

1 **Episodes of opposing survival and reproductive selection cause strong**
2 **fluctuating selection on seasonal migration versus residence**

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13

14 **Abstract**

15 Quantifying temporal variation in sex-specific selection on key ecologically relevant traits, and
16 quantifying how such variation arises through synergistic or opposing components of survival
17 and reproductive selection, is central to understanding eco-evolutionary dynamics but rarely
18 achieved. Seasonal migration versus residence is one key trait that directly shapes spatio-
19 seasonal population dynamics in spatially- and temporally-varying environments, but temporal
20 dynamics of sex-specific selection have not been fully quantified. We fitted multi-event
21 capture-recapture models to year-round ring resightings and breeding success data from
22 partially-migratory European shags (*Phalacrocorax aristotelis*) to quantify temporal variation
23 in annual sex-specific selection on seasonal migration versus residence arising through adult
24 survival, reproduction, and the combination of both (i.e. annual fitness). We demonstrate
25 episodes of strong, and strongly fluctuating, selection through annual fitness that were broadly
26 synchronised across females and males. These overall fluctuations arose because strong
27 reproductive selection against migration in several years contrasted with strong survival
28 selection against residence in years with extreme climatic events. These results indicate how
29 substantial phenotypic and genetic variation in migration versus residence could be maintained,
30 and highlight that biologically important fluctuations in selection may not be detected unless
31 both survival selection and reproductive selection are appropriately quantified and combined.

32

33 **Keywords**

34 annual fitness, extreme climatic event, fecundity selection, multi-event capture-recapture,
35 partial migration, sex-specific selection

36

37 **Introduction**

38 Quantifying temporal variation in the strength and direction of sex-specific selection on
39 ecologically-relevant phenotypic traits is central to understanding eco-evolutionary dynamics
40 [1–4]. This is because the forms and magnitudes of variation in selection will shape the
41 maintenance of genetic and phenotypic variation, and shape the rate and direction of adaptive
42 evolutionary change [2,3,5]. Temporal variation in selection will thus fundamentally affect
43 population responses to varying and changing environmental conditions. In particular, both
44 fluctuating selection and sexually antagonistic selection, respectively defined as episodes of
45 selection acting in opposite directions within short ecologically-relevant periods or between
46 the sexes, can help maintain genetic variation and alter timeframes for adaptation [3,5]. Yet,
47 temporal dynamics of sex-specific selection on key traits in wild populations have still rarely
48 been quantified [2]. Empirical evidence of temporally fluctuating selection is particularly scant,
49 once sampling variance is accounted for [4,6]. Moreover, we commonly lack insights into how
50 fluctuations are caused by environmental variation, even though such impacts are central to
51 eco-evolutionary processes and outcomes [2,7,8].

52 In general, selection on any trait can operate through differential survival and/or
53 differential reproduction in relation to phenotype, yielding survival selection and/or
54 reproductive selection [9,10]. These selection components could act in the same or opposite
55 direction, generating either strong or weak net selection within years [11]. Further, the relative
56 strength and direction of selection through each fitness component could vary among years,
57 potentially generating net fluctuating selection. Moreover, depending on sex-specific responses
58 to underlying environmental variation, fluctuations in net selection could be synchronised or
59 opposing across females and males. Comprehensive studies aiming to quantify temporal
60 variation in the overall magnitude and direction of selection should therefore quantify sex-

61 specific temporal variation through both fitness components, and through their combined
62 effects.

63 This ambition necessitates explicit estimation of temporal sequences of sex-specific
64 selection within as well as among years. In many systems, reproduction (and resulting
65 reproductive selection) occurs within discrete seasons, while survival selection could occur at
66 any time, and might not coincide with reproductive selection. Such sequential selection
67 episodes could have complex compound effects. For example, strong survival selection acting
68 during a non-breeding season will leave fewer individuals of particular phenotypes available
69 to breed subsequently, reducing the degree to which opposing reproductive selection could
70 reverse the direction of net annual selection [12]. Further, carry-over effects of non-breeding
71 season phenotypes on subsequent reproduction could cause additional components of time-
72 lagged indirect selection [13]. However, most studies of temporal variation in selection focus
73 on either survival or reproduction [2,6], and/or do not estimate combined effects of different
74 selection components across seasons. Fitness measures that combine survival and reproduction
75 to quantify individual contributions to annual population growth have been developed
76 [10,14,15], but are still rarely applied to estimate selection [16,17].

77 One key phenotypic trait that could directly link ecological and evolutionary dynamics
78 is seasonal migration (hereafter “migration”), defined as reversible individual movements
79 between locations across seasons. Migration allows individuals to exploit seasonally varying
80 resources and avoid unfavourable conditions, and directly determines individuals’ seasonal
81 locations and resulting spatio-seasonal population distributions [18,19]. Moreover, phenotypic
82 expression of migration versus residence commonly varies among individuals within
83 populations, creating opportunity for selection. Specifically, forms of ‘partial migration’,
84 where some individuals remain resident at their breeding location during the non-breeding
85 season while other individuals are seasonal migrants, occur in diverse amphibian, reptile, fish,

86 bird and mammal populations [18,20–22]. Sympatric-breeding individuals with migrant and
87 resident phenotypes are then spatially segregated in the non-breeding season. Episodes of
88 strong seasonal selection could then arise due to spatial variation in non-breeding season
89 environmental conditions that causes differences in survival and/or subsequent reproduction,
90 which may be modulated by sex-specific environmental tolerances and/or constraints on
91 reproductive success [18,23]. Quantifying among-year variation in sex-specific selection on
92 migration versus residence is therefore central to understanding how spatio-temporal
93 environmental variation could drive micro-evolution of migration, and hence drive micro-
94 evolution of spatio-seasonal population dynamics and distributions. Yet, to date, such variation
95 in selection has not been fully quantified.

96 Progress requires quantifying non-breeding season phenotype (resident or migrant),
97 survival and subsequent reproduction of numerous females and males across multiple years
98 within a sympatric-breeding partially-migratory population. This can be achieved through
99 large-scale year-round resightings of marked individuals designed to determine individuals’
100 non-breeding season locations, coupled with subsequent reproductive monitoring. However,
101 since not all individuals’ locations and reproduction will typically be observed at all times,
102 inference of selection requires advanced full-annual-cycle capture-recapture models that
103 account for the resighting process and resulting partial observation of individuals’ phenotypes
104 and uncertainty in survival and breeding outcomes. Recent analyses in European shags
105 (*Phalacrocorax aristotelis*, hereafter “shags”) demonstrated strong survival selection against
106 residence in both sexes within two of nine non-breeding seasons containing extreme late-winter
107 storms (i.e. extreme climatic events, “ECEs”), with weak selection or neutrality otherwise [24].
108 However, the degree to which such temporal variation in survival selection could be overridden
109 by sex-specific reproductive selection manifested through carry-over effects acting in

110 subsequent breeding seasons, potentially generating overall fluctuating selection, has not been
111 quantified.

112 Accordingly, we fitted multi-event capture-recapture models to year-round resightings
113 and breeding success data from adult shags to jointly estimate annual sex-specific reproductive
114 selection alongside survival selection. We then combined these estimates to quantify among-
115 year variation in overall selection on migration versus residence through annual adult
116 contribution to population growth, explicitly tested for fluctuating selection, and examined
117 whether variation and fluctuations were broadly synchronised across females and males. We
118 thereby quantify how components of seasonal selection, including selective episodes
119 associated with ECEs, can drive strong fluctuating and/or sex-specific selection on a key
120 phenotypic trait that shapes spatio-seasonal population dynamics.

121

122 **Methods**

123 *Study system and data collection*

124 The focal shag population breeds on the Isle of May (“IoM”) National Nature Reserve,
125 Scotland (56°11’N, 2°33’W). These shags are typically socially monogamous, rearing a single
126 brood per year with biparental care (Electronic Supplementary Material, “ESM”, S1). Since
127 1997, >17000 chicks (ca. 80% of all those hatched) and >900 additional adult recruits have
128 been ringed with uniquely-coded colour rings (field-readable to 150m with a telescope),
129 generating a breeding population of individually-marked adults. During ten breeding seasons
130 (April-July 2009-2018, “summers”) virtually all nest sites on IoM were monitored through
131 frequent, systematic checks (ESM S1). Colour-ringed nest owners were systematically
132 identified and hence classified as breeders, and sexed through vocalizations and/or genotyping.
133 For active nests (mean 533 year⁻¹, range 388-821), and hence their associated owners, breeding

134 success was recorded as the number of chicks fledged (0–4), or recorded as unknown in cases
135 with uncertain success (~1% of nests; ESM S1). In addition, regular (~3 week⁻¹) resighting
136 surveys at roost sites on IoM were undertaken to identify ringed adults that apparently did not
137 attempt breeding or could have failed early (hereafter early-failed/non-breeders). These
138 individuals were assigned breeding success of 0 fledglings, affecting 2–18% of all resighted
139 adult females and 1–30% of males (means 5%, ESM S1). Due to the intensive ringing,
140 comprehensive nest monitoring and high overall breeding season resighting probability (mean
141 0.95 during 2010–2018; range 0.90–0.98; [24]), annual breeding success was assigned for a
142 very high proportion of the total adult population. Ringing and nest monitoring were licensed
143 by British Trust for Ornithology and NatureScot.

144 Because shags have partially wettable plumage and hence must return to shore every day
145 to dry, ringed individuals can be resighted at coastal locations throughout the non-breeding
146 season (“winter”). Hence, throughout each winter (September–February) during 2009–2018,
147 major roost sites on IoM and across the known winter range of migrant IoM shags (eastern and
148 northern Scotland) were surveyed approximately every two weeks and resightings of colour-
149 ringed individuals recorded (ESM S1, [24,25]). Since breeding dispersal from IoM is very rare
150 [24,26], these winter surveys allowed individuals to be directly classified as residents when
151 resighted on IoM, and as migrants when resighted elsewhere. These resightings also effectively
152 inform on true survival, with virtually no confounding permanent emigration.

153

154 ***Model design***

155 To estimate survival and reproductive selection on migration versus residence, we devised a
156 discrete-time multi-event capture-recapture model that considers hidden transitions between
157 individual states and imperfect observation of these states. States are defined as locations (i.e.
158 residence on IoM, versus migratory areas elsewhere; ESM S1), and breeding outcomes (i.e.

159 breeding status and number of fledglings). The state transition process thus represents seasonal
160 movement and survival, and subsequent breeding success. The observation process represents
161 spatially and temporally varying resighting effort, and uncertainty in breeding success
162 assessment. The model thereby allows robust probabilistic inference on the (partially-
163 observed) full-annual-cycle sequence of individual phenotypes (migrant or resident), and hence
164 migration-dependent survival and breeding success (i.e. survival and reproductive selection;
165 Fig. 1a).

166 To maximise use of available year-round resighting data to make probabilistic inference
167 on individuals' winter locations, and hence phenotypes and resulting selection, we divided each
168 annual cycle (y ; one breeding season to the next) into five capture-resighting occasions (o),
169 comprising the breeding season and four subsequent winter occasions (Fig. 1a; ESM S1, [24]).
170 In each breeding season, new adults enter the dataset and all alive individuals are assumed to
171 be in the residency area (on IoM). Through the four subsequent winter occasions (Fig. 1a),
172 alive individuals can be in the residency area or a migratory area (corresponding to resident
173 and migrant states). At each occasion, alive individuals can be seen where they are located or
174 not seen, according to occasion- and location-dependent resighting probability (p). To model
175 spatial heterogeneity in the observation process, we defined multiple migrant states, including
176 a "ghost area" encompassing sites with no resighting effort (i.e. an unobservable state with
177 $p=0$, ESM S1; [24]). Between occasions, survival probability (ϕ) is sex, time- (i.e. occasion by
178 year) and migration-dependent (i.e. all migrants versus residents). Individuals can move
179 between residency and migratory areas, according to probabilities of departing from residency
180 (ϵ), moving to a particular migratory area conditional on departure (δ), returning from a
181 migratory area to the residency area (ω), and switching between migratory areas conditional
182 on not returning (σ ; [24]). The model was parameterised with interacting sex-, location-, and
183 time-dependence in movement and resighting probabilities. However, σ was set constant across

184 locations and time, because switching between migratory areas between winter occasions was
185 rarely observed [24]. Since the data did not suggest any major sex bias in migrants'
186 destinations, δ and σ were modelled as sex-independent. Since an individual cannot be a
187 migrant during the breeding season, parameters were constrained such that individuals can only
188 move from or remain in the residency area between occasion 1 (breeding season) and 2 (first
189 winter occasion), and can only move to or remain in the residency area between occasion 5
190 (late-winter occasion) and 1 (Fig. 1a). Full details of non-breeding season model structure and
191 parameterisation are in [24].

192 In each breeding season (occasion $o=1$), adults that survived the previous winter
193 transition to one of six possible breeding states conditional on whether they were resident or
194 migrant in the preceding late-winter occasion ($o=5$; Fig. 1b). Specifically, individuals first
195 become breeders (B), or conversely transition to the early-failed/non-breeder state (\mathcal{B})
196 according to migration-dependent breeding probability ζ . Breeders then produce n fledglings
197 ($0 \leq n \leq 4$) and thus transition to the corresponding states (B_n), following the migration-dependent
198 set of nest outcome probabilities χ_n (with $\sum_{n=0}^4 \chi_n = 1$; Fig. 1b). The model was parameterised
199 with interacting migration- and year-dependence in ζ and χ_n . Because there are as yet no
200 capture-recapture methods allowing breeding outcome to be modelled as a joint state for two
201 paired individuals, breeding outcome was modelled for one sex at a time (hereafter 'focal sex')
202 and hence treated as independent from the other sex. Corresponding observation events for
203 focal sex individuals are resighted as early-failed/non-breeder (\mathcal{B}), resighted as breeder with
204 success of n fledglings (B_n) or unknown success ($B_?$), or not resighted (\emptyset) (Fig. 1b). We assume
205 that, since nests are exhaustively monitored (ESM S1), all breeders are resighted (i.e. $p_B=1$ for
206 each breeder state). Breeder states are consequently either recorded with certainty or unknown
207 (i.e. a breeder that produced n fledglings can only have observation event B_n or $B_?$), following
208 state-dependent assignment probability α_{Bn} (Fig. 1b). However, early-failed/non-breeders can

209 be resighted or not, with resighting probability p_B . All surviving non-focal sex individuals
210 transition into a single live state unlinked to reproduction, and are resighted with probability p
211 [24]. However, winter observations of non-focal sex individuals inform movement parameters
212 of both sexes, and therefore improve precision and accuracy of estimates for the focal sex.

213

214 *Data*

215 We used 42322 year-round resightings to compile individual capture-resighting histories (i.e.
216 sequences of observation events) of 2147 known-sex adult shags that bred on IoM at least once
217 during 2009–2017 (19011 resightings of 1108 females; 23311 resightings of 1039 males). Each
218 individual was first assigned to the residency area in the summer of its first observed breeding
219 attempt during 2009-2017, then assigned as observed in an area or unobserved in each
220 subsequent occasion, with a specific breeding observation in summer (ESM S1).

221 Breeding season events comprised 2569 and 3004 direct observations of breeding success
222 (and 31 and 25 unknown success) for females and males respectively. Success of each
223 individual's first observed breeding attempt during 2009-2017 is excluded from current
224 analyses. This is because previous winter location (and hence migrant versus resident state)
225 cannot be inferred for individuals that entered the dataset in summer 2009 (before winter
226 resightings started; 340 females, 382 males), or were ringed as breeding adults during 2010-
227 2017 (187 females, 127 males). Other individuals originally ringed as chicks entered the dataset
228 at recruitment, typically aged three years (563 females, 508 males). However, individual pre-
229 recruitment histories cannot be included without further assumptions, model developments,
230 and data regarding natal dispersal and recruitment processes. Since first breeding attempts were
231 necessarily excluded, we did not aim to test general hypotheses regarding age-specific breeding
232 success. Accordingly, we retained individuals of known and unknown ages (ringed as chicks

233 and adults respectively) in the data. However, to confirm that estimated differences in breeding
234 success between residents and migrants, and hence apparent reproductive selection, were not
235 simply due to correlated effects of age (e.g. if younger individuals were independently likely
236 to migrate and to have low breeding success) we fitted further multi-event models that included
237 basic age structure in transitions to breeding state (ESM S6).

238

239 *Model analyses*

240 The model was built and analysed using Stan, a Bayesian probabilistic programming language
241 using Hamiltonian Monte Carlo, with package rstan [27] in R v3.6.3 (code in ESM S2; [28]).
242 Objective (“uninformative”) uniform priors were used for all parameters (ESM S2). Posterior
243 predictive checks showed no major discrepancies between the data and posterior predictions,
244 implying good model fit (ESM S3). Complete details on posterior samples, including for
245 elementary model parameters, are in ESM S5 and [48].

246 We derived posterior distributions for compound quantities of biological interest that are
247 not elementary parameters, thus synthesising key effects while propagating associated
248 uncertainty. Annual survival probability (Φ_s) for possible phenotypic sequences (s) of
249 seasonal residence versus migration through the annual cycle (Fig. 1a) was calculated as the
250 product of survival probabilities of focal migratory phenotypes π (R or M) across the five
251 successive occasions within each year ($\phi_{\pi,o}$). For current purposes we focused on two
252 stereotypical and biologically relevant sequences: “full-winter migration” (leaving the
253 residency area by September and returning next breeding season, $s=R-M-M-M-M$, hence
254 $\Phi_{RMMMM,j}=\phi_{R,1}\phi_{M,2}\phi_{M,3}\phi_{M,4}\phi_{M,5}$), and “full-winter residence” ($s=R-R-R-R-R$,
255 $\Phi_{RRRRR,j}=\phi_{R,1}\phi_{R,2}\phi_{R,3}\phi_{R,4}\phi_{R,5}$). Model estimates show that these sequences are the two most
256 frequently realised: across 2009–2018, the posterior mean of the probability of full-winter

257 residence ranged from ca. 20–50% (grand mean 30%) and full winter migration from ca. 10–
 258 30% (grand mean 20%; [24]). Each alternative path was unlikely: grand mean range 0-7% [24].
 259 The two stereotypical sequences also capture key biological variation because major
 260 differences in Φ_s among sequences are driven primarily by late-winter survival; all sequences
 261 ending as migrant (or resident) in late-winter occasion have similar survival probabilities [24].
 262 Based on model estimates across years, approximately 35-75% of individuals were residents
 263 in the late-winter occasion (grand mean 60%) while 25–65% of individuals were migrants
 264 (grand mean 40%). There was no strong sex bias in the proportion of migrants, or hence of
 265 sexual dimorphism in late-winter location (female-male difference ranged -0.18–0.07, grand
 266 mean -0.04; [24]).

267 To summarize the distribution of breeding success across all focal sex individuals
 268 (including defined breeders and early-failed/non-breeders) dependent on residence or
 269 migration in late-winter occasion, we derived the expected number of fledglings per individual
 270 (hereafter ‘expected breeding success’, $E(BS_\pi)$ where π denotes resident or migrant phenotype):
 271 effectively $E(BS_\pi) = \sum_{n=1}^4 \zeta_\pi \chi_{\pi,n} n$ (ESM S5). Underlying full probability distributions of
 272 breeding outcomes are summarised in ESM S5.

273 We computed annual fitness as the expected contribution to population growth ($E(C_s)$)
 274 of adult residents and migrants encompassing survival probability from year y to $y+1$ followed
 275 by breeding success in year $y+1$, for a given annual phenotypic sequence s ending with
 276 phenotype π , such that $E(C_s) = \Phi_s(1 + \frac{1}{2}E(BS_\pi))$. This measure represents the expected direct
 277 contribution of an adult alive following a given breeding season to the population immediately
 278 following the next breeding season (i.e. a post-breeding census), conditional on being resident
 279 or migrant. It comprises the expected contribution of an individual itself and half its expected
 280 number of offspring (given that all offspring have two parents), both conditional on annual
 281 survival. It is broadly analogous to the pre-breeding census formulation utilised elsewhere [14].

282 To quantify sex-specific selection on residence versus migration, we computed full posterior
283 distributions of the differences (Δ) in Φ_s , $E(BS\pi)$ and $E(C_s)$ between residents and migrants
284 within each sex and year. We assessed evidence for each difference through the posterior
285 probability that it was positive ($\Pr(\Delta>0)$). $\Pr(\Delta>0)$ values close to 1 or 0 indicate substantial
286 evidence for positive or negative differences respectively (and hence for selection in one
287 direction or the other), while values close to 0.5 indicate no clear evidence for selection in
288 either direction. To explicitly test for variation in components of selection between sexes and
289 years, we computed the difference in the resident-migrant difference (Δ_Δ , and corresponding
290 $\Pr(\Delta_\Delta>0)$) between females and males within each year, and between every pair of years
291 within each sex (ESM S4). Because ordering of years within pairwise comparisons and
292 resulting directionality is arbitrary when summarising across several comparisons, we report
293 values as the distance from the [0,1] boundaries rather than as the absolute values ($\Pr(\Delta_\Delta)$;
294 ESM S4). Accordingly, $\Pr(\Delta_\Delta)$ values close to 0 indicate substantial evidence for a
295 difference in selection between two focal years (in a given direction), while values close to
296 0.5 indicate no clear evidence in either direction. These measures of differences in selection
297 combine differences in magnitude and direction. To explicitly test for fluctuating selection
298 (i.e. differences in direction), we calculated the posterior probability of a sign change in
299 selection between every pair of years within each sex (ESM S4; [4]). $\Pr(\Delta_\Delta\pm)$ values close to
300 1 indicate strong evidence that selection acted in opposite directions between two focal years,
301 whereas values close to 0 indicate no evidence that selection differed in direction.

302 **Results**

303 *Annual survival selection*

304 Estimated annual adult survival probabilities (Φ_s) were notably lower in 2012-13, 2013-14 and
305 2017-18 than in the other six study years (Fig. 2). There were clear episodes of strong survival

306 selection against full-winter residence in two of these years (2012-13 and 2017-18; Fig. 2).
307 Here, Φ_s was approximately 0.2 higher for full-winter migrants than residents in both sexes
308 (Fig. 2; ESM S5). These episodes of mortality and survival selection were previously noted to
309 coincide with late-winter ECEs comprising severe storms [24].

310 In contrast, there was no evidence of substantial differences in Φ_s between migrants and
311 residents, or hence of survival selection, in the other seven years (Fig. 2; grand mean Δ was
312 0.00 in females and 0.02 in males; ESM S5). Survival selection in 2012-13 and 2017-18
313 exceeded that in the other years in both sexes (Fig. 2), as confirmed by pairwise comparisons
314 ($\Pr(\Delta_{\Delta})'$ was <0.03 and <0.11 for 2012-13 and <0.01 and <0.12 for 2017-18, in females and
315 males respectively; ESM S5). Further, survival selection in 2012-13 did not differ from that in
316 2017-18 ($\Pr(\Delta_{\Delta})'$ was 0.45 in females and 0.20 in males; ESM S5). There were no marked
317 differences in selection among the other seven years, except for some evidence that selection
318 against resident males differed between 2015-16 and other years apart from 2009-10 and 2010-
319 11 (Fig. 2, $\Pr(\Delta_{\Delta})'$ ranged 0.05–0.09; ESM S5).

320 There was no evidence of strong or consistent sex-specific survival selection in any year
321 (Fig. 2; $\Pr(\Delta_{\Delta}>0)$ ranged 0.11–0.81 across years; ESM S5). Hence, overall, there was strong
322 among-year variation in survival selection, driven by two extreme years with low survival and
323 strong selection against residents in both sexes. However, there was little definitive evidence
324 of fluctuating survival selection, defined as sign changes, in either sex ($\Pr(\Delta_{\Delta\pm})$ ranged 0.04–
325 0.80 in females and 0.04–0.89 in males across all pairs of years; ESM S5).

326

327 ***Reproductive selection***

328 Expected breeding success ($E(BS_{\pi})$) varied substantially among years, and there was evidence
329 of strong reproductive selection against late-winter migrants in multiple years (Fig. 3, recall

330 that for $E(BS_\pi)$, phenotype π reflects location in late-winter occasion $o=5$; Figure 1).
331 Specifically, there was strong evidence of selection against migrants in both sexes in 2011,
332 2012 and 2014, and in females in 2016. For these years, posterior means of Δ ranged 0.26–0.64
333 and 0.28–0.45 fledglings in females and males respectively (Fig. 3, ESM S5).

334 Evidence of reproductive selection was weaker in other years, but estimated effects were
335 typically in the same direction (i.e. against late-winter migrants, Fig. 3). However, there was
336 weak evidence for reversed selection (i.e. against late-winter residents) in females in 2013 and
337 2018 (Fig. 3; ESM S5), which are the two years that also showed strong survival selection
338 against residence (Fig. 2). Consequently, pairwise comparisons confirmed that reproductive
339 selection varied among years in females. In particular, there was strong evidence that selection
340 was different in 2013 and 2018 compared to other years (Fig. 3; $\text{Pr}(\Delta_\Delta)'$ ranged 0.00–0.14 and
341 0.01–0.26 respectively; ESM S5), but not to each other ($\text{Pr}(\Delta_\Delta)'$ =0.37). Among the other seven
342 years, there was some evidence that selection was different in 2011 and 2012 compared to later
343 years ($\text{Pr}(\Delta_\Delta)'$ ranged 0.05–0.26), but not otherwise ($\text{Pr}(\Delta_\Delta)'$ ranged 0.22–0.45). However,
344 there was only weak evidence of fluctuating reproductive selection in females; $\text{Pr}(\Delta_{\Delta\pm})$ ranged
345 0.72–0.82 when comparing 2013 with other years excluding 2017 and 2018, but ranged 0.01–
346 0.64 otherwise (Fig. 3; ESM S5).

347 Evidence of among-year variation in reproductive selection was weaker in males. Here,
348 selection against migrants differed between 2012 and later years (Fig. 3; apart from 2014,
349 $\text{Pr}(\Delta_\Delta)'$ ranged 0.07–0.10; ESM S5), but did not differ between any other years ($\text{Pr}(\Delta_\Delta)'$ ranged
350 0.14–0.48; ESM S5). There was consequently no strong evidence of fluctuating reproductive
351 selection in males ($\text{Pr}(\Delta_{\Delta\pm})$ ranged 0.04–0.51). Finally, even though there was stronger
352 evidence of among-year variation in reproductive selection in females than males, there was
353 no strong evidence of sex-specific reproductive selection on residence versus migration in any
354 year (Fig. 3, $\text{Pr}(\Delta_\Delta>0)$ ranged 0.13–0.91; ESM S5).

355

356 *Selection through annual fitness*

357 Analyses of the composite measure of annual fitness ($E(C_s)$) showed clear evidence of episodes
358 of strong fluctuating selection on full-year residence versus migration (Fig. 4). Specifically,
359 there was strong evidence of sign changes in selection in 2012-13 and 2017-18 compared to
360 several other years: 2009-2010, 2010-2011 and 2011-12 in females, and 2011-12 and 2013-14
361 in males ($\Pr(\Delta_{\Delta\pm})$ for these pairwise years ranged 0.92–0.99 in females and 0.94–1.00 in
362 males; ESM S5). However, 2012-13 and 2017-18 did not differ from each other ($\Pr(\Delta_{\Delta\pm})$ was
363 0.01 in both sexes; ESM S5). There was no strong evidence of sex-specific overall selection
364 on residence versus migration within any year ($\Pr(\Delta_{\Delta>0})$ ranged 0.22–0.89; Fig. 3; ESM S5).
365 Variation and fluctuations in selection were consequently broadly synchronised across both
366 sexes.

367 The fluctuations were caused by the underlying episodes of strongly opposing survival
368 and reproductive selection that occurred in different years. Specifically, $E(C_s)$ was substantially
369 higher in migrants than residents in both sexes in the two years with strong survival selection
370 (2012-13 and 2017-18; Fig. 4; ESM S5). Conversely, $E(C_s)$ was substantially higher in
371 residents than migrants in years with strong reproductive selection, most notably in 2009-10 to
372 2011-12 and 2015-16 in females and in 2011-12, 2013-14 and 2014-15 in males (Δ ranged
373 0.15–0.34 and 0.15–0.32 in females and males respectively; Fig. 4; ESM S5).

374

375 **Discussion**

376 Eco-evolutionary dynamics will partly depend on the magnitude and between-sex synchrony
377 of temporal variation in the strength and direction of selection on key ecologically-relevant

378 traits that shape spatio-temporal population dynamics. We demonstrate episodes of strong, and
379 strongly fluctuating, selection on one such key trait, seasonal migration versus residence,
380 through annual fitness in adult European shags (Fig. 4). Fluctuations were broadly
381 synchronised across males and females, and arose because strong reproductive selection
382 against migration in several years contrasted with episodes of strong survival selection against
383 residence in two other years, coupled with weakened reproductive selection in the subsequent
384 summers (Figs 2 & 3). While the underlying components of both survival and reproductive
385 selection varied substantially among years, including episodes of approximate neutrality,
386 neither fluctuated strongly (strictly defined as a change in direction). Other empirical studies
387 testing for fluctuating selection commonly consider only one component or the other, or do not
388 quantitatively combine them into a single annual fitness measure [e.g. 2,4,6]. Our analyses
389 demonstrate the value of doing so, since the presence of overall strong fluctuating selection
390 would not otherwise have been evident. Predictions regarding micro-evolutionary outcomes
391 based on single-component estimates of selection might consequently be misleading.

392 In our system, the two notable episodes of strong survival selection against residence
393 were associated with ECEs that occurred during late winter in 2012-13 and 2017-18 [24]. Here,
394 prolonged periods of strong onshore wind, rain or cold, which reduce foraging efficiency and
395 incur high thermoregulatory costs in shags [29], primarily impacted the residency area, likely
396 causing increased mortality in residents [24]. Location, and hence migrant versus resident
397 phenotype, would then directly affect survival probability, constituting direct selection.
398 However, because these phenotypes are only expressed during the non-breeding season, any
399 reproductive selection against migration must constitute time-lagged indirect selection. This
400 could reflect ‘carry-over’ effects, for example if an individual’s migrant versus resident
401 phenotype affects its condition and/or capability to acquire or retain a breeding site, which then
402 affects its subsequent breeding success [30–32]. Reproductive selection against migrants was

403 also weakened, or perhaps even reversed in females, in the summers following the ECE winters
404 (2013 and 2018), particularly in older individuals (ESM S6). Such patterns could arise if
405 residents that survived through selective events were in poorer condition (e.g. due to poorer
406 foraging conditions; [33]). This effect could be more pronounced in females, because females'
407 foraging efficiency is more negatively impacted by strong winds than that of males [29].
408 Temporal variation in selection may therefore predominantly reflect underlying environmental
409 conditions. However, formally demonstrating such links, and the intermediate physiological
410 and/or behavioral mechanisms, is generally challenging and rarely achieved [2,7,8,34]. Our
411 results set up valuable opportunities to attempt such analyses once longer timeseries, including
412 multi-dimensional environmental data at appropriate spatio-temporal scales, can be assembled
413 [24]. Nevertheless, our current results indicate that environmental variation including ECEs
414 can generate major reversals of the direction of net selection in annual fitness, encompassing
415 both direct and time-lagged indirect components. Depending on the frequency of ECEs, and
416 on underlying environmental versus additive genetic (co)variances and forms of phenotypic
417 plasticity, such fluctuations may contribute to maintaining additive genetic and phenotypic
418 variation [3], yet alter the optimal genotype and phenotype and constrain rates of adaptive
419 micro-evolution [35–37].

420 Classic examples of strongly fluctuating selection on other traits in other systems have
421 also been linked to extreme environmental variation. For example, drought-induced changes in
422 food supply changed the direction of selection on beak morphology in Darwin's finches [38].
423 Seasonal migration versus residence is a good candidate trait for such effects because
424 sympatric-breeding migrant versus resident phenotypes are, by definition, completely spatially
425 segregated in the non-breeding season and hence subject to different environmental conditions.
426 However, although studies across diverse taxa have now quantified differences in components
427 of survival and/or reproduction between such residents and migrants [18,22], none have

428 explicitly quantified selection through composite measures of annual fitness. Further, some
429 previous studies pooled data across years to generate sufficient sample sizes, precluding
430 estimation of temporal variation in selection (e.g. elk (*Cervus elaphus*) [39], moose (*Alces*
431 *alces*) [40], European blackbird (*Turdus merula*) [41]. Others showed little or no temporal
432 variation and no strong evidence of fluctuating selection, albeit across few years and
433 individuals (e.g. red-spotted newt (*Notophthalmus viridescens*) [23], skylark (*Alauda orvensis*)
434 [42], pronghorn (*Antilocapra americana*) [43]). Our findings (which encompass the whole
435 adult population) broadly concur with earlier analyses in the same study system, which used a
436 subset of resighted individuals with known winter locations during 2009–2012 to show that
437 resident shags had consistently higher breeding success than migrants (Fig. 3; [30]). Our longer
438 time-series now shows temporal variation in selection in subsequent years. In general, very
439 short timeframes are a common limitation across studies of variation and fluctuations in
440 selection (median 3 years; [2]) and may miss biologically important fluctuations caused by
441 infrequent environmental perturbations.

442

443 ***Estimation and implications***

444 In general, estimates of selection can be biased by missing or error-prone phenotypic and/or
445 fitness data [44,45], and evidence of varying and fluctuating selection should be evaluated
446 given sampling variance [4]. These challenges are ubiquitous but commonly ignored, and come
447 to the fore when focal phenotypes are not always directly observed with certainty [46].
448 Uncertainty is inevitable for resident versus migrant phenotypes inferred from resighting data.
449 Our multi-event analyses accounted for key uncertainties by modelling missing phenotypic and
450 survival data due to resighting failure (including due to migration outside surveyed locations),
451 and missing reproduction data due to non-breeding and unobserved nest outcomes. The

452 Bayesian implementation allowed straightforward computation of posterior distributions of
453 between-sex and among-year differences and sign changes that evidence varying, fluctuating
454 and cross-sex synchrony in selection. This approach differs somewhat from standard regression
455 approaches to estimating selection, and recent extensions, designed for readily observable
456 continuous traits. For example, we did not estimate variance in selection through temporal
457 random effects [4,8]. Such estimation is not straightforward in our case, since annual survival
458 and expected breeding success and annual fitness are all derived parameters. Further, variances
459 may be poorly estimated across relatively few years, and assumptions regarding Gaussian
460 distributions may be violated (ESM S5). Our analyses illustrate how variation and fluctuations
461 in selection can be robustly quantified in such (common) circumstances.

462 The variation and fluctuations in selection on the defined migrant versus resident
463 phenotypes estimated in adult shags could appreciably affect phenotypic dynamics and
464 underlying additive genetic variation. Since both phenotypes are frequently expressed, there is
465 considerable phenotypic variance on which selection can act. Indeed, such variance could be
466 partly maintained by fluctuating selection, and the apparent lack of sexual dimorphism in
467 migration is consistent with the cross-sex synchrony in selection. Nevertheless, further steps
468 that consider how the effects of fluctuating selection are propagated across years and life-
469 history stages are required to fully consider the eco-evolutionary consequences. In a moderately
470 long-lived species such as shags, selection through adult survival is likely to impact strategy-
471 specific population growth rates at multi-year scales more than selection through reproduction.
472 However, such effects will also depend on the degree of phenotypic plasticity following
473 selection episodes, and on forms of selection acting before recruitment, which remain to be
474 quantified in our system. Moreover, while our focus on individual full-winter migration versus
475 residence captures considerable annual phenotypic and fitness variation, subtle forms of
476 selection might act on the full diversity of possible phenotypic sequences of seasonal residence

477 versus migration [24,47] and on the joint phenotypes of breeding pairs [30]. Future analyses
478 with further data and methodological developments, including analyses of paired capture-
479 resighting histories, will allow us to quantify these components and thereby reveal the full form
480 and consequences of varying and fluctuating selection on liability for migration.

481

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490

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631 **Figure 1:** Multi-event capture-recapture model structure. Panel (a) illustrates the full annual
632 cycle, indicating possible transitions of surviving individuals between ‘resident’ (R) and
633 ‘migrant’ (M) states across five defined occasions ($o=1$ April–June; $o=2$ September; $o=3$
634 October; $o=4$ mid-November–mid-December; $o=5$ mid-January–mid-February). Different
635 possible annual paths through the annual cycle could be followed, such that surviving
636 individuals are resident or migrant in late-winter occasion ($o=5$). From $o=5$ to the next breeding
637 season ($o=1$), focal sex individuals transition to different breeding states conditional on
638 previous state (i.e. phenotype R or M in $o=5$). Panel (b) illustrates possible fates of focal sex
639 individuals at this time step (see [24] for other time steps and non-focal sex individuals). Circles
640 denote states, defined in $o=1$ as early-failed/non-breeder (\mathcal{B}), breeder with n fledglings (\mathcal{B}_n ;
641 $n \in \llbracket 0, 4 \rrbracket$), or dead (D). Squares denote observation events, defined as seen as early-failed/non-
642 breeder (\mathcal{B}), seen as breeder with known success (\mathcal{B}_n), seen as breeder with unknown success
643 ($\mathcal{B}_?$), or not seen (\mathcal{O}). Arrows indicate possible paths in the state-transition and observation
644 steps, with corresponding probabilities as indices; dashed arrows indicate multifurcations (see
645 bottom box). Parameters are elementary probabilities: ϕ for survival, ζ for breeding, χ_n for n
646 fledglings conditional on breeding, p for resighting, and α for recording a breeding outcome.
647 Additional subscripts indicate state-dependence.

648 **Figure 2:** Annual survival probabilities (Φ_s) for full-winter resident (red) and full-winter
649 migrant (orange) females and males in each biological year from 2009-10 to 2017-18. Points
650 show posterior means, and inner and outer line segments show 50% and 95% credible intervals.
651 Posterior probabilities that each resident-migrant difference is positive are shown (values close
652 to zero or one indicate strong evidence of selection).
653

654

655 **Figure 3:** Expected breeding success ($E(BS_{\pi})$, number of fledglings) for late-winter resident
656 (red) and migrant (orange) females and males in each summer during 2010–2018. Points show
657 posterior means, and inner and outer line segments show 50% and 95% credible intervals.
658 Posterior probabilities that each resident-migrant difference is positive are shown.

659

660 **Figure 4:** Annual fitness ($E(C_s)$, expected demographic contribution, number of genes
661 copies) for full-winter resident (red) and full-winter migrant (orange) females and males in
662 each biological year from 2009-10 to 2017-18. Points show posterior means, and inner and
663 outer line segments show 50% and 95% credible intervals. Posterior probabilities that each
664 resident-migrant difference is positive are shown.