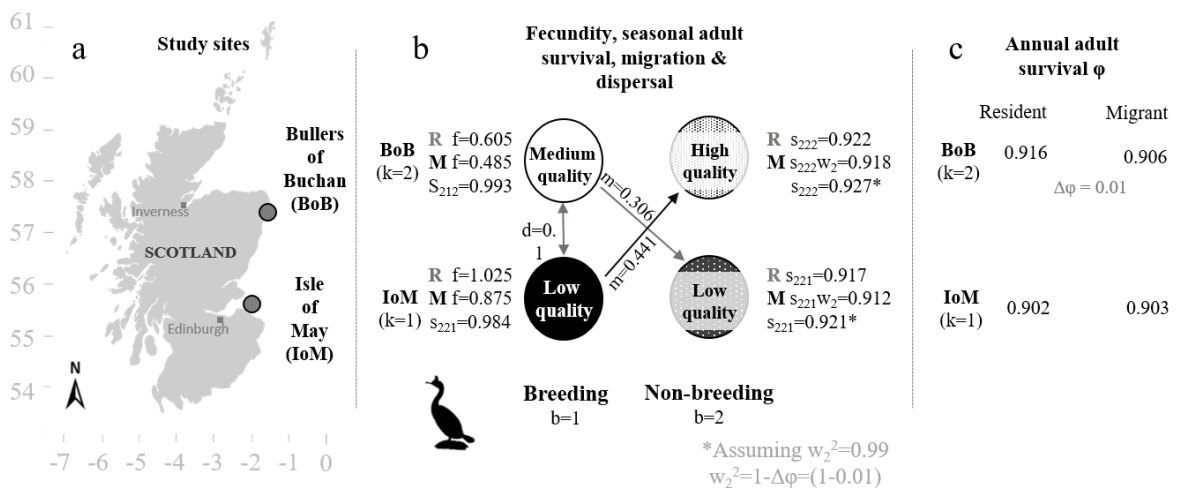
458 **4 | FROM THEORY TO APPLICATION: AN EMPIRICAL CASE STUDY**

459 **4.1 | Empirical parameterization**

460 Applying our conceptual framework to real systems requires estimating seasonal vital rates,
461 including movement probabilities, in partially migratory systems. This is challenging (Marra
462 et al., 2015; Sample et al., 2018), but will become increasingly feasible as individual tracking
463 technologies, large-scale monitoring programs and associated statistical tools reach maturity
464 (Eggeman et al., 2016; Grist et al., 2017; Reid et al., 2018). For instance, combinations of
465 breeding and non-breeding season monitoring data can allow estimation of season and location
466 specific vital rates (Acker, Daunt, et al., 2021; Grayson et al., 2011), carry-over effects
467 (Gillanders et al., 2015; Grist et al., 2017), and forms of within-individual repeatability (or
468 plasticity) in non-breeding location (Grist et al., 2014, Eggeman et al. 2016). Given such
469 estimates, our models allow quantitative evaluation of the impact of changing seasonal
470 migration probability, and associated survival probability, on metapopulation dynamics.

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

485



486

487 **FIGURE 6** Summary of vital rates estimated for a European shag (*Gulosus aristotelis*)
 488 partially-migratory metapopulation in Scotland to illustrate a landscape with seasonal and

489 spatial variation in survival and fecundity. (a) Location of Isle of May (IoM) and Bullers of
490 Buchan (BoB) colonies. (b) Spatio-temporal vital rates: f_k , fecundity; s_{2bk} , seasonal adult
491 survival probabilities (i.e. $y \geq 2$) during each season ($b = 1$, breeding, solid fill and $b = 2$,
492 non-breeding, dotted fill) at IoM ($k = 1$; dark fill) and BoB ($k = 2$; light fill) for resident (R)
493 and migrant (M) population fractions; w and w^2 , seasonal and annual movement survival
494 probabilities; m , seasonal movement/migration probability and d , dispersal probability. (c)
495 Realized annual survival probabilities for residents and migrants breeding at IoM and BoB.

496

497 As shags typically first breed aged three years (Aebischer et al., 1995), we formulate
498 M_{life} considering three stages (Fig.3): yearlings ($a = 1$, 1-2years), sub-adults ($a = 2$, 2-3years)
499 and breeding adults ($a = 3$, ≥ 3 years). We take previously estimated values of local breeding
500 success for residents and migrants (f_k) and seasonal survival probabilities (s_{abk}) (Acker,
501 Burthe, et al., 2021; Acker, Daunt, et al., 2021; Grist et al., 2017; Reid et al., 2020). As seasonal
502 movement survival probabilities (w_{abk}) have not previously been explicitly estimated, we
503 derive an estimate from the maximum observed difference in annual survival between residents
504 and migrants (Appendix S7) and assume that w is season- and site-independent but age-
505 dependent (w_a). We use proportional age-specific survival rates estimated by Frederiksen et
506 al. (2008, Appendix S7). We take seasonal movement probability m_k as the realized migratory
507 fraction estimated following (Acker, Daunt, et al., 2021) averaged across years and assume that
508 m is age independent ($m_1 = 0.441$, $m_2 = 0.306$). As the IoM and BoB breeding populations
509 are connected through occasional dispersal (Barlow et al. 2013), we extend M_{life} to allow age-
510 independent dispersal probability $\delta = 0.1$, assuming that demography and dispersal occur
511 sequentially within the annual projection interval (Appendix S6). All resulting parameter
512 values are shown in Fig. 6 (further details in Appendix S7).

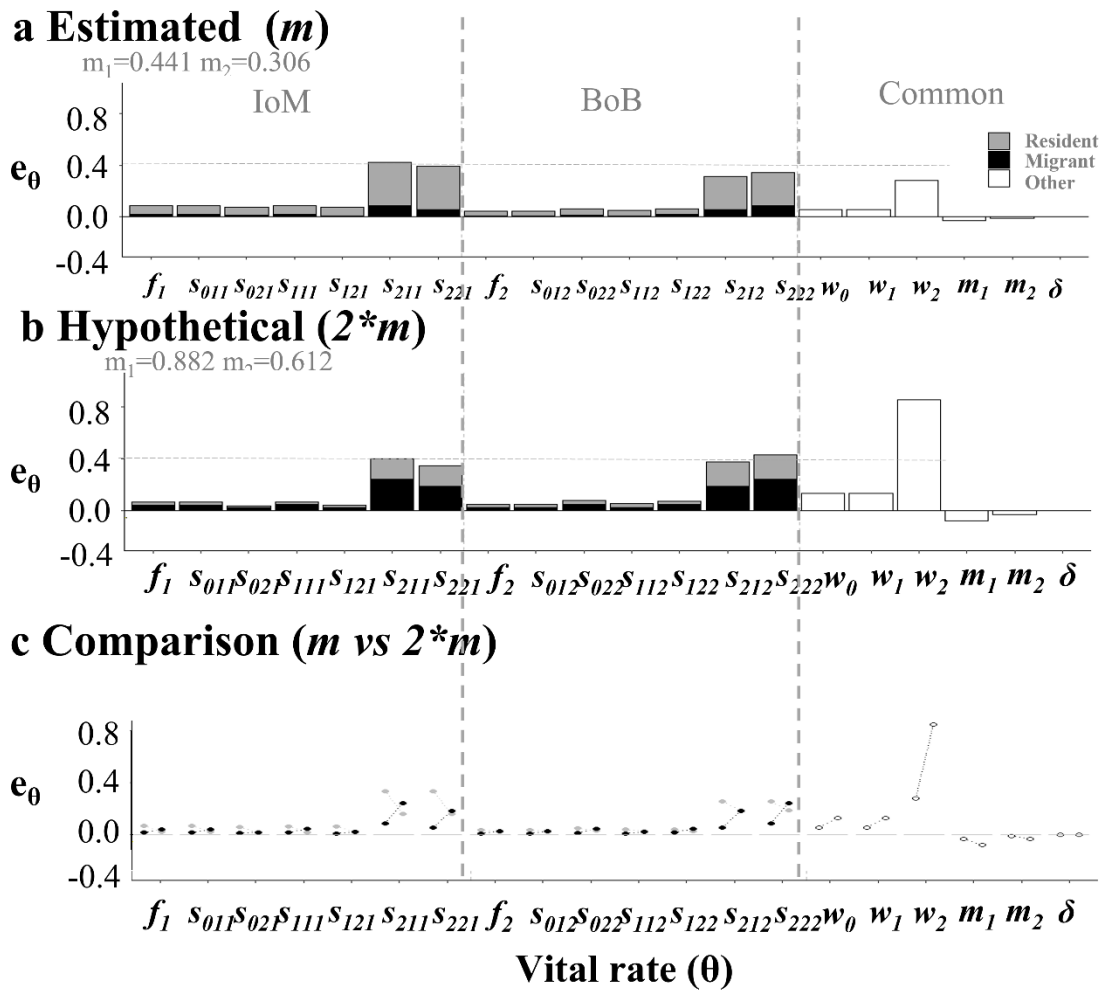
513 We calculate metapopulation growth rate (λ), mobile fraction (Ω) and associated
514 elasticities of λ to vital rates (e_θ) at the asymptotic equilibrium. Our assumption that m_k equals
515 the realized (observed) mobile fraction will likely underestimate the true value of m_k , because
516 some individuals will die before achieving movement. Further, previous studies suggested that
517 movement probability can increase with increased environmental stochasticity (Kokko &
518 Lundberg, 2001). Therefore, we explore potential metapopulation consequences of higher m_k
519 by doubling the initial values (i.e. $2m_k$).

520

521 **4.2 | Results from empirical case study: Growth rate (λ), mobile fraction (Ω) and** 522 **elasticity of λ to vital rates (e_θ).**

523 Estimated λ s were 1.11 and 1.05 given m_k and $2m_k$ respectively. Both scenarios therefore
524 allow metapopulation growth and persistence. Migrants are the less fit strategy and are selected
525 out, leaving increasing proportions of residents. Accordingly, in both scenarios, Ω is lower than
526 the imposed value of m_k . Specifically, Ω is only 0.14 at IoM and 0.09 at BoB given m_k , and
527 0.37 at IoM and 0.26 at BoB given $2m_k$.

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



537

538 **FIGURE 7** Elasticity of metapopulation growth rate (λ) to vital rates (θ) for estimated value
 539 of seasonal movement probability (a) m , (b) $2m$, and (c) their comparison. Parameter notation:
 540 f_k , fecundity in patch k ; s_{abk} , age a , season b and patch k survival; w_a , age a movement
 541 survival; m_k , seasonal migration probability from patch k and δ dispersal probability; $a = 0$,
 542 newborns; $a = 1$, sub-adults; $a = 2$, adults. Parameters from Isle of May (IoM) and Bullers of
 543 Buchan (BoB) or both are separated by dashed lines and noted in grey, black and white
 544 respectively. In c dashed lines between the two scenarios are used as reference in the change
 545 of value but they do not denote trends as these are often non-linear (see Appendix S6).

546

547 Elasticities also differ between the two focal populations breeding on IoM and BoB,
548 and between residents and seasonal migrants. Elasticities of λ to breeding season vital rates are
549 greater at IoM, while elasticities of non-breeding season vital rates are greater at BoB. The
550 pattern of differences in elasticities of λ to breeding and non-breeding season vital rates is
551 consistent given m_k and doubled m_k , but the magnitude is greater for doubled m_k (Fig. 7). With
552 m_k , λ is more elastic to changes in f_k and s_{abk} than in w_a , m_k and δ (Fig. 7a). Moreover, λ is
553 most elastic to the vital rates of the population fraction breeding at IoM (i.e. f_1 and s_{ab1} s_{ab1} Fig.
554 7a). Likewise, λ is most elastic to vital rates of the resident fraction of the population (Fig. 7a).
555 However, with doubled m_k , λ is most elastic to $m_2 w_2$ (Fig. 7b). Overall, elasticities of λ to w_a
556 approximately doubled. Still, λ is more elastic to changes in vital rates of the resident fraction
557 than the migrant fraction (Fig. 7c). However, the overall relative contribution of the resident
558 fraction decreases. With doubled m_k , the effect of seasonality becomes more obvious with
559 notable increase in the differences between the elasticities of λ to the breeding and non-
560 breeding season vital rates.

561

562 **5 | DISCUSSION**

563 Increasingly important aims in fundamental and applied ecology are to identify which seasonal
564 vital rates, life-history stages and locations regulate the size and persistence of partially-
565 migratory metapopulations, and thereby forecast likely impacts of deteriorating seasonally-
566 occupied habitats (Reid et al., 2018; Small-Lorenz et al., 2013). In such systems, individuals
567 can potentially respond to seasonal environmental variation by migrating between discrete
568 locations. Yet, while the metapopulation dynamic consequences of variable dispersal rates have
569 been widely studied (Akçakaya, 2000; Hokit et al., 2001; Lecomte et al., 2020; Travis et al.,
570 2012), effects of structured variation in seasonal migration on dynamics of partially-migratory
571 metapopulations remain largely unexplored. We provide a general conceptual framework that

572 explicitly incorporates seasonal movement probability (m), and movement survival probability
573 (w), as population-level vital rates, and conceptualizes several forms of within-individual
574 variation (i.e., ‘plasticity’) in seasonal movement. Our example theoretical and empirical
575 example parameterizations illustrate how movement vital rates and plasticity can interact to
576 shape the dynamics and persistence of partially-migratory metapopulations across different
577 life-histories.

578

579 **5.1 | Implications of variation in seasonal migration for metapopulation dynamics**

580 Our illustrative theoretical parameterizations provide proof of concept of how our framework
581 can identify regions of movement parameter space where partially-migratory metapopulations
582 can persist ($\lambda > 1$), and identify what values of m are sustainable for any given values of w .
583 The point that when m is high, persistence is only possible when w is also high (Fig. 4), is
584 qualitatively intuitive. However, our analyses quantitatively evaluate such relationships, and
585 show how they can vary with life-history. For example, our hypothetical longer-lived species
586 persisted in a wider range of the explored movement parameter space. Additionally, our
587 parameterizations show how such outcomes can depend on the level of individual plasticity.
588 Persistence occurred across wider movement parameter space when seasonal migration or
589 residence are lifelong fixed strategies than given seasonal or annual plasticity, especially in the
590 longer-lived species. With fixed strategies, the less fit phenotype (migrants in our examples) is
591 selected out, causing the mobile fraction Ω to be lower than m . Effects of such within-
592 generation selection are smaller in the short-lived species, leaving a higher proportion of the
593 metapopulation susceptible to movement costs.

594 Our results highlight the potentially key contributions of variable seasonal migration
595 rates to metapopulation dynamics. Specifically, elasticities highlight that perturbations in m
596 and associated w can have comparable (or even larger) effects on λ than perturbations in the

597 vital rates that are typically taken to have the greatest impacts (i.e. fecundity for short-lived
598 species; adult survival for longer-lived species). As vital rates are location- and season-specific,
599 our framework can identify critical locations and seasons that could underlie system dynamics
600 (Erickson et al., 2018; Sample et al., 2020). Such understanding could aid effective
601 conservation or management of vulnerable seasonally-mobile species (Møller et al., 2008;
602 White et al., 2018), including eradication of pest or invasive species (Stuart et al., 2006).
603 However, as elasticities of λ to vital rates varied non-linearly with seasonal movement rates,
604 and interacted with plasticity levels (Appendix S5), simple overarching generalizations cannot
605 be readily drawn. To make progress towards identifying general principles of constraints on
606 partially-migratory metapopulations, we now need empirical estimates of key vital rates
607 comprising stage-, season- and location-specific seasonal movement probability and associated
608 survival and plasticity, alongside seasonal survival and reproduction (see also Norris & Taylor,
609 2006; Reid et al., 2018; Runge & Marra, 2005; Small-Lorenz et al., 2013).

610 Accordingly, our empirical case study illustrates how year-round demographic
611 monitoring can allow initial parameterization of required models. We characterized the
612 relevant $m - w$ parameter space, and other vital rates, for a shag metapopulation where
613 individuals are consistently resident or migrant across years (Fig. 6). By parameterizing the
614 model M_{life} , we show that λ would be most elastic to perturbations of adult survival probability
615 for the resident fraction of the metapopulation breeding at the Isle of May colony. However,
616 under a hypothetical scenario with higher m , adult survival during seasonal movement would
617 become the vital rate to which λ is most elastic. Thus, our framework can be used to consider
618 the relative value of managing the breeding colony versus the larger-scale coastal environment.
619 As technologies develop, the required estimates of key seasonal movement vital rates such as
620 m and w will soon become available for diverse seasonally-mobile species (Eggeman et al.,
621 2016; Grayson et al., 2011; Grist et al., 2017). Future ambitions should be to systematically

622 include such estimates within comparative demography databases (e.g., Salguero-Gómez et al.
623 2016). This would also facilitate further exploration of how matrix dimensions can affect
624 calculated elasticities of λ to vital rates, and hence affect demographic inferences (Reid et al.,
625 2004; Salguero-Gómez & Plotkin, 2010). Meanwhile our current analyses illustrate how, when
626 explicit vital rate estimates are not yet available, reasonable assumptions can allow exploration
627 of biologically plausible or postulated scenarios.

628

629 **5.2 | Extensions and open questions**

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

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

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

665 Indeed, our current models could be extended to explicitly consider density-
666 dependence, environmental and demographic stochasticity and resulting transient dynamics, as
667 previously done for matrix models that do not consider variable seasonal migration (Caswell,
668 2007; Haridas & Tuljapurkar, 2007). Yet, such extensions would yield additional interesting
669 challenges, due to the implied demographic, spatial and seasonal structure. Environmental
670 stochasticity and extreme climatic events might differentially affect vital rates of seasonally
671 mobile versus resident subpopulations rather than have system-wide effects (Acker, Daunt, et

672 al., 2021). Further, environmental changes could potentially directly affect movement
673 probabilities and associated survival probabilities; indeed it has been previously suggested that
674 increasing environmental stochasticity can increase movement propensity (Kokko &
675 Lundberg, 2001).

676 Seasonal movement probabilities could also be density-dependent (Grayson et al.,
677 2011; Mysterud et al., 2011), and will certainly alter local seasonal densities and thereby affect
678 other density-dependent vital rates. Indeed, intrinsic relationships between the frequency of
679 seasonal migration and local density have been suggested to cause frequency-dependent
680 selection on seasonal migration, and thereby maintain partial migration (Kokko & Lundberg,
681 2001; Runge & Marra, 2005). However, such tight relationships between migration probability
682 and density only arise when migratory subpopulations move to otherwise unoccupied patches.
683 Much more complicated relationships could potentially arise in partially-migratory
684 metapopulations inhabiting weakly seasonal landscapes where different locations can hold
685 residents alongside incoming and outgoing migrants, as envisaged by our current models (Reid
686 et al., 2018). Such effects may ultimately be best considered by placing our concepts within a
687 spatially-explicit individual-based model framework, which could track local density and
688 effects of differing spatio-temporal regimes of environmental perturbations. Individual-based
689 models would also facilitate eco-evolutionary extensions to examine evolutionary dynamics of
690 partial migration and associated plasticity or canalization. This approach will ultimately
691 facilitate integration of holistic understanding of metapopulation dynamic consequences of
692 variation in seasonal migration into forecasting and management tools (e.g. Bocedi et al.,
693 2014).

694

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701

702 **AUTHORS' CONTRIBUTIONS**

703 APP conceived the ideas, undertook the analyses and drafted the manuscript, assisted by JMR
704 and PA. JR and PA provided empirical estimates. FD, SW, SB, MN, MPH, and JMR collected
705 the data. All authors contributed to conceptual, technical and manuscript development and
706 gave final approval for publication.

707

708 **DATA AVAILABILITY STATEMENT**

709 There are no primary data associated with this manuscript.

710

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932 **APPENDICES**

933 **APPENDIX S1** | Possible sequences of movement states for a two-year trajectory under the
934 different temporal scales of plasticity considered

935 **APPENDIX S2** | Seasonal (B_b) and annual (A) metapopulation Leslie matrices.

- 936 **APPENDIX S3** | Defining the seasonal and spatial environmental landscape.
- 937 **APPENDIX S4** | Multidimensional representation of results.
- 938 **APPENDIX S5** | Elasticities of metapopulation lambda to vital rates in detail.
- 939 **APPENDIX S6** | Empirical case study: dispersal matrix formulation.
- 940 **APPENDIX S7** | Empirical case study: vital rate estimation.
- 941 **APPENDIX S8** | Code.