

1 **Among-individual and within-individual variation in seasonal migration**  
2 **covaries with subsequent reproductive success in a partially-migratory bird**

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17 Running head: Plastic migration & reproductive success

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23 **Abstract**

24 Within-individual and among-individual variation in expression of key environmentally-  
25 sensitive traits, and associated variation in fitness components occurring within and between  
26 years, determine the extents of phenotypic plasticity and selection and shape population  
27 responses to changing environments. Reversible seasonal migration is one key trait that  
28 directly mediates spatial escape from seasonally-deteriorating environments, causing spatio-  
29 seasonal population dynamics. Yet, within-individual and among-individual variation in  
30 seasonal migration versus residence, and dynamic associations with subsequent reproductive  
31 success, have not been fully quantified. We used novel capture-mark-recapture mixture  
32 models to assign individual European shags (*Phalacrocorax aristotelis*) to 'resident, 'early  
33 migrant' or 'late migrant' strategies in two consecutive years, using year-round local  
34 resightings. We demonstrate substantial among-individual variation in strategy within years,  
35 and directional within-individual change between years. Further, subsequent reproductive  
36 success varied substantially among strategies, and relationships differed between years;  
37 residents and late migrants had highest success in the two years respectively, matching the  
38 years in which these strategies were most frequently expressed. These results imply that  
39 migratory strategies can experience fluctuating reproductive selection, and that flexible  
40 expression of migration can be partially aligned with reproductive outcomes. Plastic seasonal  
41 migration could then potentially contribute to adaptive population responses to currently  
42 changing forms of environmental seasonality.

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44 **Key words:** Annual reproductive success; capture-mark-recapture mixture model; fluctuating  
45 selection; partial migration; phenotypic plasticity; spatial population dynamics.

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## 47 **1. Introduction**

48 Population responses to changing environments depend on dynamic relationships between  
49 components of fitness and within-individual and among-individual variation in expression of  
50 environmentally-sensitive phenotypic traits [1-6]. Specifically, population outcomes depend  
51 on the degrees to which individuals' phenotypes, and the fitness consequences of those  
52 phenotypes, vary within and among seasons and years, representing labile plasticity and  
53 temporal variation in selection [1,6]. They also depend on the degree to which temporal  
54 variation in individual phenotype is aligned with temporal variation in the fitness  
55 consequences, representing adaptive plasticity [6,7]. Quantifying such effects is prerequisite  
56 for predicting individual and population responses to environmental variation and change,  
57 and for identifying mechanisms that maintain or constrain the critical phenotypic variation  
58 [5-8].

59         One key trait that directly mediates spatial escape from seasonally-deteriorating local  
60 environments, and thereby directly causes spatial population dynamics on short (within-year)  
61 time scales, is seasonal migration (i.e. reversible cross-season movements). Phenotypic  
62 expression of seasonal migration, versus year-round residence at one location, commonly  
63 varies substantially among individuals within populations. Many populations are therefore  
64 'partially migratory', including many fish, birds, mammals and amphibians [9-15]. Further,  
65 experiments show that expression of migration can be state-, condition- and density-  
66 dependent, representing rapid labile plasticity (i.e. within-individual variation [16-18], also  
67 termed phenotypic flexibility [19]). Hence, individuals can switch between residence and  
68 migration both between years, and on shorter timeframes within years. For example,  
69 individuals may be 'early' (pre-emptive or anticipatory) migrants that move in advance of  
70 predictable local environmental deterioration (e.g. onset of winter or other forms of

71 seasonality), or 'late' (responsive) migrants that move upon experiencing further  
72 environmental deterioration [12,14,20-22]. Dynamic relationships between such variable  
73 expression of migration versus residence and major fitness components must then be  
74 quantified in order to understand the maintenance of within-individual and among-individual  
75 variation and to consider the short-term and longer-term population consequences; but this  
76 is rarely achieved [13,14,23,24].

77         Recent studies show that survival probability can be higher in migrants [25,26] or  
78 residents [10,13], or be similar for both groups [27], and that such relationships can vary with  
79 environmental conditions [28]. Carry-over effects can then cause subsequent reproductive  
80 success to differ between surviving sympatric-breeding residents and migrants [29], but such  
81 effects are not always evident [13,24]. However, no studies have yet quantified variation in  
82 subsequent reproductive success across multiple co-existing phenotypes, for example across  
83 early migrants versus late migrants versus residents (hereafter termed 'migratory strategies').  
84 Consequently, no studies have quantified the degree to which associations between such  
85 migratory strategies and reproductive success can vary between years, or hence examined  
86 whether migratory strategies that yield the highest success in any particular year are more  
87 frequently expressed. Evidence of any such adaptive labile plasticity would imply that  
88 dynamic seasonal migration could contribute to maintaining populations experiencing  
89 changing forms of environmental seasonality, by rapidly reshaping spatio-seasonal  
90 population distributions [14].

91         Quantifying such effects requires quantifying variation in reproductive success in  
92 relation to individual location(s) during the preceding non-breeding season, which is still very  
93 challenging. Retrieval of location data from non-transmitting archival loggers or bio-markers  
94 (e.g. stable isotopes) is often restricted to individuals that return and breed and can

95 consequently be (re-)captured. Such state-dependent sampling could bias estimated  
96 relationships with reproductive success, and bio-markers may not clearly distinguish  
97 migratory strategies that differ in timing. Meanwhile, technologies that directly transmit  
98 individuals' locations are still typically deployed on relatively few (often non-random)  
99 individuals. Systems where marked individuals can be directly observed all year therefore  
100 provide valuable opportunities to relate reproductive success to preceding non-breeding  
101 season locations, but require advanced statistical analyses to account for inevitably  
102 incomplete observations and resulting uncertainty.

103         Accordingly, we fitted novel capture-mark-recapture mixture models to year-round  
104 local (i.e. breeding area) resightings of colour-ringed European shags (*Phalacrocorax*  
105 *aristotelis*) in a partially-migratory population to probabilistically assign individuals as 'early  
106 migrant', 'late migrant' or 'resident' in each of two winters. We thereby quantified variation  
107 in phenotypic expression of seasonal migration arising within and among individuals, within  
108 and between the two years, with associated uncertainty. We then tested whether subsequent  
109 reproductive success differed between the three migratory strategies, whether observed  
110 relationships differed between the two years, and whether between-year directional changes  
111 in individual migratory strategy occurred and were aligned with reproductive outcomes. We  
112 thereby consider the scope for adaptive labile plasticity in a key trait, seasonal migration, that  
113 directly shapes spatio-seasonal population dynamics.

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## 119 2. Methods

### 120 (a) Overall approach

121 One approach to quantifying variation in reproductive success in relation to preceding non-  
122 breeding season location (and hence migratory strategy) is to mark individuals with field-  
123 readable tags, then undertake intensive non-breeding season resighting surveys followed by  
124 comprehensive reproductive monitoring. However, even in readily observable systems, not  
125 all present individuals are typically detected in any one survey. Utilising 'capture-mark-  
126 recapture' (CMR) analyses can then minimise bias in parameter estimates, but basic analyses  
127 assume that all individuals within defined model strata have identical occasion-specific  
128 detection probabilities (i.e. no heterogeneity). In partially-migratory populations, this  
129 assumption will be strongly violated regarding local (breeding area) detection probability ( $P_L$ )  
130 during non-breeding season surveys. Here, individuals that have migrated away (i.e.  
131 temporarily emigrated) cannot be locally detected, while individuals that remain resident are  
132 locally detectable. However, this heterogeneity provides information with which to infer  
133 individuals' migratory strategies solely from local resightings; locally detected individuals are  
134 by definition currently resident, while individuals that are not locally detected on any occasion  
135 have a non-zero probability of being a departed migrant. Repeated surveys can then allow  
136 individuals to be assigned to strategies with high probability.

137 Finite mixture models, that consider a specified number of latent (i.e. unobserved)  
138 classes of individuals with different detection probabilities (and/or other parameters, [30-  
139 34]), provide one means of utilising heterogeneity in  $P_L$  to infer individual migratory strategy.  
140 Such models can assign individuals to latent classes (representing different migratory  
141 strategies) given their observed encounter history, yielding posterior probabilities of class  
142 membership [30]. Advantages are that classes need not be defined *a priori* but can emerge

143 from analyses, and uncertainty in class assignments can be formally quantified and  
144 propagated through subsequent analyses [30,31,33] (e.g. relating individuals' probabilistic  
145 class membership to subsequent reproductive success). Potential challenges are that  
146 biological interpretations of model-estimated classes may not be clear or necessarily  
147 consistent across different datasets. These challenges can be mitigated by formulating model  
148 structures with clear objectives and biological knowledge of the focal system; by using  
149 additional information and/or heuristic criteria to validate class interpretations; and by  
150 explicitly evaluating uncertainty in class assignments and consistency across datasets  
151 [30,32,35].

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### 153 **(b) Field data**

154 We collected the required data for two full annual cycles (2017-2018, 2018-2019) for shags  
155 breeding at Bullers of Buchan, Aberdeenshire, Scotland (hereafter 'BoB', Supplementary  
156 Material S1, [36]). During 2009-2018, shags hatched or breeding at BoB were marked with  
157 individually-coded colour-rings (licenced by British Trust for Ornithology), creating a sample  
158 of identifiable adults (age  $\geq 3$  years) alive during 2017-2019 (Supplementary Material S1). Each  
159 breeding season (April-July), the breeding area was intensively surveyed every 5-10 days (19,  
160 18 and 20 surveys in 2017-2019 respectively). All nests were mapped and systematically  
161 monitored through to offspring fledging or nest failure following established protocols [37],  
162 and all adults were systematically identified as unringed or colour-ringed, and ring codes  
163 recorded (Supplementary Material S1). Coastal rocks were also surveyed for roosting shags,  
164 yielding observations of additional colour-ringed individuals that were apparently not  
165 currently breeding (sub-adults, skipping adults or failed breeders). This systematic effort  
166 ensured overall breeding season  $P_L \approx 1$  (Supplementary Material S1).

167            These observations identified 121 and 127 colour-ringed individuals alive in summers  
168 2017 and 2018 that would be age  $\geq 3$  years, and hence deemed capable of breeding, in  
169 summers 2018 and 2019 respectively (conditional on over-winter survival, Supplementary  
170 Material S1). The reproductive success of all surviving individuals was measured as the  
171 number of chicks fledged (range: 0-4) following standard protocols [37] (Supplementary  
172 Material S1). Surviving individuals that apparently did not breed (or could have failed early)  
173 were assigned values of zero, thereby preventing bias due to excluding failed or non-breeders  
174 [38] (Supplementary Material S4).

175            Since shags have partially-wettable plumage they must return to land daily to dry,  
176 facilitating year-round resightings [29,39]. Accordingly, during winters (Sept 1<sup>st</sup>–Feb 28<sup>th</sup>)  
177 2017-2018 and 2018-2019, all daytime and pre-dusk roost sites within daily foraging range of  
178 BoB (ca. 16km) were regularly surveyed for colour-ringed shags (Supplementary Material S1).  
179 This provided substantial data on local non-breeding season presence in the BoB area, overall  
180 77 positive survey days (i.e.  $\geq 1$  colour-ringed individual locally resighted) totalling 1250  
181 resightings of 111 individuals in 2017-2018; and 48 positive survey days totalling 942  
182 resightings of 117 individuals in 2018-2019. Further winter surveys were undertaken across  
183 multiple other night roost sites and their adjacent day roosts spanning >500km of UK east  
184 coast, providing direct resightings of some colour-ringed individuals that bred at BoB and had  
185 definitely migrated away [28,29,39] (Supplementary Material S1). However, since surveys did  
186 not cover the entire UK coastline, not all departed migrants would be directly identified.

187

### 188 **(c) Mixture model analyses**

189 Individuals' local encounter histories were compiled by defining 17 consecutive 10-day  
190 'occasions' spanning Sept 1<sup>st</sup>–Feb 18<sup>th</sup> through each winter. This is the maximum number (i.e.



191 shortest duration) of equal-duration occasions for which there was  $\geq 1$  local positive survey  
192 day within each occasion in both winters. Later ( $\geq$ Feb 19<sup>th</sup>) sightings were excluded because  
193 data inspection showed that some known (i.e. directly observed elsewhere) migrants had  
194 already returned, meaning that local breeding area resightings were no longer highly  
195 informative of an individual's migratory strategy (Supplementary Material S2). Two occasions  
196 representing the breeding seasons before and after each focal winter were also included.  
197 Each individual's full encounter history for each year therefore comprised 19 occasions, on  
198 which it was locally observed or not (Supplementary Material S3). Winter resightings from  
199 other locations (i.e. direct observations of migrants elsewhere) were not included in  
200 encounter histories, but were used to validate mixture model class interpretations (i.e. assess  
201 whether known migrants were assigned as migrants based on local resightings), as is good  
202 practice with mixture models (details below and Supplementary Material S3).

203 Resightings during 2010-2017 strongly suggested three broad categories of  
204 individuals: those regularly locally resighted throughout winter ('residents'); those never  
205 resighted locally in autumn or winter, or only very early in autumn (early September, putative  
206 'early migrants'); and those resighted locally through autumn (September-November) but not  
207 later in winter (late November-January, putative 'late migrants'). Accordingly, CMR mixture  
208 models with three latent classes in  $P_L$  were fitted to data from 2017-2018 and 2018-2019 (full  
209 technical details, Supplementary Material S2). Initial analyses showed that three-class models  
210 were substantially better supported than two-class alternatives, providing formal support for  
211 the three-class structure ( $\Delta AIC_c \geq 20$ , Supplementary Material S2). Occasion-specific  
212 parameter structures for  $P_L$  were then defined to broadly capture the three postulated  
213 migratory strategies (full details, Supplementary Material S2). These constraints ensured that  
214 all estimated  $P_L$  values exceeded zero, allowing estimation of individual class assignment

215 probabilities. They also facilitate inference since local resightings in different winter occasions  
216 are not equally informative regarding migratory strategy (e.g. residence is more strongly  
217 implied by local mid-winter resightings than by early September resightings). However, note  
218 that all  $P_L$  values are estimated from the local resighting data, not set *a priori*. Annual survival  
219 probabilities ( $\phi_A$ ) were known to be high in both years. Of 121 and 127 focal individuals  
220 observed in summers 2017 and 2018, 111 and 122 were resighted in summers 2018 and 2019  
221 respectively. This implies  $\phi_A \geq 0.92$  and  $\geq 0.96$  respectively, and hence  $\phi_l \geq 0.995$  and  $\geq 0.998$  for  
222 each inter-occasion interval ( $\phi_l = \phi_A^{1/18}$  given 19 occasions and 18 intervals, assuming time-  
223 independent mortality). Consequently, we fitted constant  $\phi_l$  across all 18 intervals within  
224 each annual cycle, and did not attempt to estimate class-specific survival probabilities with  
225 the current dataset and analysis (Supplementary Material S2).

226 CMR mixture models were fitted in programme E-Surge, and individual class  
227 probabilities extracted [30,31,40] (Supplementary Material S2). Separate models were fitted  
228 to encounter histories for 2017-2018 and 2018-2019, facilitating model validation and  
229 estimation of class probabilities (Supplementary Material S2). General goodness of fit (GoF)  
230 tests for CMR mixture models are not yet available. We therefore structured the encounter  
231 histories into three fixed *post hoc* groups according to their most probable latent class, and  
232 assessed GoF of models fitted to the group-structured approximation. There was no evidence  
233 of substantial lack of fit (bootstrap p: 0.16 and 0.11 for 2017-2018 and 2018-2019  
234 respectively) or additional overdispersion (median  $\hat{c}$ : 1.07 and 1.09 respectively; full details,  
235 Supplementary Material S2).

236 The biological interpretation of resultant mixture model latent classes as distinct  
237 'resident', 'late migrant' and 'early migrant' migratory strategies was validated in four ways.  
238 First, we summarised the distributions of individual class membership probabilities and

239 thereby quantified the degree to which individuals were assigned to distinct classes with high  
240 probabilities (versus more continuously distributed probabilities, [30]). Second, we examined  
241 whether estimated  $P_L$  values concurred with patterns expected for each postulated strategy  
242 (e.g. low mid-winter  $P_L$  for migrants, higher for residents). Third, we examined whether each  
243 individual's most probable class matched heuristic interpretation of its local encounter history  
244 based on its last autumn resighting occasion and total positive winter occasions (i.e. early last  
245 observation and few positive occasions for early migrants; late last observation and many  
246 positive occasions for residents; intermediate values for late migrants). Fourth, for directly  
247 observed migrants (i.e. individuals resighted at night roosts elsewhere in winter), we  
248 evaluated whether the total summed mixture model probabilities that these individuals were  
249 migrants (early plus late) were close to one. Additionally, to assess across-year consistency of  
250 class assignment probabilities, we quantified the differences in probabilities for the set of  
251 identical or very similar encounter histories that occurred in both 2017-2018 and 2018-2019.

252 Mixture models also directly estimate initial class probabilities [30,33], here  
253 interpretable as the proportions of early migrants, late migrants and residents at the start of  
254 each annual cycle. To further quantify these proportions among individuals that survived each  
255 winter and whose reproductive success was observed, we drew each individual's class from  
256 the multinomial distribution defined by its simplex of estimated class probabilities (which sum  
257 to one), and recorded the total number of individuals assigned to each class. We tested  
258 whether estimated class frequencies differed between the two years using a robust  $\chi^2$  test on  
259 the 3-strategy by 2-year contingency table. This process was repeated for 10000 independent  
260 realisations of each individual's class, thereby propagating uncertainty resulting from class  
261 probabilities  $<1$ . Resulting distributions of class frequencies and  $\chi^2$  statistics are summarised  
262 as the mean and 95% confidence interval across 10000 iterations.

263 Finally, to quantify the degree and form of between-year change in migratory strategy  
264 within individuals that survived through both years, the frequencies with which individuals  
265 were assigned to the same or different classes across the two years were extracted. Robust  
266  $\chi^2$  tests on the 3x3-strategy contingency table were used to test whether these frequencies  
267 differed from a null expectation generated by random resampling from the overall class  
268 frequencies estimated in 2018-2019, conditional on classes assigned in 2017-2018 (full details  
269 and other null models, Supplementary Material S3). These analyses were also repeated for  
270 10000 independent realisations, and distributions of frequencies and  $\chi^2$  statistics summarised  
271 as above.

272

#### 273 **(d) Reproductive success**

274 We fitted a generalised linear model (GLM) to test whether mean annual reproductive success  
275 differed between the three mixture classes (specified as a three-level fixed effect), and hence  
276 between the three inferred migratory strategies. We explicitly tested for a class-by-year  
277 interaction, and hence for between-year variation in the relationship between reproductive  
278 success and migratory strategy. Models with and without the interaction were fitted  
279 assuming a quasi-Poisson distribution of reproductive success, and the comparative ANOVA  
280 test statistic ( $\chi^2_{\text{Obs}}$ ) extracted. This analysis was again repeated for 10000 independent  
281 realisations of each individual's probabilistic class assignment. Each model was then refitted  
282 with individual reproductive success randomly resampled from the focal year's observations,  
283 yielding a null  $\chi^2_{\text{Rand}}$ . The statistic  $\chi^2_{\text{Diff}} = \chi^2_{\text{Obs}} - \chi^2_{\text{Rand}}$  was computed, where positive values imply  
284 that the class-by-year interaction effect was greater given observed versus randomised  
285 reproductive success. The proportion of iterations for which this difference was negative  
286 ( $P(\chi^2_{\text{Diff}} < 0)$ ) was extracted.

287           To broadly capture variation in reproductive success with age, and hence minimise the  
288 degree to which current analyses could potentially be confounded by age-specific variation,  
289 we also fitted a two-level factor defining individuals as young (aged 3-4 years) or older (5+  
290 years) adults (details in Supplementary Material S4). While most focal colour-ringed  
291 individuals had unringed mates, there were 17 breeding attempts where both adults were  
292 colour-ringed. Their observed reproductive success consequently occurred in the dataset  
293 twice. To account for resulting non-independence, reproductive success was resampled at  
294 the level of breeding attempts (rather than individuals). Across 103 individuals that appeared  
295 in the dataset in both years, the between-year correlation in individual reproductive success  
296 was small (Spearman correlation  $r_s=-0.08$ ). Individual reproductive success was therefore  
297 resampled independently for each year. In practice, since most individuals were assigned to  
298 one mixture class with very high probability (see Results), conclusions were the same if  
299 models were directly fitted taking each individual's most probable class and hence migratory  
300 strategy in each year, with random individual effects. Possible effects of sex on relationships  
301 between migratory strategy and reproductive success were not considered because ~55% of  
302 adults were of unknown sex. Across known-sex individuals, frequencies of assigned migratory  
303 strategies did not differ between females and males (Supplementary Material S4). Similarly,  
304 there was no consistent age-specific variation in migratory strategy across the current dataset  
305 (Supplementary Material S4). Analyses were run in R v3.5.1 [40].

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### 311 **3. Results**

#### 312 **(a) Migratory strategies**

313 The mixture models successfully assigned encounter histories, and hence individuals, to  
314 distinct classes that were clearly and consistently interpretable as resident, late migrant and  
315 early migrant (Fig. 1). In each year, most individuals were assigned to one class with very high  
316 probability (overall  $\geq 0.95$  for  $\geq 83\%$  of individuals,  $\geq 0.75$  for  $\geq 97\%$  of individuals; Fig. 1,  
317 Supplementary Material S1). Estimated class-specific  $P_L$  for the 17 winter occasions concurred  
318 with patterns expected for the three migratory strategies. Specifically,  $P_L$  was always low for  
319 early migrants and close to zero through mid-winter, and initially high and then lower for late  
320 migrants (Fig. 1).  $P_L$  for residents varied among occasions, reflecting variable survey success,  
321 but was often substantially higher than for the migrant classes through mid-winter (Fig. 1).  
322 Consequently, encounter histories assigned with high probabilities clearly matched heuristic  
323 interpretations; early and late migrants were typically last seen before winter occasion 4  
324 (early October) and 11 (early December) respectively while residents were seen  
325 subsequently, with more positive occasions in total (Fig. 1). The few less certain assignments  
326 were probabilistically split between early and late migrant, or between late migrant and  
327 resident (Fig. 1, Supplementary Material S3). In total, 17 and 29 focal individuals were  
328 resighted at night roosts elsewhere in winters 2017-2018 and 2018-2019 respectively (46  
329 encounter histories of 36 different individuals), and hence were known migrants  
330 (Supplementary Material S1). The mixture models assigned all 46 histories as migrant with  
331 very high total probabilities (mean: 0.999, range: 0.964-1.000). By corollary, zero individuals  
332 assigned as resident by the mixture models were resighted elsewhere. Comparisons of 15  
333 identical or similar encounter histories observed in both years showed that class assignment

334 probabilities were highly consistent across years (mean absolute difference: 0.008, range:  
335 0.000-0.090, Supplementary Material S2).

336

### 337 **(b) Strategy frequencies and between-year change**

338 Estimated initial probabilities ( $\pm 1SE$ ) for the three mixture classes representing residents, late  
339 migrants and early migrants were  $0.42 \pm 0.05$ ,  $0.26 \pm 0.04$  and  $0.32 \pm 0.06$  respectively in 2017-  
340 2018, and  $0.22 \pm 0.04$ ,  $0.39 \pm 0.05$  and  $0.39 \pm 0.06$  respectively in 2018-2019. The relative class  
341 frequencies estimated across individuals with observed reproductive success were  
342 quantitatively similar (Supplementary Material S1). These frequencies differed between years  
343 (mean  $\chi^2$ : 11.2, 95%CI: 8.5-14.0; mean p: 0.005, 95%CI: 0.001-0.016 across 10000  
344 realisations). Overall, residents were most frequent in 2017-2018 but least frequent in 2018-  
345 2019, while late migrants, and to some degree early migrants, were more frequent in 2018-  
346 2019 than 2017-2018. The population sample was therefore more migratory in 2018-2019  
347 than in 2017-2018.

348         These changes in frequencies between years arose partly because, of 103 individuals  
349 that survived through both years, a mean proportion of 0.36 (95%CI: 0.32-0.40) were assigned  
350 to different classes in the two years and hence changed strategy (Table 1A, hence mean  
351 proportion assigned to the same class in both years: 0.64, 95%CI: 0.60-0.68). The frequencies  
352 of individuals assigned to the same and different classes differed substantially from null  
353 expectation (mean  $\chi^2$ : 76.2, 95%CI: 38.4-140.9, all  $p < 0.001$  across 10000 realisations, Table 1,  
354 Supplementary Material S3). More individuals than expected retained the same strategy  
355 across both years, while few or no individuals changed from late or early migrant to resident,  
356 from early migrant to late migrant or from resident to early migrant (Table 1B). Individuals  
357 that changed strategy therefore predominantly became slightly more migratory (i.e. resident

358 to late migrant, and late migrant to early migrant, Table 1, Supplementary Material S3). There  
359 was therefore evidence of substantial between-year individual repeatability in migratory  
360 strategy, but also of substantial directional change.

361

### 362 **(c) Reproductive success**

363 Mean reproductive success ( $\pm 1SD$ ) across all observed focal individuals was  $1.1 \pm 1.1$  and  
364  $1.0 \pm 1.1$  fledged chicks in 2018 and 2019 respectively. In 2018, individuals assigned as  
365 residents during the preceding winter had substantially higher mean reproductive success  
366 than early migrants, while late migrants had intermediate success (Fig. 2). In 2019, late  
367 migrants had higher mean reproductive success than residents and early migrants (Fig. 2).  
368 Consequently, there was a strong class-by-year interaction, largely reflecting that residents  
369 had high mean success in 2018 but low mean success in 2019 (Fig. 2, Supplementary Material  
370 S4). Residents and late migrants, and to some extent early migrants, therefore had highest  
371 relative reproductive success in the year in which they were most frequent (Fig. 2). As  
372 anticipated, young adults had lower success than older adults (Fig. 2, Supplementary Material  
373 S4).

374 The substantial decrease in mean reproductive success of residents in 2019 compared  
375 to 2018, and the corresponding relative increase in success of late migrants (Fig. 2), could  
376 potentially arise if the most successful resident individuals in 2017-2018 became late migrants  
377 in 2018-2019 and remained successful. High reproductive success would then be associated  
378 primarily with individuals rather than migratory strategies. However, additional analyses  
379 provided no evidence of such individual effects. Specifically, reproductive success of late  
380 migrants in 2019 did not differ between surviving individuals that had been residents or late  
381 migrants in 2017-2018 (Table 2A). Further, reproductive success of residents in 2018 did not



382 differ between individuals that subsequently remained as residents or became late migrants  
383 in 2018-2019 (Table 2B). If anything, individuals that became late migrants tended to have  
384 lower reproductive success in 2018, opposing the between-year change in mean reproductive  
385 success estimated across all individuals (Fig. 2).

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#### 388 **4. Discussion**

389 Population responses to environmental variation and change depend on patterns of variation  
390 and covariation in individual phenotypes and fitness, representing plasticity and selection  
391 [1,2,6,8]. Seasonal migration (versus residence) is one key phenotype that allows rapid spatial  
392 escape from temporarily deteriorating environments, but patterns of dynamic (co)variation  
393 in migratory phenotypes and fitness components have not been fully quantified. We show  
394 that substantial phenotypic variation, with individuals classified with high probabilities as  
395 early migrants (inferred to depart from the breeding area in early autumn), late migrants  
396 (depart in late autumn) and year-round residents, is evident within a European shag  
397 population, and that these 'migratory strategies' can have substantially differing subsequent  
398 mean year-specific reproductive success. Further, strategy frequencies and associated  
399 reproductive success varied markedly between two study years, and in each year the strategy  
400 associated with the highest estimated success in each year was more frequently expressed.  
401 These results highlight that seasonal migration can be an individually- and temporally-variable  
402 non-neutral trait, and imply that flexible seasonal migration may have capacity to mediate  
403 adaptive plastic responses to currently changing forms of environmental seasonality.

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405

## 406 **(a) Migratory strategy**

407 Objectively classifying individual migratory strategy is generally challenging, requiring year-  
408 round location data and appropriate analyses [22,24]. We used capture-mark-recapture  
409 mixture models to assign individuals to latent classes representing distinct migratory  
410 strategies, with explicit uncertainty, solely using local (breeding area) observations (further  
411 commentary, Supplementary Material S2). CMR mixture models were originally devised to  
412 overcome ‘nuisance’ heterogeneity in detection probability and minimise resulting bias in  
413 estimated survival probabilities and population sizes [30,32,35]. In that context, support for  
414 a model with  $K$  classes does not necessarily mean that  $K$  biologically meaningful distinct  
415 groups exist, but simply that  $K$  latent classes adequately capture heterogeneity [30,34,35].  
416 However, in our analyses, most encounter histories were assigned to one of three mixture  
417 classes with very high probability, and these classes are clearly biologically interpretable as  
418 ‘resident’, ‘late migrant’ and ‘early migrant’ (Fig. 1). While there may not in fact be three  
419 entirely distinct strategies, this structure clearly provides a very good approximation that  
420 allows strong individual-level inference. The few less typical cases with higher class  
421 uncertainty (Fig. 1, Supplementary Material S3), might represent slightly different strategies  
422 (e.g. mid-autumn departure), or could reflect further individual heterogeneity in  $P_L$   
423 conditional on presence, or simply chance sequences of local resighting failure. Nevertheless,  
424 our results strongly imply the existence of different ‘migratory strategies’, such that some  
425 sympatric-breeding individuals spend considerably more time per year than others in the  
426 breeding area environment.

427 Our analyses also demonstrate substantial within-individual variation in non-breeding  
428 season location within years, and in defined migratory strategy between years. Defining  
429 individual state at any instant as resident (i.e. in the breeding area) or migrant (i.e. away),

430 individuals were inferred to transition between these states at different times of year, or  
431 never, generating emergent early migrant, late migrant and resident strategies that can be  
432 viewed as differential within-year plasticity. Further, while 64% of surviving individuals were  
433 assigned to the same class in both study years, representing high between-year repeatability  
434 of migratory strategy, 36% changed class, demonstrating between-year plasticity. Indeed,  
435 evidence of labile plasticity in migration, both within and between years, is accumulating in  
436 diverse taxa (but see [15]). For example, European blackbirds (*Turdus merula*) can show early  
437 or late migration alongside residence [21]; storms can induce altitudinal migration in white-  
438 ruffed manakins (*Corapipo altera*, [20]); and adult roach (*Rutilus rutilus*, [42]), elk (*Cervus*  
439 *elaphus*, [12]) and skylarks (*Alauda arvensis*, [24]) can switch between migration and  
440 residence between years.

441           In European shags, the form of between-year variation differed substantially from null  
442 expectations, and resulted in directional change that contributed to making the population  
443 more migratory in 2018-2019 than 2017-2018. Specifically, approximately 42% of surviving  
444 residents became late migrants and 31% of surviving late migrants became early migrants,  
445 but other transitions were infrequent to the degree that zero surviving early migrants became  
446 residents (Table 1, Supplementary Material S3). Overall, these observed patterns of within-  
447 year and between-year migratory plasticity and repeatability are consistent with a ‘threshold  
448 model’, which proposes that discrete phenotypes are expressed when an underlying  
449 continuously-distributed ‘liability’ exceeds some threshold [43] (Supplementary Material S5).  
450 This model was previously suggested to apply to migration versus residence in birds and fish  
451 [23,44], and to other discrete phenotypes including wingless versus winged (dispersive)  
452 morphs in hemimetabolous insects [45]. The patterns of phenotypic variation observed in  
453 shags could arise given among-individual variation and time-of-season dependence in liability,

454 and increased population mean liability in 2018-2019 compared to 2017-2018  
455 (Supplementary Material S5). Any effects of migratory strategy on subsequent reproductive  
456 success would then impose selection on a threshold trait, and hence on underlying migratory  
457 liability.

458

#### 459 **(b) Reproductive success**

460 Despite recent interest in partial migration and its consequences [9,11-29], no studies have  
461 yet quantified within-year and between-year variation in sympatric reproductive success  
462 across diverse migratory strategies (more than simply resident versus migrant). For example,  
463 a leading study that used stable isotopes to assign individual skylarks as resident or migrant  
464 found no difference in breeding success across four years, but sample sizes were small and  
465 individuals that were not clearly assigned as simply resident or migrant were excluded [24].  
466 Previous analyses of a different shag population breeding on Isle of May, Scotland, showed  
467 that residents had higher breeding success than migrants across three years, but did not  
468 distinguish early and late migrants [29].

469         Our comprehensive reproductive monitoring of shags that survived through each  
470 winter revealed substantial variation in mean reproductive success with migratory strategy,  
471 and showed that the most successful strategy differed between years (Fig. 2). The estimated  
472 mean between-class differences exceeded 0.7 fledged chicks in both years, constituting  
473 notable effects compared to the grand mean success of approximately 1 fledged chick. Direct  
474 causal effects of migratory strategy on subsequent reproductive success cannot, of course,  
475 be proved by phenotypic associations. However, there was no evidence that observed  
476 differences in relative reproductive success between residents and late migrants across the  
477 two years arose because individuals that switched strategies had consistent reproductive

478 success (Table 2). Instead, the observed relationships could potentially reflect varying carry-  
479 over effects of winter location(s), perhaps including lasting effects on physiology or  
480 acquisition of breeding sites or local ecological information. Such mechanisms can be  
481 investigated in future. Our results then imply time-lagged indirect selection on migratory  
482 liability, and imply that such selection can act on both the occurrence and within-year timing  
483 of migration, and can also differ markedly between consecutive years.

484 Further, in each study year, more individuals expressed the migratory strategy that  
485 yielded highest mean reproductive success; residents were most frequent and had high  
486 reproductive success in 2018, while late migrants were more frequent and had highest  
487 reproductive success in 2019 (Fig. 2). Switching from residence to late migration is therefore  
488 expected to yield the highest mean reproductive success across the two years  
489 (Supplementary Material S4), and this was indeed the most frequently observed form of  
490 between-year switching. Strong evidence of adaptive plasticity of course cannot be  
491 definitively inferred across two years. However, the observed patterns could indicate  
492 adaptive labile plasticity expressed by some individuals, which is still surprisingly infrequently  
493 demonstrated for any trait or system [3,5,7,23]. This would in turn imply selection for  
494 migratory liability values near the threshold, thereby maintaining both within-year and  
495 between-year environmental responsiveness and generating substantial phenotypic  
496 variation.

497 However, this interpretation would raise the question of why plasticity was far from  
498 complete. Many individuals were early migrants in both years, even though repeated early  
499 migration is expected to yield low mean reproductive success (Supplementary Material S4),  
500 and some 2017-2018 residents remained resident in 2018-2019. Proximately, this implies that  
501 some individuals have high or low migratory liabilities, whether due to genetic or permanent

502 environmental effects, and may consequently be quasi-obligate migrants and residents [e.g.  
503 42]. High migratory liabilities could be maintained in a population if early migration yields the  
504 highest probability of over-winter survival, at least in some years, as recently shown for  
505 blackbirds (*Turdus merula*, [26]) and shags breeding on Isle of May [28].

506 Overall, our current results provide evidence of among-individual variation, within-  
507 individual plasticity and fluctuating reproductive selection on a key phenotype across two  
508 years, and indicate that plasticity and selection could be aligned. More years of data are  
509 clearly now required to ascertain which, if either, currently observed pattern of variation in  
510 reproductive success with migratory strategy (Fig. 2) is more typical; whether early migration  
511 is ever associated with high reproductive success; to identify underlying environmental  
512 drivers; and to quantify relative reproductive success of individuals that do and do not change  
513 migratory strategies between years. Partially-migratory systems then provide exciting  
514 opportunities to quantify the magnitude and form of adaptive labile plasticity, the direct and  
515 constitutive costs, and hence the direct implications of such processes for spatio-seasonal  
516 population dynamics (e.g. [6,14]).

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652 **Table 1.** Frequencies of inferred two-year migratory strategies for 103 European shags  
653 included in analyses for both focal years, given (A) mixture model-assigned strategies for both  
654 years, and (B) model-assigned strategy for 2017-2018 and a randomly resampled strategy for  
655 2018-2019 (full details, Supplementary Material S3). Rows and columns index strategies in  
656 2017-2018 and 2018-2019 respectively, showing the mean frequency and 95% confidence  
657 interval across 10000 realisations. In (A), dark grey shading (leading diagonal) identifies  
658 individuals assigned to the same strategy in both years. Light grey and white identify  
659 individuals that became more and less migratory in 2018-2019 respectively. In (B), dark and  
660 light grey indicate two-year strategies that occurred more and less frequently than expected  
661 respectively (compared to frequencies in A). White indicates strategies whose frequencies did  
662 not differ from overall expectation, but occurred more frequently than expected conditional  
663 on change (Supplementary Material S3). In addition, 17 new individuals entered the dataset  
664 in 2018-2019 (and hence do not contribute to estimates of between-year individual  
665 variation): 2, 6 and 9 residents, late migrants and early migrants respectively.

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			2018-2019		
			Resident	Late migrant	Early migrant
(A)	2017-2018	Resident	22.4 (21,24)	19.1 (17,21)	3.1 (2,4)
		Late migrant	2.0 (1,3)	17.3 (14,20)	8.7 (6,11)
		Early migrant	0.0 (0,0)	4.1 (2,6)	26.3 (24,29)
(B)	2017-2018	Resident	10.6 (5,17)	17.5 (11,24)	16.5 (10,23)
		Late migrant	6.6 (2,11)	11.0 (6,16)	10.4 (5,16)
		Early migrant	7.2 (3,12)	12.0 (7,17)	11.2 (6,17)

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700 **Table 2.** Comparisons of (A) reproductive success in 2019 of individuals assigned as late  
701 migrants (LM) in 2018-2019 that were residents (R) or late migrants in 2017-2018, and (B)  
702 reproductive success in 2018 of individuals assigned as residents in 2017-2018 that remained  
703 as residents or became late migrants in 2018-2019. Statistics are the number of individuals in  
704 each group (N), the group mean and standard deviation (SD) of reproductive success in the  
705 focal year, and the Wilcoxon test statistic (W) for the difference in mean and associated p  
706 value (all presented as means and 95% confidence intervals across 10000 realisations).  
707 Statistics for reproductive success in 2018 of individuals assigned as late migrants in both  
708 years are shown for comparison, but do not contribute to current hypothesis tests.

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Year	Classes	N	Mean	SD	W	p
<b>(A) 2019</b>	<b>R → LM</b>	19.0	1.32	1.01		
		(17,21)	(1.21,1.42)	(0.95,1.08)	154.4	0.71
	<b>LM → LM</b>	17.2	1.42	1.07	(118.0,194.0)	(0.30,1.00)
		(14,20)	(1.21,1.61)	(0.98,1.16)		
<b>(B) 2018</b>	<b>R → R</b>	19.3	1.74	0.88		
		(18,21)	(1.65,1.80)	(0.86,0.96)	144.7	0.36
	<b>R → LM</b>	18.2	1.35	1.21	(123.0,166.5)	(0.11,0.74)
		(16,20)	(1.21,1.50)	(1.15,1.26)		
<b>LM → LM</b>	17.2	1.02	1.09			
	(14,20)	(0.84,1.20)	(1.05,1.13)			

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737 **Figure 1.** Summaries of mixture model latent class assignments for European shags observed  
738 in (A-E) 2017-2018 and (F-J) 2018-2019. (A,F): Frequencies of individual maximum class  
739 membership probability. (B,G): Ternary plots visualising each individual's simplex of class  
740 probabilities. Vertices represent classes interpreted as resident (R, left), early migrant (EM,  
741 right) and late migrant (LM, top). Points represent individuals, line segments indicate multiple  
742 identical points. Most points are at or near the vertices, indicating individuals assigned to one  
743 class with very high probability. Points on intervening dashed lines indicate individuals  
744 assigned to two classes with non-zero probabilities. Few points are within the triangular  
745 space, indicating little three-way uncertainty. (C,H): Estimated local (breeding area) resighting  
746 probabilities ( $P_L$ , with 95% confidence intervals) across 19 occasions for the classes  
747 representing residents (black, solid line), late migrants (mid-grey, dashed line) and early  
748 migrants (light grey, dotted line). (D,I): Last autumn observation occasion for individuals  
749 assigned as resident, late migrant or early migrant with probability  $\geq 0.95$  (96 and 101  
750 individuals in 2017-2018 and 2018-2019 respectively, occasion zero is the initial summer).  
751 (E,J): Total positive winter occasions for these individuals.

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760 **Figure 2.** (A) Predicted mean reproductive success in 2018 and 2019 for individuals assigned  
761 as resident (R), late migrant (LM) or early migrant (EM) during the preceding winter. Open  
762 and filled symbols denote young (age 3-4 years) and older (age 5+) adults respectively. (B)  
763 Relative (mean-standardised) predicted reproductive success for each migratory strategy  
764 versus the proportion of individuals assigned to that strategy in each year (shown for older  
765 adults only for clarity). On both panels, squares, circles and triangles represent residents, late  
766 migrants and early migrants respectively. Black and grey symbols denote 2017-2018 and  
767 2018-2019 respectively. Points denote back-transformed mean predicted values and vertical  
768 solid and dashed lines denote back-transformed mean standard errors and 95% confidence  
769 intervals estimated across 10000 realisations. Horizontal solid and dashed lines denote mean  
770 standard errors and 95% confidence intervals for initial class probabilities.

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1 **Supplementary material**

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3 **Among-individual and within-individual variation in seasonal migration**  
4 **covaries with subsequent reproductive success in a partially-migratory bird**

5

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13 **S1. Details of the field system**

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15 European shags are seabirds that are restricted to coastal areas all year round, and have  
16 patchy breeding and wintering distributions due to their requirements for appropriate nest  
17 and night roost sites (typically on rocky islands and cliffs). They additionally use coastal rocks  
18 as day roosts between foraging bouts, where colour-ringed individuals can be readily  
19 observed all year round [1].

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21 Figure S1 shows the locations of the Bullers of Buchan ('BoB') study area and adjacent day  
22 roosts and breeding colonies. During 2009-2018, samples of chicks and adults were ringed at  
23 BoB, using colour-rings with three-letter individual codes (licensed by British Trust for

24 Ornithology). The ringed individuals comprised those that could be accessed without undue  
25 risk to researchers or other breeding seabirds in the cliff colony. Totals ringed per year varied  
26 through approximately 60-110 chicks and 2-12 adults, representing 5-10% of the total  
27 individuals present. Some ringing occurred within nine widely-distributed and accessible sub-  
28 colonies within the overall colony. Recruited and surviving colour-ringed adults could  
29 subsequently breed at any nest site, including many sites that were not accessible for ringing  
30 but could still be readily viewed from cliff tops to record reproductive success. Consequently,  
31 breeding attempts made by ringed adults are likely to be broadly representative of the whole  
32 colony. Reproductive success of these individuals was ascertained by systematically recording  
33 nest contents every 5-10 days throughout the breeding period following well-established and  
34 widely used seabird monitoring protocols [2]. Offspring were deemed to have reached  
35 fledging age once observed with fully grown wing and tail feathers, with little or no down  
36 remaining on the back and upper wings [2].

37

38 Most breeding shags that had been ringed at BoB and recruited locally bred within the main  
39 study area. However, adjacent breeding areas (~3km south and north) were also intensively  
40 surveyed to locate colour-ringed adults that had dispersed slightly further (Fig. S1). Beyond  
41 these areas, there are no further shag breeding areas for >40km (Fig. S1). Data from three  
42 immigrants that were originally ringed at colonies further south in Scotland (Isle of May and  
43 Craigleith, Firth of Forth), and then dispersed to breed at BoB, were included in analyses.  
44 There is no evidence of long-distance breeding dispersal of recruited adults.

45

46 European shags typically breed from age three years. Although they can attempt to breed  
47 aged two years, this was rarely observed at Bullers of Buchan in 2018 and 2019 (only two

48 attempts by known ringed two year-olds). Individuals that would have been two years old in  
49 the summer following each focal winter were consequently excluded from current analyses  
50 of reproductive success. All surviving three year-olds were defined as adults and included  
51 (Table S1). The frequent breeding season surveys ensured that most colour-ringed individuals  
52 were resighted on multiple occasions during in each summer (Figure S2). Adults that were not  
53 seen in a particular breeding season were never seen subsequently, either in subsequent  
54 breeding seasons or winters, implying that breeding season resighting probability was close  
55 to 1 during 2017-2019.

56

57 During 2017-2019, local (i.e. breeding area) winter resighting surveys of all local roost sites  
58 were undertaken by experienced observers, primarily JMR and MS, typically at times of day  
59 and tide that surveys undertaken during 2009-2017 had shown to maximise the probability  
60 of observing roosting shags (including pre-dusk gatherings). Roosting groups were repeatedly  
61 scanned with 60x magnification telescopes, and colour-ring codes recorded and checked. This  
62 core survey effort was supplemented with substantial additional effort from numerous other  
63 observers, who checked diverse local sites at diverse times of day and tide. This substantial  
64 combined effort reduced heterogeneity in local resighting probability per defined 10-day  
65 'occasion', and increased the probability that colour-ringed shags that were locally present  
66 would be resighted on multiple occasions during the winter.

67

68

69

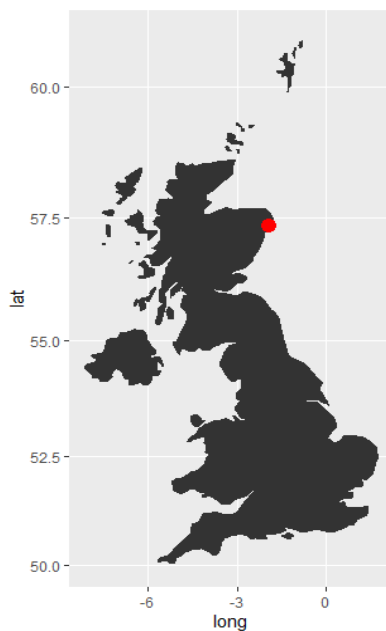
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71

72 **Figure S1.** (A) Location of the main Bullers of Buchan study area, and (B) zoomed-in locations  
73 of the main breeding colony (red), two adjacent sub-colonies (orange, Whinnyfold to the  
74 south and Longhaven to the north), and three main winter day roost sites (blue) ranging up  
75 to 16km north of the main breeding area. The next nearest breeding colonies to the north  
76 and south are also shown (yellow). Wider surveys showed that few shags utilised winter day  
77 roost sites south of Bullers of Buchan, since the main foraging areas are slightly north.

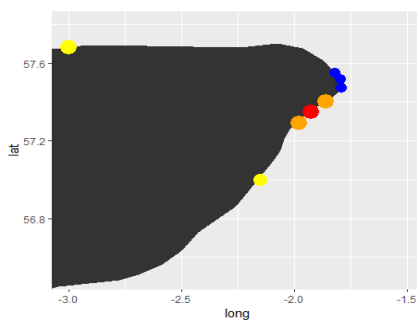
78

79 **(A)**



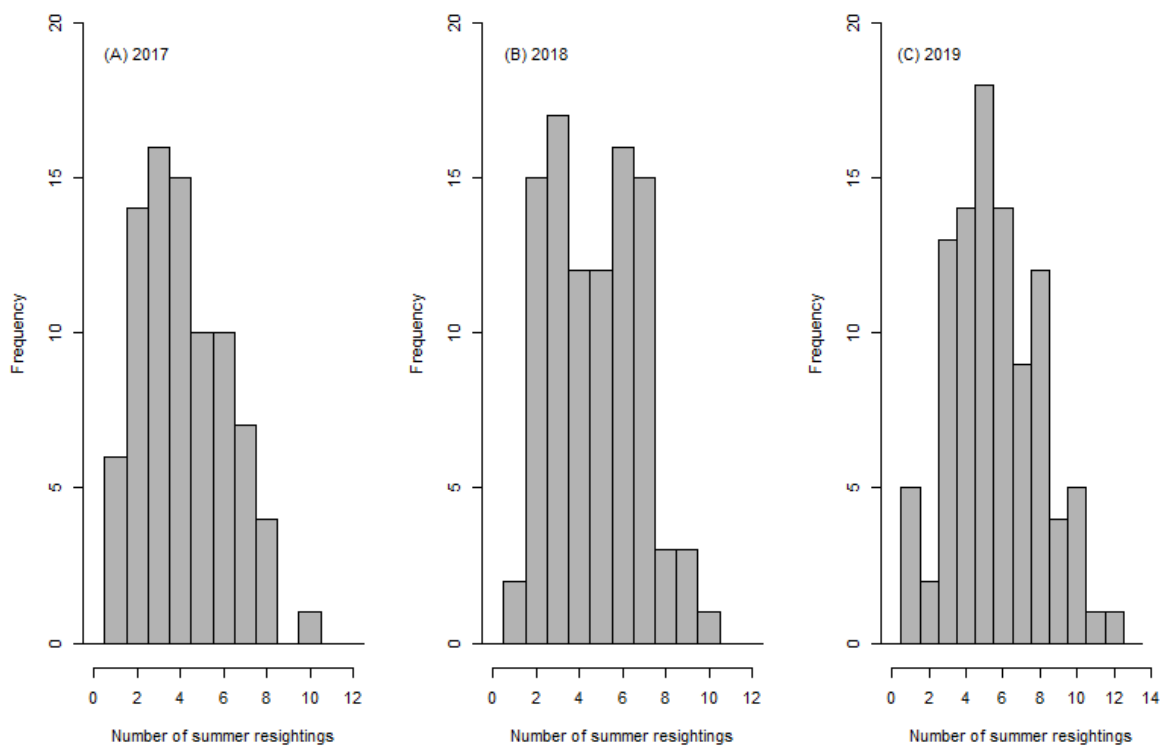
80

81 **(B)**



82

83 **Figure S2.** Frequency distributions of the number of times that an adult colour-ringed shag  
84 was resighted at Bullers of Buchan during the breeding season in (A) 2017, (B) 2018 and (C)  
85 2019. Y-axes show the numbers of individuals. Mean numbers of resightings per individual  
86 were 4.1, 4.7 and 5.6 in 2017-2019 respectively, and variances were 4.1, 4.4 and 5.8  
87 respectively. Consequently, there was therefore little or no overdispersion compared to  
88 expectation given a Poisson distribution of resightings.

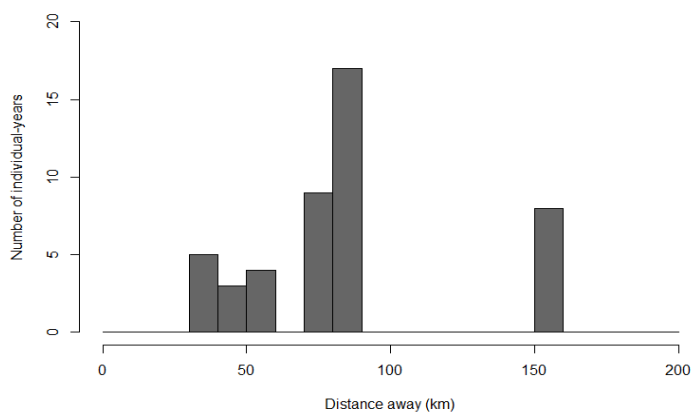


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96 Winter surveys for colour-ringed shags were also carried out at numerous other sites along  
97 the east coast of Scotland, primarily ranging from Northumberland to Caithness [1,2-4]. These  
98 surveys focussed on key night roost locations where shags could be observed pre-dusk, as  
99 well as day roosts adjacent to the night roosts. Totals of 17 and 29 colour-ringed individuals  
100 known to breed at Bullers of Buchan were resighted at night roosts elsewhere in winters  
101 2017-2018 and 2018-2019 respectively (36 different individuals), and hence were directly  
102 observed to be migrants. These individuals were observed between ~35km and 160km away  
103 from Bullers of Buchan (Fig. S3). These individuals were seen at these locations on multiple  
104 occasions through the winter, with no intervening sightings in the Bullers of Buchan area.  
105 They consequently provide direct evidence that focal individuals had moved away for a  
106 protracted period, representing migration rather than solely daily foraging trips. The total of  
107 46 individual-year encounter histories comprised 24 and 22 that the mixture models assigned  
108 as late migrants and early migrants respectively. Individuals that were never observed in any  
109 of the survey areas in either of the two winters are likely to have moved further away.

110

111 **Figure S3.** Distribution of distances (km) that migrant individual shags were observed away  
112 from Bullers of Buchan across winters 2017-2018 and 2018-2019. The discrete distribution  
113 reflects the distances to major surveyed night roost sites.



114

115 **Table S1.** Data summaries for 2017-2018 and 2018-2019: numbers of (A) focal individuals, (B)  
116 observed surviving individuals, (C) individuals with observed reproductive success and unique  
117 breeding events, (D) focal individuals originally ringed as chicks or adults, (E) individuals  
118 observed as young or older adults, (F) estimated initial class (i.e. state) probabilities ( $\pm 1$   
119 standard error) and 95% confidence interval, (G) surviving individuals assigned to their most  
120 likely class with probabilities  $P_{Max} \geq 0.95$  or  $\geq 0.75$ , (H) individuals with observed reproductive  
121 success assigned to the classes interpreted as resident (R), late migrant (LM) or early migrant  
122 (EM). H shows means and 95% confidence intervals across 10000 realisations of individuals'  
123 probabilistic class assignments. In B, C, G and H, proportions are shown in parentheses.

	<b>2017-2018</b>	<b>2018-2019</b>
(A) Focal individuals	121	127
(B) Surviving individuals	111 (0.92)	122 (0.96)
(C) Observed reproductive success	Individuals: 105 (0.95) Breeding events: 95	Individuals: 118 (0.97) Breeding events: 111
(D) Chicks, adults	72, 33	87, 31
(E) Young, older	41, 64	34, 84
(F) Initial class probabilities	R: 0.42 $\pm$ 0.05, 95%CI: 0.33,0.52 LM: 0.26 $\pm$ 0.04, 95%CI: 0.19,0.35 EM: 0.32 $\pm$ 0.05, 95%CI: 0.22,0.41	R: 0.22 $\pm$ 0.04, 95%CI: 0.16,0.30 LM: 0.39 $\pm$ 0.05, 95%CI: 0.30,0.50 EM: 0.39 $\pm$ 0.05, 95%CI: 0.29,0.51
(G) Confident assignments	$P_{Max} \geq 0.95$ : 96 (0.86) $P_{Max} \geq 0.75$ : 109 (0.98)	$P_{Max} \geq 0.95$ : 101 (0.83) $P_{Max} \geq 0.75$ : 118 (0.97)
(H) Individuals assigned as R, LM or EM	R: 43.9 (0.42), 95%CI: 42,46 LM: 28.6 (0.27), 95%CI: 26,31 EM: 32.4 (0.31), 95%CI: 31,34	R: 25.2 (0.21), 95%CI: 24,27 LM: 46.7 (0.40), 95%CI: 43,50 EM: 46.2 (0.39), 95%CI: 43,49

124



## 125 **S2. Details of capture-mark-recapture mixture models**

126

127 Diverse methods of extending basic capture-mark-recapture (CMR) models to estimate  
128 movement probabilities and account for temporary emigration have been devised, including  
129 utilising multiple secondary occasions (robust design), multi-site observations in multi-state  
130 models, and individual covariates that predict emigration [5-8]. Our analyses illustrate use of  
131 CMR mixture models to assign encounter histories, and hence individuals, to latent classes  
132 that represent different migratory strategies. We illustrate that individuals can be assigned to  
133 interpretable classes with high probability solely using frequent local (breeding area)  
134 resightings. This approach could be logistically feasible in diverse systems, and particularly  
135 useful for systems where individuals that have migrated away (i.e. temporarily emigrated) are  
136 not readily observable. Here, we provide further details of current analyses, and highlight  
137 some considerations for applying similar analyses to other datasets.

138

139 ***Number of mixture classes:*** Support for modelling any particular number of classes within a  
140 mixture model can be formally assessed by using standard information criteria (including AIC)  
141 to compare candidate models with different numbers of classes [9-11]. This approach has  
142 been validated using simulated CMR datasets with two classes of detection probability,  
143 showing that AIC commonly identifies the correct model structure (i.e. two classes versus one  
144 or three classes, [9]; see also [10]). These simulations assumed no temporal (i.e. among-  
145 occasion) variation in detection probability, meaning that straightforward comparison  
146 between candidate models with constant detection probability within one, two or three  
147 mixture classes was appropriate. However, specifying an appropriate set of candidate models  
148 becomes more complex when detection probabilities vary among occasions and such

149 variation can differ between mixture classes. A large number of models, with different class  
150 structures, could then be postulated.

151

152 Consequently, to validate the foundations of our inferences for shags, we first fitted mixture  
153 models that assumed two or three latent classes in resighting (i.e. detection) probability  
154 assuming constant probability across all occasions, and used AIC adjusted for small sample  
155 sizes (AICc) to assess support for these different structures. These models were fitted to  
156 separate datasets for 2017-2018 and 2018-2019. The three-class model was considerably  
157 better supported than the two-class model in both years ( $\Delta AICc > 20$ , Table S2). It has  
158 previously been suggested that it may rarely be useful to fit mixture models with more than  
159 three classes to typical CMR datasets, due to high resulting uncertainty [9]. Exploratory  
160 analyses of models with four mixture classes fitted to the current shag dataset supported this  
161 view. AICc values were similar to those for three-class models, but class assignments were  
162 highly uncertain and no longer easily interpretable. Further, simulations have shown that in  
163 these circumstances AIC may tend to indicate support for models with too many classes,  
164 especially for long-lived species with substantial heterogeneity ([9], see also [10]).  
165 Consequently, four-class models were not considered further in current analyses.

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172 **Table S2.** Summaries of capture-mark-recapture (CMR) mixture models fitted to encounter  
173 histories observed in 2017-2018 and 2018-2019 with (A) two or three mixture classes in local  
174 resighting probability with constant class-specific probability, and (B) three mixture classes in  
175 local resighting probability with class-specific probabilities that varied among occasions. Here,  
176 probabilities were constrained either following Table S3 (model i), with additional  
177 independent variation in resighting probability for the postulated late migrant and resident  
178 classes (model ii), and with resighting probability for the final summer occasion fixed to one  
179 (model iii). Model deviance, number of parameters (Par.), AIC adjusted for small sample sizes  
180 (AICc) and the difference in AICc between each model and the best supported model in each  
181 section ( $\Delta$ AICc) are shown. The model with three mixture classes and constraints on local  
182 resighting probability following Table S3 was best supported in both years (model i, bold).  
183 This model was consequently used to compute individual class assignment probabilities and  
184 infer individual migratory strategy, and hence to quantify relationships with subsequent  
185 reproductive success.

186

	<b>2017-2018</b>				<b>2018-2019</b>			
	Deviance	Par.	AICc	$\Delta$ AICc	Deviance	Par.	AICc	$\Delta$ AICc
(A) Two classes	2511.5	4	2519.5	+20.2	2609.3	4	2617.3	+29.8
Three classes	2487.2	6	2499.3	-	2575.4	6	2587.5	-
(B) <b>Model i</b>	<b>1871.3</b>	<b>31</b>	<b>1935.4</b>	-	<b>1776.4</b>	<b>31</b>	<b>1840.9</b>	-
Model ii	1865.3	34	1935.7	+0.2	1771.3	34	1842.3	+1.4
Model iii	1877.1	30	1939.0	+3.6	1780.1	30	1842.3	+1.4

187

188

189 **Parameter constraints:** We took the well-supported three-class model and applied  
190 constraints on the form of temporal (i.e. among-occasion) variation in local resighting  
191 probability ( $P_L$ ) according to our biological understanding of the system and the postulated  
192 existence of three broad migratory strategies (i.e. resident, late migrant and early migrant,  
193 Table S3). These constraints were implemented primarily because exploratory analyses of  
194 models with full unconstrained occasion-dependence in  $P_L$  for all three mixture classes  
195 showed that estimates of  $P_L$  were bounded at zero for the putative migrant classes in some  
196 winter occasions. This makes biological sense; local resighting probability for migrant classes  
197 will be zero at times of year when all migrants are locally absent. However, estimated values  
198 of  $P_L=0$  prevented useful estimation of individual class assignment probabilities, or hence  
199 quantitative inference of individual migratory strategies. Consequently, values of  $P_L$  for the  
200 migrant classes were constrained to be identical across restricted sets of winter occasions  
201 (Table S3). Since migrants were occasionally locally present and resighted in early and late  
202 winter (i.e. before departure or after return), the constrained values of  $P_L$  were then  
203 estimated as slightly above zero (main text Figure 1C,H), thereby allowing individual class  
204 assignment probabilities to be computed. Further exploratory analyses with different  
205 parameter constraints showed that imposing some biologically-informed constraints also  
206 facilitated inference. This is because local resightings in different winter occasions are not  
207 equally informative regarding individual migratory strategy. For example, a local mid-winter  
208 resighting strongly implies that an individual is 'resident', but an early September resighting  
209 does not. Finally, imposing constraints that differed among mixture classes also meant that  
210 the order of identity of the three emerging mixture class was consistent across different  
211 analyses and datasets (rather than varying according to starting values and the input order of  
212 encounter histories, which occurs in the absence of any other constraints). This facilitated

213 subsequent analyses and model comparisons. However, it is important to note that while  
 214 parameter constraints are set *a priori*, parameter values are estimated from the encounter  
 215 history data. Consequently, values will not necessarily concur with those that would be  
 216 expected for the three postulated migratory strategies, and there are no *a priori* defined exact  
 217 'cut-off' dates that define strategies (e.g. early versus late migrants).

218

219 **Table S3.** Structure of occasion-specific local resighting probabilities ( $P_L$ ) for a three-class  
 220 mixture model specified to capture postulated resident (R), late migrant (LM) and early  
 221 migrant (EM) strategies. Occasions (Occ.) comprise 17 winter occasions ( $W_i$ ) and the previous  
 222 and subsequent summer breeding seasons ( $S_1$  and  $S_2$ , hence 19 occasions in total).  $P_L$   
 223 parameters for each winter are specified as  $X_y$ , where X is e, l or r denoting the EM, LM and R  
 224 strategies respectively, and y is the first winter occasion for that parameter. Some  $X_y$  values  
 225 for early and late migrants were constrained to be identical across multiple occasions,  
 226 primarily to prevent estimation of occasion-specific  $P_L=0$ . Since individuals only enter the  
 227 dataset if observed in summer  $S_1$ , initial  $P_L=1$  for all classes (i.e. conditioning on initial  
 228 encounter). Since there was no expectation that  $P_L$  in summer  $S_2$  would differ between  
 229 classes, this parameter was set equal ( $s_2$ ).  $P_L$  was also set equal for the LM and R strategies  
 230 for occasions  $W_1$ - $W_3$ , when all such individuals are locally present and are expected to be  
 231 equally observable. Groups of adjacent parameters that were constrained to be equal are  
 232 highlighted in shades of grey.

Occ.	S <sub>1</sub>	W <sub>1</sub>	W <sub>2</sub>	W <sub>3</sub>	W <sub>4</sub>	W <sub>5</sub>	W <sub>6</sub>	W <sub>7</sub>	W <sub>8</sub>	W <sub>9</sub>	W <sub>10</sub>	W <sub>11</sub>	W <sub>12</sub>	W <sub>13</sub>	W <sub>14</sub>	W <sub>15</sub>	W <sub>16</sub>	W <sub>17</sub>	S <sub>2</sub>
<b>R</b>	1	r <sub>1</sub>	r <sub>2</sub>	r <sub>3</sub>	r <sub>4</sub>	r <sub>5</sub>	r <sub>6</sub>	r <sub>7</sub>	r <sub>8</sub>	r <sub>9</sub>	r <sub>10</sub>	r <sub>11</sub>	r <sub>12</sub>	r <sub>13</sub>	r <sub>14</sub>	r <sub>15</sub>	r <sub>16</sub>	r <sub>17</sub>	S <sub>2</sub>
<b>LM</b>	1	r <sub>1</sub>	r <sub>2</sub>	r <sub>3</sub>	l <sub>4</sub>	l <sub>5</sub>	l <sub>6</sub>	l <sub>7</sub>	l <sub>8</sub>	l <sub>9</sub>	l <sub>9</sub>	l <sub>9</sub>	l <sub>9</sub>	l <sub>9</sub>	l <sub>9</sub>	l <sub>15</sub>	l <sub>15</sub>	l <sub>15</sub>	S <sub>2</sub>
<b>EM</b>	1	e <sub>1</sub>	e <sub>1</sub>	e <sub>1</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>4</sub>	e <sub>15</sub>	e <sub>15</sub>	e <sub>15</sub>	S <sub>2</sub>

233 Observations from previous years suggested that migrants could start to return from late  
234 January, with most returning from late February. Consequently, the last winter occasion for  
235 which resighting data were collected (Feb 19<sup>th</sup>–28<sup>th</sup>) was excluded from encounter histories  
236 because sightings were no longer strongly informative of an individual’s migratory strategy.  
237 Local resighting probability was constrained to be constant across the three previous late  
238 winter occasions for both early and late migrants, but allowed to differ from mid-winter  
239 values (Table S3). This allows  $P_L$  to increase in late winter, as migrants return. However, in  
240 practice, late winter  $P_L$  was estimated to be only slightly higher than mid-winter  $P_L$  for both  
241 migrant classes (main Figure 1). There was therefore no evidence that early and late migrants  
242 returned at substantially different times (up to mid-February) as well as departing at different  
243 times.

244

245 ***Additional constrained models:*** We fitted two sets of additional models to verify whether  
246 conclusions were robust given slightly different parameter constraints from those defined in  
247 the primary model (Table S3).

248

249 **1. *Different constraints on winter  $P_L$ :*** We fitted a set of 7 additional models with slightly  
250 different constraints on winter  $P_L$  (codes in Box 1). These models were considerably less well  
251 supported than the primary model ( $\Delta AIC_c \gg 2$ ), except for a model where  $P_L$  values for the  
252 postulated late migrant class for the first three winter occasions varied independently from  
253 those for the postulated resident class (rather than being constrained to be equal, as in Table  
254 S3). This model was only slightly less well supported than the primary model in both years  
255 (lower deviance, but more parameters, Table S2B model ii versus model i). Individual class

256 assignment probabilities calculated from the two models were quantitatively very similar,  
257 meaning that the choice between these models did not alter subsequent inferences.

258

259 **2. Different constraints on final summer  $P_L$  (i.e. parameter  $S_2$ ):** The primary model estimated  
260 the constant between-occasion survival probability  $\phi_l$  to be 1.00 in both years. Consequently,  
261 local resighting probability in each subsequent summer ( $S_2$ ) was estimated as  $<1$ . In reality,  
262 some or all individuals that were unobserved in the subsequent summer will have died during  
263 winter, implying that  $\phi_l$  was slightly overestimated and  $S_2$  slightly underestimated. These  
264 small biases probably arose because  $\phi_l$  was constrained to be equal across all occasions for  
265 all three classes. This in turn was because estimation of fully time- and class-specific  $\phi_l$  was  
266 not feasible given current sample sizes of individuals (~120 encounter histories per year)  
267 relative to the large number of survival parameters in a fully saturated model (3 classes x 18  
268 intervals = 54 parameters), coupled with high overall annual survival probabilities ( $\geq 0.92$ ) and  
269 no *a priori* expectation of when mortality would occur or that it should be concentrated into  
270 specific occasions. Consequently, to evaluate the implications of minor biases for individual  
271 class assignment probabilities and hence inference of individual migratory strategy, an  
272 additional model was fitted, parameterised following Table S3 but with  $s_2$  fixed to equal 1.  
273 This forced estimation of  $\phi_l < 1$ , in practice yielding estimates of 0.995 (95%CI: 0.991,0.997)  
274 and 0.997 (95%CI: 0.994,0.999) for 2017-2018 and 2018-2019 respectively). This model was  
275 slightly less well supported than the primary model in both years (Table S2B model iii versus  
276 model i). Class assignment probabilities estimated for surviving individuals were  
277 quantitatively very similar across both models. The primary model was consequently used for  
278 subsequent inference, but class assignment probabilities for individuals that were not  
279 observed during the second summer or subsequently, and hence most likely died during the

280 focal winter, were not interpreted. These individuals anyway do not enter analyses of  
281 variation in reproductive success during the subsequent summer.

282

283 **Goodness of fit:** General goodness of fit (GoF) tests for CMR mixture models are not yet  
284 available. We therefore used a group-structured approximation to evaluate GoF and  
285 overdispersion. We assigned each observed encounter history to its most likely class  
286 according to mixture model probabilities, then structured the encounter histories into three  
287 fixed groups defined by the assigned classes. Standard approaches to evaluating GoF of  
288 group-structured CMR models can then, in principle, be applied. However, in the current case,  
289 fully time-dependent group-structured CMR models could not be usefully fitted and  
290 evaluated because local resighting probability ( $P_L$ ) was estimated as zero for the migrant  
291 groups in some mid-winter occasions (as makes biological sense, see above). We therefore  
292 fitted models with constrained group-structured temporal variation in  $P_L$  (following Table S3),  
293 and used simulation utilities in programme MARK to assess GoF and overdispersion ( $\hat{c}$ , full  
294 methodological details and explanations in [12]). In brief, we simulated 1000 independent  
295 datasets given estimated parameters of the group-structured model and with the same  
296 number of encounter histories as in the real datasets, refitted the model, and quantified the  
297 proportion of instances in which the deviance exceeded that estimated when the model was  
298 fitted to the real data. This gives a bootstrap probability that the fitted model does not fit the  
299 data; values  $>0.05$  can be interpreted that the observed deviance can arise by chance.  
300 Overdispersion was estimated from these simulations as the ratios of observed to mean  
301 simulated deviance or  $\hat{c}$ . As a further measure, the value of  $\hat{c}$  for which the proportions of  
302 simulated values that were higher and lower were exactly 0.5 (i.e. 'median  $\hat{c}$ ') was computed  
303 (see [12]).



304

305 In summary, these analyses suggested that a model with three fixed classes of resighting  
306 probability, fitted by assigning each observed encounter history to its most likely class as  
307 estimated by the mixture model, adequately fitted the data with little additional  
308 overdispersion (Table S4). This implies that the three-class mixture model also adequately  
309 fitted the data; indeed the mixture model likely fits even better than the group-structured  
310 approximation, since encounter histories can be assigned to multiple classes with some  
311 probability, better capturing remaining heterogeneity.

312

313 Note that this approach to assessing GoF for mixture models would not work so well for  
314 datasets and models where most individual encounter histories are not assigned to single  
315 classes with high probability (as they were in our current analyses). The simple group-  
316 structured approximation would then be less useful.

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329 **Table S4.** Summary of (A) bootstrap goodness of fit (GoF) tests and (B) median  $\hat{c}$  simulations  
 330 for group-structured CMR models, where each encounter history was assigned to its most  
 331 likely class of resighting probability as estimated by mixture models. In (A) the GoF probability  
 332 is the proportion of bootstrap replicates where the deviance of the model fitted to simulated  
 333 data exceeded that of the model fitted to the real observed data. Overdispersion was  
 334 estimated as the ratio of observed to simulated (i) deviance and (ii)  $\hat{c}$ .  
 335

		2017-2018	2018-2019
(A)	GoF probability	0.164	0.110
(i)	Observed model deviance	857.1	745.4
	Mean simulated deviance	814.3	698.8
	Observed / mean simulated deviance	1.05	1.07
(ii)	Observed model $\hat{c}$	14.3	13.3
	Mean simulated $\hat{c}$	12.8	11.6
	Observed / mean simulated $\hat{c}$	1.12	1.15
<hr/>			
(B)	Median $\hat{c}$	1.07	1.09

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343 **Box 1. E-SURGE specifications for a CMR mixture model with three mixture classes in**

344 **detection (resighting) probability:**

345

346 Number of states: 4 (3 live states and dead)

347

348 **GEPAT code:**

349 Initial state probabilities:

$\pi$	$\pi$	*
-------	-------	---

350

351 State transition probabilities (assuming no transitions among classes):

$\psi$	-	-	*
-	$\psi$	-	*
-	-	$\psi$	*
-	-	-	*

352

353 Event probabilities:

*	$\beta$
*	$\beta$
*	$\beta$
*	-

354

355 **GEMACO code:**

356 Initial state: to

357 Transition: i

358 Event (following Table S3):

359 firste+nexte.[from(1:2).t(2\_4)+from(1).t(5\_18)+from(2).t(5\_9,10:15,16:18)+from(3).t(2:4,5:15,16:18)  
360 +from(1:3).t(19)]

361

362 First detection probability was fixed to 1. Replicate models were fitted with multiple random starting  
363 values, yielding no evidence of local minima of the deviance. Individual class assignment probabilities  
364 were calculated (following [5,12]) and saved by selecting 'View history state dependent probability' in  
365 the 'Run & See' menu [13].

366

367 GEMACO event code for 7 additional candidate models, with slightly different constraints on occasion-  
368 specific local resighting probability, that were less well supported (all with firste+nexte.):

- 369 • [from+t]
- 370 • [from(1).t(2\_18) + from(2).t(2\_8,9:18) + from(3).t(2:18) + from(1:3).t(19)]
- 371 • [from(1).t(2\_18) + from(2).t(2\_8,9:18) + from(3).t(2:4,5:15,16:18) + from(1:3).t(19)]
- 372 • [from(1:2).t(2,3,4,5,6) + from(1).t(7\_18) + from(2).t(7,8,9) + from(3).t(1:9) + from(2:3).t(10:15,16:18)  
373 + from(1:3).t(19)]
- 374 • [from(1).t(2\_18) + from(2).t(2\_8,9:15,16:18)+ from(3).t(2:4,5:15,16:18) + from(1:3).t(19)]
- 375 • [from(1).t(2\_18) + from(2).t(2\_9,10:15,16:18)+ from(3).t(2:4,5:15,16:18) + from(1:3).t(19)]
- 376 • [from(1:2).t(2,3,4) + from(1).t(5\_18) + from(2).t(5\_8,9:15,16:18)+ from(3).t(2:4,5:15,16:18) +  
377 from(1:3).t(19)]

378

379

380

381 The use of CMR mixture models to assign encounter histories, and hence individuals, to  
382 different latent classes that represent different migratory strategies worked well with our  
383 dataset, but some points should be considered for application to other datasets or questions.

384

385 **Separate year models:** We fitted separate models to separate encounter histories for 2017-  
386 2018 and 2018-2019 (hence, in Table S3,  $S_1=2017$  and  $S_2=2018$ , or  $S_1=2018$  and  $S_2=2019$ ). This  
387 facilitated: (i) direct estimation of initial class probabilities for each year (i.e. the proportions  
388 of individuals entering each winter that were assigned to the classes interpreted as residents,  
389 late migrants and early migrants); (ii) direct estimation of individual class assignment  
390 probabilities for each year; (iii) comparison of class assignment probabilities for identical or  
391 similar encounter histories that were observed in both years, thereby validating whether class  
392 interpretations were consistent; and (iv) assessment of goodness of fit and overdispersion  
393 using tractable group structured approximations. Comparisons of 15 identical or very similar  
394 encounter histories showed that class assignment probabilities were indeed very similar  
395 across the two years (Table S5). ‘Very similar’ encounter histories were defined as those with  
396 the same number of positive occasions, with broadly similar distributions across each winter  
397 (Table S5).

398

399

400 **Table S5.** Comparisons of class assignment probabilities for (A) 10 identical and (B) 5 very  
401 similar encounter histories observed in both 2017-2018 and 2018-2019. The probability  $P_A$   
402 that each encounter history is assigned to the resident (R), late migrant (LM) or early migrant  
403 (EM) class in each year is shown, with the absolute magnitude of the between-year difference.  
404 The focal encounter histories comprise 5, 4 and 6 that were assigned to the R, LM and EM  
405 classes with high probabilities respectively (grey shading).

2017-2018				2018-2019				Absolute difference		
Encounter history	$P_A(R)$	$P_A(LM)$	$P_A(EM)$	Encounter history	$P_A(R)$	$P_A(LM)$	$P_A(EM)$	$P_A(R)$	$P_A(LM)$	$P_A(EM)$
(A) 10000000000000000001	0.000	0.001	0.999	10000000000000000001	0.000	0.001	0.999	0.000	0.001	0.001
100000000000000000011	0.000	0.002	0.998	100000000000000000011	0.000	0.003	0.997	0.000	0.001	0.001
100100000000000000001	0.000	0.014	0.986	100100000000000000001	0.000	0.017	0.983	0.000	0.003	0.003
100101000000000000001	0.000	0.821	0.179	100101000000000000001	0.000	0.824	0.176	0.000	0.003	0.003
101000000000000000001	0.000	0.001	0.999	101000000000000000001	0.000	0.006	0.994	0.000	0.005	0.005
110000000000000000001	0.000	0.005	0.995	110000000000000000001	0.000	0.003	0.997	0.000	0.002	0.002
110100000000000000001	0.000	0.134	0.866	110100000000000000001	0.000	0.044	0.956	0.000	0.090	0.090
110101000000000000001	0.000	0.980	0.020	110101000000000000001	0.000	0.923	0.077	0.000	0.057	0.057
110110111000000000001	0.000	1.000	0.000	110110111000000000001	0.001	0.999	0.000	0.000	0.000	0.000
111111100000000000001	0.000	1.000	0.000	111111100000000000001	0.000	1.000	0.000	0.000	0.000	0.000
(B) 111111111110011001	1.000	0.000	0.000	111111110110101111	1.000	0.000	0.000	0.000	0.000	0.000
111111111110101011	1.000	0.000	0.000	111111111101001011	1.000	0.000	0.000	0.000	0.000	0.000
1111110011101111001	1.000	0.000	0.000	111111110100101011	1.000	0.000	0.000	0.000	0.000	0.000
1111110110110111011	1.000	0.000	0.000	111111110100111011	1.000	0.000	0.000	0.000	0.000	0.000
1101111101000111001	0.980	0.020	0.000	1101111011000101011	0.999	0.001	0.000	0.019	0.019	0.000

406

407

408 It would in principle be possible to fit a single CMR mixture model to individuals' two-year  
409 encounter histories. By allowing class (i.e. state) transitions in the middle summer, the  
410 probability of changing class between years could then be estimated (at the population level).  
411 However, such two-year models would not necessarily define the same biologically  
412 interpretable mixture classes as the single-year models, and individual class assignment  
413 probabilities cannot be so easily estimated when individuals can change class. Such additional  
414 analyses therefore provide no major benefit given our current aims. Indeed, since no  
415 parameter values are shared between the two years and most individuals were assigned to  
416 one class in each year with very high probability, the frequencies of individual class transitions  
417 can be estimated *post hoc*, while propagating the small remaining uncertainty (see main text).  
418 However, CMR mixture models that directly consider multiple years may be appropriate for  
419 other datasets and questions.

420 **Encounter history structure:** Given our datasets for 2017-2018 and 2018-2019, the mixture  
421 models assigned most individuals to one of three classes with very high probability (Fig. 1).  
422 However, in general, such assignments, and hence the success of the mixture model  
423 approach, will be sensitive to the structures of the defined encounter history. For example,  
424 exploratory analyses showed that defining encounter histories with fewer longer winter  
425 resighting occasions yielded less clear assignments for some individuals. This is because there  
426 was less information to distinguish late migrants from unobserved residents, or to distinguish  
427 early migrants from unobserved late migrants. However, defining more shorter occasions also  
428 caused problems since local detection probability  $P_L$  for all classes was then very low for some  
429 occasions with little field effort, impeding discrimination. The specification of 17 10-day  
430 winter occasions represents a heuristic balance; similar exploratory analyses and decisions  
431 should be undertaken to successfully apply similar analyses to other datasets. In principle,  
432 encounter occasions do not necessarily have to be of uniform duration. For example, when  
433 two successful surveys were undertaken within the same 10-day period these could have  
434 been split into two occasions, potentially further increasing power for class assignments.  
435 However, since the fine-scale distribution of survey dates differed somewhat between our  
436 two focal years, further targeted sub-division of encounter occasions would have impeded  
437 between-year comparisons and consistency.

438

439 **Individual assignments and survival:** Individual class assignments can be uncertain for  
440 individuals that died at some (unknown) early time in winter, for example because there is  
441 little information to distinguish a dead (and hence unobserved) potential resident from a  
442 migrant that survived until late winter but cannot be locally observed (see also [10]). The very  
443 high breeding season resighting probability in our system likely contributed substantially to

444 the high individual assignment probabilities, since it allowed clear distinction between winter  
445 mortality and low winter-long local detection probability. [6] note that individual class  
446 assignments will also be highly uncertain for individuals that enter a dataset at later occasions.  
447 This does not affect our current analyses, which focus on multiple occasions within one year,  
448 since all individuals enter the dataset in the initial summer. Note that individual class  
449 assignments should not be used to estimate class-specific survival probabilities *post hoc*.  
450 Rather, such probabilities should be directly estimated within the CMR mixture model. This is  
451 technically feasible, but was not attempted in our current analyses because overall adult  
452 survival probabilities across both focal years were very high (see above). This implies that  
453 there will be low power to detect variation in survival among the relatively large number of  
454 between-occasion intervals, but also implies that survival is unlikely have varied substantially  
455 among strategies across the current dataset.

456

457 ***Between-class transitions:*** A further possibility would be to consider two mixture classes of  
458 detection probability relating to resident and migrant states, and then allow transitions  
459 between them (thereby capturing 'late migrants' that switch between resident and migrant  
460 states during mid-winter). However, exploratory analyses of the current datasets suggested  
461 that this approach did not work as well as specifying three mixture classes. It required further  
462 constraints on the transition process to allow transitions away from the resident state at the  
463 end of the initial summer and transitions back to that state before the subsequent summer,  
464 and allow transitions away from the resident state in late autumn (to capture 'late migrants'),  
465 but prevent estimation of repeated transitions between resident and migrants states within  
466 winters (which system-wide observations suggest very rarely occur). This required tight *a*  
467 *priori* specification of time windows when 'early migrants' and 'late migrants' could depart



468 and hence what classes of individuals existed. In contrast, the three-class mixture model  
469 allowed these classes to emerge without requiring strong *a priori* definitions.

470

471 Note that for other kinds of datasets and structures, for example with sparse local winter  
472 sightings but larger numbers of sightings across one or multiple other sites, relationships  
473 between winter location and subsequent reproductive success might be best estimated using  
474 other approaches, for example using multi-state models that consider multiple observable  
475 (and/or unobservable) winter locations and reproductive outcomes as explicit states. Our  
476 clear interpretation of different mixture classes as early and late migrants and residents also  
477 assumes that there is no further major heterogeneity in resighting (i.e. detection) probability  
478 within classes; for example that there were no residents that were consistently not observed.  
479 This assumption is likely to be valid in our system, as evidenced by the goodness of fit tests  
480 that showed no major lack of fit of the group-structured approximation. This is facilitated  
481 because individual shags using day roost sites are highly visible, and these sites are highly  
482 spatially restricted (meaning that all individuals can in principle be observed). However,  
483 caution may be required in other systems whose ecologies could foster greater individual  
484 heterogeneity in local detection.

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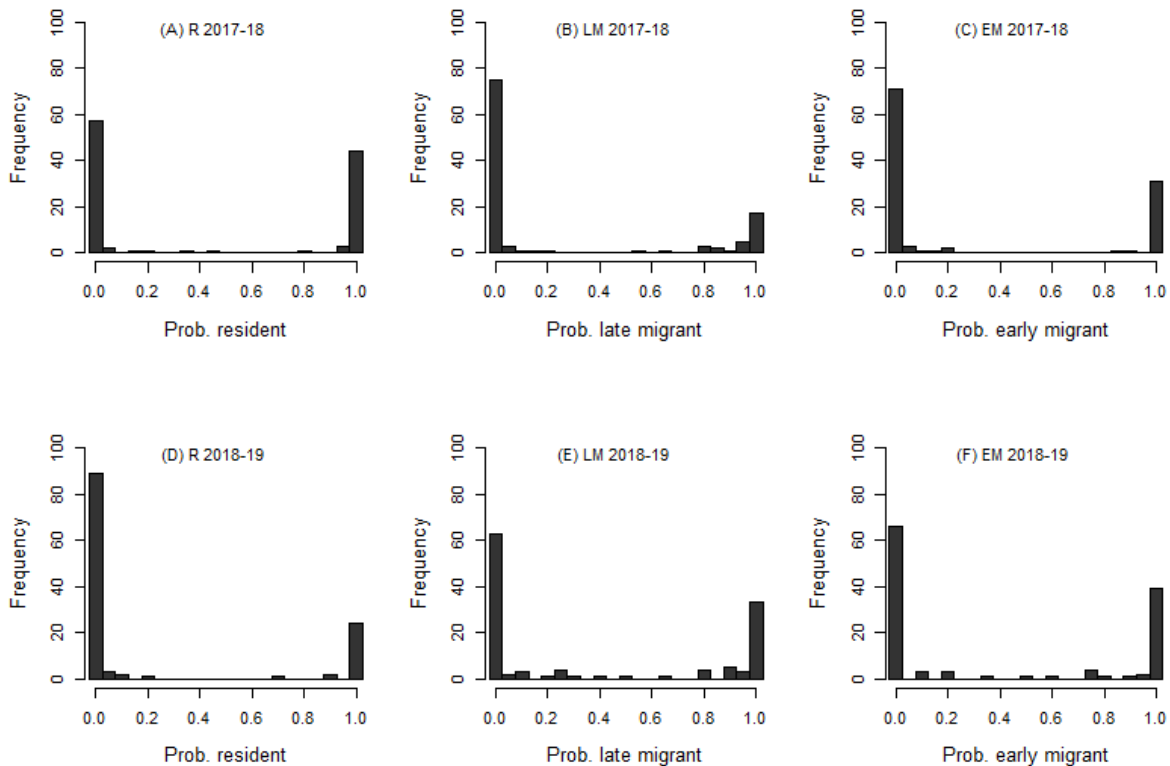
492 **S3. Details of class assignments**

493

494 Figure S4 summarises the probabilities with which individual shags were assigned to the three  
495 mixture model classes interpreted as residents, late migrants and early migrants in 2017-2018  
496 and 2018-2019, further illustrating that individuals could be assigned to any of the three  
497 strategies with high probabilities. Table S6 provides examples of individual encounter  
498 histories that were assigned to each class with high probability, and with lower probability.  
499 All encounter histories are provided in the supporting datafiles.

500

501 **Figure S4.** Frequencies of the probabilities with which individuals were assigned to the  
502 mixture model classes interpreted as (A and D) resident (R), (B and E) late migrant (LM) or (C  
503 and F) early migrant (EM) in (A-C) 2017-2018 and (D-F) 2018-2019.



504

505 **Table S6.** Illustrative examples of individual encounter histories (*i-xi*) from 2017-2018  
506 assigned with high probability ( $P_A \approx 1$ ) to the mixture classes interpreted as (A) resident (R), (B)  
507 late migrant (LM) and (C) early migrant (EM), or (D) assigned with lower probability. For each  
508 of the 19 occasions ( $S_1$ ,  $W_1$ - $W_{17}$  and  $S_2$ , representing the 17 winter occasions and the  
509 preceding and subsequent summers), 1 (grey shading) and 0 respectively denote that an  
510 individual was or was not locally resighted. Assignment probabilities ( $P_A$ ) are shown, where  
511  $P_A(R) + P_A(LM) + P_A(EM) = 1$ .

Occ.	$S_1$	$W_1$	$W_2$	$W_3$	$W_4$	$W_5$	$W_6$	$W_7$	$W_8$	$W_9$	$W_{10}$	$W_{11}$	$W_{12}$	$W_{13}$	$W_{14}$	$W_{15}$	$W_{16}$	$W_{17}$	$S_2$	$P_A(R)$	$P_A(LM)$	$P_A(EM)$
(A) <i>i</i>	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1	1.00	0.00	0.00
R <i>ii</i>	1	0	1	1	1	1	1	1	1	0	1	0	0	1	1	1	0	1	1	1.00	0.00	0.00
<i>iii</i>	1	0	0	1	1	1	1	1	1	0	1	0	0	1	0	1	1	1	1	1.00	0.00	0.00
(B) <i>iv</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0.00	1.00	0.00
LM <i>v</i>	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0.00	1.00	0.00
<i>vi</i>	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0.00	1.00	0.00
(C) <i>vii</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.00	0.00	1.00
EM <i>viii</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.00	0.01	0.99
<i>ix</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.00	0.00	1.00
(D) <i>x</i>	1	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	0	1	1	0.34	0.66	0.00
<i>xi</i>	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.00	0.82	0.18

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514 Testing whether patterns of change in individual migratory strategy between years differ from  
515 null expectation requires definition of an appropriate expectation. Table S7 shows the  
516 expected frequencies of two-year migratory strategies given different null models. The  
517 conclusion that more surviving individuals than expected retained the same strategy across  
518 both years, and that plasticity was directional, was consistent across all considered null  
519 models. It was also consistent given a further null expectation that all strategies occurred with  
520 an equal probability of 0.33 in 2018-2019 (data not shown).

521

522 **Table S7.** Frequencies of two-year migration strategies for 103 individual European shags  
523 included in analyses for both focal years, given (A) observed (probabilistic) strategies for both  
524 years, (B) a strategy randomly sampled (with replacement) from the observed strategies in  
525 both years, (C) observed (probabilistic) strategy for 2017-2018 and a strategy for 2018-2019  
526 randomly sampled with replacement from the strategies observed in 2018-2019, and (D)  
527 observed (probabilistic) strategy for 2017-2018 and a strategy for 2018-2019 randomly  
528 sampled with replacement from the strategies observed in 2017-2018. Block C matches the  
529 results presented in main Table 1. In addition, (E) shows the expected null frequencies of two-  
530 year strategies conditional on change, assuming that new strategies occur with equal  
531 probability of 0.5. Rows and columns index strategies assigned in 2017-2018 and 2018-2019  
532 respectively, with the mean frequency and 95% confidence interval across 10000 realisations.  
533 In A, dark grey shading (leading diagonal) identifies strategies where individuals were  
534 assigned to the same class in both years. Light grey and white identifies strategies where  
535 individuals became more and less migratory in 2018-2019 respectively. In B-D, italics show  
536 the mean and 95% confidence interval of the difference between the observed and  
537 randomised frequencies. Yellow and blue shading indicate two-year strategies that occurred  
538 more and less frequently than expected respectively, and green shading indicates strategies  
539 whose frequencies did not differ from overall expectation (but were more frequent than  
540 expected conditional on change). Comparison between A and E shows that individuals that  
541 changed strategy between years became more migratory than expected by chance (mean  $\chi^2$ :  
542 20.1, 95%CI: 15.5-24.8, all  $p < 0.005$  across 10000 realisations).

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				2018-2019		
				Resident	Late migrant	Early migrant
(A)	2017-2018	Resident	Obs.	22.4 (21,24)	19.1 (17,21)	3.1 (2,4)
		Late migrant	Obs.	2.0 (1,3)	17.3 (14,20)	8.7 (6,11)
		Early migrant	Obs.	0.0 (0,0)	4.1 (2,6)	26.3 (24,29)
(B)	2017-2018	Resident	Samp.	5.8 (2,11)	9.6 (4,16)	9.1 (4,15)
			Diff.	16.6 (12,21)	9.5 (3,15)	-6.0 (-12,-1)
		Late migrant	Samp.	9.6 (4,16)	15.9 (9,24)	14.9 (8,22)
			Diff.	-7.5 (-14,-2)	1.4 (-7,9)	-6.2 (-14,1)
		Early migrant	Samp.	9.1 (4,15)	14.9 (8-22)	14.1 (7,22)
			Diff.	-9.1 (-15,-4)	-10.8 (-18,-4)	12.2 (5,19)
(C)	2017-2018	Resident	Samp.	10.6 (5,17)	17.5 (11,24)	16.5 (10,23)
			Diff.	11.8 (6,16)	1.6 (-3,8)	-13.4 (-20,-7)
		Late migrant	Samp.	6.6 (2,11)	11.0 (6,16)	10.4 (5,16)
			Diff.	-4.6 (-9,0)	6.3 (1,12)	-1.7 (-7,4)
		Early migrant	Samp.	7.2 (3,12)	12.0 (7,17)	11.2 (6,17)
			Diff.	-7.2 (-12,-3)	-7.9 (-13,-2)	15.1 (10,20)
(D)	2017-2018	Resident	Samp.	10.6 (5,16)	17.4 (11,24)	16.5 (10,23)
			Diff.	11.8 (6,17)	1.6 (-5,8)	-13.4 (-20,-7)
		Late migrant	Samp.	6.6 (3,11)	11.0 (6,16)	10.4 (6,16)
			Diff.	-4.6 (-9,0)	6.3 (1,12)	-1.7 (-7,4)
		Early migrant	Samp.	7.2 (3,12)	11.9 (7,17)	11.3 (6,17)
			Diff.	-7.2 (-12,-3)	-7.8 (-13,-2)	15.1 (9,20)
		Early migrant	Samp.	2.1 (1,3.5)	2.1 (1,3.5)	-

546

(E)	2017-2018	Resident	Samp.	-	11.1 (10,12)	11.1 (10,12)
		Late migrant	Samp.	5.4 (4,6.5)	-	5.4 (4,6.5)
		Early migrant	Samp.	2.1 (1,3.5)	2.1 (1,3.5)	-

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552 **S4. Details of reproductive success analyses**

553

554 Raw distributions of annual reproductive success of individual European shags classified as  
555 most likely to be resident, late migrant and early migrant are shown in Figure S5. All focal  
556 individuals that were resighted in each summer were included in analyses. The only  
557 exceptions were 6 and 4 individuals in 2018 and 2019 respectively whose nests were  
558 unobservable (in sea-caves); these outcomes were assumed ‘missing completely at random’  
559 with respect to migratory strategy. Full results of models fitted to estimate variation in  
560 reproductive success as a function of inferred migratory strategy are shown in Table S8. The  
561 mean expected reproductive success for each possible two-year migratory strategy is shown  
562 in Table S9.

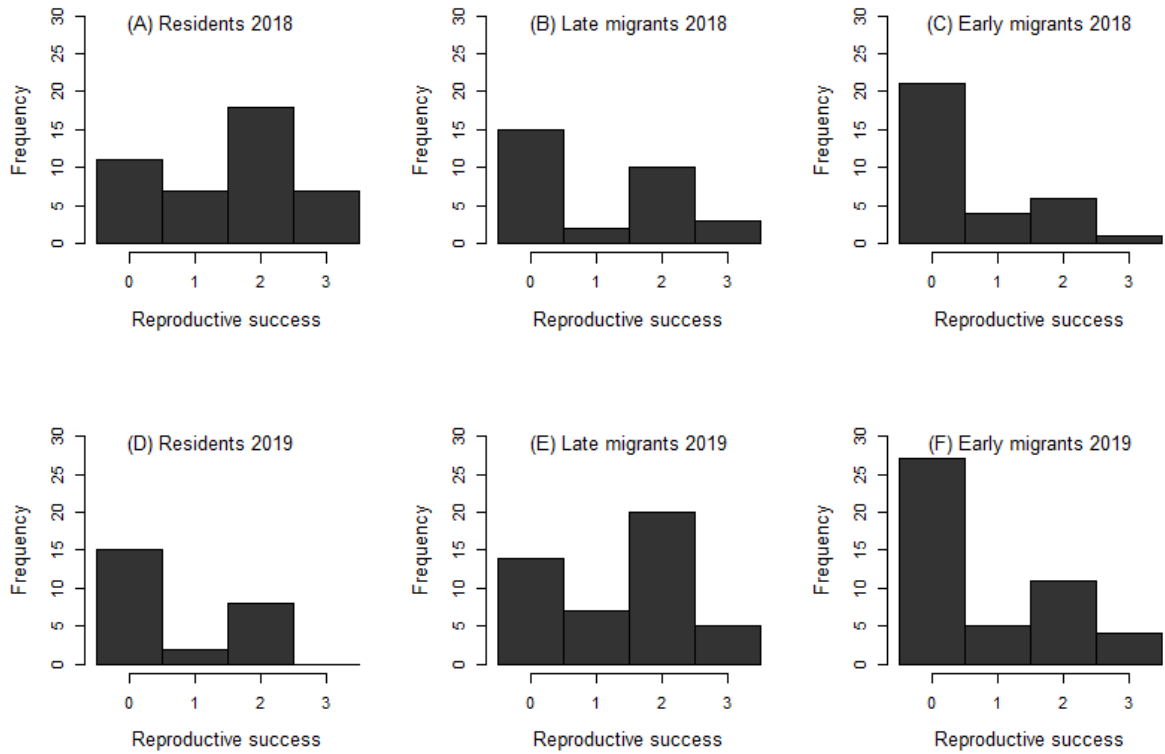
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567 **Figure S5.** Frequency distributions of reproductive success of shags classified as (A and D)  
568 resident, (B and E) late migrant and (C and F) early migrant in (A-C) 2018 and (D-F) 2019.



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580 **Table S8.** Summaries of models estimating effects of assigned class and hence migratory  
581 strategy (resident, late migrant or early migrant) and age category (young or older adults) on  
582 reproductive success in (A) 2018, (B) 2019 and (C) both years combined. Estimated effect sizes  
583 (on the latent log scale) and associated standard errors (SE) and probabilities (p) are  
584 presented.  $\chi^2$  is the overall test statistic comparing models (A,B) with and without effects of  
585 migratory strategy, or (C) with and without effects of the strategy by year interaction.  $\chi^2_{\text{Diff}}$  is  
586 the difference in  $\chi^2$  between models with observed and randomised reproductive success. All  
587 statistics are presented as means and 95% confidence intervals over 10000 realisations of  
588 each individual's probabilistic migratory strategy.  $P(\chi^2_{\text{Diff}} < 0)$  is the proportion of realisations  
589 where  $\chi^2_{\text{Diff}}$  was negative. Late migrant, early migrant and older age effects are estimated as  
590 contrasts from young residents. There was no evidence of a migratory strategy by age class  
591 interaction in either 2018 or 2019.

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<b>(A) 2018</b>	<b>Estimate</b>	<b>SE</b>	<b>p</b>
Resident	0.17 (0.10,0.25)	0.22 (0.21,0.23)	0.45 (0.26,0.66)
Late Migrant	-0.30 (-0.48,-0.15)	0.25 (0.24,0.27)	0.25 (0.06,0.55)
Early Migrant	-0.88 (-0.98,-0.75)	0.27 (0.25,0.27)	0.0014 (0.0005,0.0046)
Older age	0.31 (0.22,0.35)	0.23 (0.22,0.23)	0.18 (0.12,0.27)
$\chi^2$	13.6 (10.5,16.3)		0.0025 (0.0005,0.0087)
$\chi^2_{\text{Diff}}$	11.5 (5.3,15.4)		$P(\chi^2_{\text{Diff}} < 0)$ : 0.002
<b>(B) 2019</b>			
Resident	-0.84 (-0.92,-0.74)	0.32 (0.31,0.34)	0.011 (0.007,0.021)
Late Migrant	0.67 (0.55,0.78)	0.28 (0.26,0.29)	0.018 (0.007,0.044)
Early Migrant	0.20 (0.07,0.33)	0.30 (0.28,0.31)	0.50 (0.28,0.80)
Older age	0.61 (0.57,0.64)	0.24 (0.24,0.25)	0.015 (0.010,0.021)
$\chi^2$	9.3 (5.9,13.0)		0.019 (0.0021,0.065)
$\chi^2_{\text{Diff}}$	7.0 (0.45,11.9)		$P(\chi^2_{\text{Diff}} < 0)$ : 0.020
<b>(C) Both years</b>			
Resident	0.06 (-0.002,0.11)	0.19 (0.18,0.19)	0.76 (0.53,0.98)
Late Migrant	-0.25 (-0.42,-0.10)	0.24 (0.23,0.26)	0.32 (0.09,0.67)
Early Migrant	-0.87 (-0.96,-0.75)	0.27 (0.25,0.27)	0.002 (0.0005,0.004)
Year	-0.76 (-0.85,-0.66)	0.28 (0.26,0.29)	0.007 (0.003,0.014)
Late Migrant:Year	0.92 (0.72,1.12)	0.37 (0.35,0.38)	0.016 (0.003,0.045)
Early Migrant:Year	1.06 (0.88,1.23)	0.40 (0.38,0.41)	0.010 (0.003,0.025)
Older age	0.45 (0.42,0.48)	0.16 (0.16,0.17)	0.007 (0.004,0.012)
$\chi^2$	10.5 (8.1,13.2)		0.009 (0.002,0.024)
$\chi^2_{\text{Diff}}$	8.3 (2.2,12.2)		$P(\chi^2_{\text{Diff}} < 0)$ : 0.009

607 **Table S9.** Expected mean reproductive success ( $\pm 1SE$ ) for two-year migratory strategies  
 608 comprising combinations of resident (R), late migrant (LM) and early migrant (EM) for (A)  
 609 young (aged 3-4 years) adults and (B) older (aged 5+ years) adults. Rows and columns identify  
 610 strategies in 2017-2018 and 2018-2019 respectively. Expectations are simply calculated as the  
 611 means of predicted strategy-specific reproductive success in 2017-2018 and 2018-2019 and  
 612 are consequently cross-sectional rather than individual-based. Standard errors are calculated  
 613 using the Delta method. Darker colours highlight strategies with higher expected reproductive  
 614 success. Thick borders highlight the most frequently observed two-year strategies (Table 1).

615

		<b>(A) Young adults</b>			<b>(B) Older adults</b>		
		<b>2018-2019</b>			<b>2018-2019</b>		
		<b>R</b>	<b>LM</b>	<b>EM</b>	<b>R</b>	<b>LM</b>	<b>EM</b>
<b>2017-2018</b>	<b>R</b>	0.78 $\pm$ 0.12	1.01 $\pm$ 0.13	0.83 $\pm$ 0.12	1.22 $\pm$ 0.14	1.58 $\pm$ 0.15	1.30 $\pm$ 0.14
	<b>LM</b>	0.66 $\pm$ 0.11	0.89 $\pm$ 0.12	0.71 $\pm$ 0.11	1.03 $\pm$ 0.17	1.40 $\pm$ 0.17	1.11 $\pm$ 0.16
	<b>EM</b>	0.47 $\pm$ 0.09	0.70 $\pm$ 0.11	0.52 $\pm$ 0.09	0.74 $\pm$ 0.13	1.10 $\pm$ 0.13	0.82 $\pm$ 0.12

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625 **Age and sex effects**

626 The dataset included individuals that had been ringed as chicks and hence were of exact  
627 known age, and individuals that had been ringed as full breeding adults and hence were  $\geq 3$   
628 years old at first capture (Table S1). Since local ringing commenced in 2009 and shags regularly  
629 live up to  $\sim 15+$  years, the available data do not yet cover the full likely age range, or hence  
630 allow detailed analyses of age-specific variation in migratory strategy or reproductive success.  
631 However, to capture coarse age structure, and thereby examine whether observed  
632 relationships between reproductive success and migratory strategy could potentially be  
633 confounded by age, we classified all focal individuals in each year as young adults (aged 3-4  
634 years) or older adults (aged 5+ years). This classification was designed to capture expected  
635 lower reproductive success in young adults, as was apparent in exploratory analyses of a  
636 larger dataset on shags breeding on Isle of May, Scotland.

637

638 Classification was straightforward and accurate for known-age individuals ringed as chicks. All  
639 individuals ringed as adults were classified as older adults. This classification is correct for  
640 individuals observed  $\geq 2$  years after ringing (i.e. ringed before 2017 and 2018 for analyses of  
641 reproductive success in 2018 and 2019 respectively), but could be incorrect for some  
642 individuals observed the year after ringing (which could be aged 4 years). In practice, such  
643 mis-categorisation is likely to be infrequent, since individuals ringed as adults are most likely  
644 to have been  $>3$  years old at capture. Conclusions were unchanged when analyses of age  
645 effects were repeated after excluding the few individuals that could potentially have been  
646 misclassified. Note that no individuals were included in analyses of reproductive success in  
647 their ringing year, since their migratory strategy in the preceding winter is unknown.

648

649 Individuals were assigned as male or female based on call during ringing of adults or  
650 subsequent field encounters (following [15]). There were no conflicts across 20 instances  
651 where individuals were independently assigned twice. When a known-sex individual was  
652 paired with another ringed individual that individual was assigned as the opposite sex. This  
653 process yielded totals of 56 assigned-sex focal individuals in both 2018 and 2019, comprising  
654 21 females and 35 males in both years. This slight bias towards assigned males likely arises  
655 because male calls are more audible.

656

657 These additional analyses showed that the frequencies with which individuals were assigned  
658 as resident, late migrant or early migrant differed between young and older age classes in  
659 2017-2018. Here, late migrants were more likely to be young, and less likely to be older, than  
660 expected by chance (Table S10). However, there was no evidence of a similar pattern in 2018-  
661 2019 (Table S10), meaning that there was little evident age-specific variation in migratory  
662 strategy over the whole dataset. Similar patterns were evident when analyses were restricted  
663 to individuals whose age category was known with certainty. Sex-specific frequencies of the  
664 different migratory strategies also did not differ from random expectation in either year  
665 (Table S10).

666

667 There was no evidence that mated pairs systematically stay together over winter. For 10 and  
668 7 pairs observed in 2018 and 2019 where both adults were colour-ringed, both adults were  
669 assigned to the same most-likely class in only 1 and 2 instances respectively (always both  
670 assigned as early migrants).

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673 **Table S10.** Frequencies of assigned migration strategies for (A and B) young versus older  
674 individuals and (C and D) females versus males in (A and C) 2017-2018 and (B and D) 2018-  
675 2019, and  $\chi^2$  test statistics and associated p values. Mean statistics and 95% confidence  
676 intervals calculated across 10000 realisations of each individual's probabilistic migratory  
677 strategy are shown.

					$\chi^2$ test statistic
		Residents	Late migrants	Early migrants	p value
<b>(A) 2017-2018</b>	<b>Young</b>	11.2 (10,12)	18.5 (16,21)	11.3 (10,13)	$\chi^2$ : 11.8 (8.1,16.1)
	<b>Older</b>	32.8 (32,34)	10.1 (8,12)	21.1 (20,22)	p: 0.005 (0.001,0.02)
<b>(B) 2018-2019</b>	<b>Young</b>	5.0 (5,5)	14.1 (12,15)	14.9 (14,17)	$\chi^2$ : 1.4 (0.9,2.2)
	<b>Older</b>	20.2 (19,22)	32.6 (30,36)	31.2 (29,34)	p: 0.52 (0.34,0.70)
<b>(C) 2017-2018</b>	<b>Female</b>	11.4 (11,12)	3.4 (2,4)	6.1 (6,7)	$\chi^2$ : 1.2 (0.5,2.2)
	<b>Male</b>	14.2 (14,15)	7.8 (6,9)	13.0 (12,14)	p: 0.61 (0.38,0.83)
<b>(D) 2018-2019</b>	<b>Female</b>	4.7 (4,5)	7.7 (6,9)	8.6 (7,10)	$\chi^2$ : 0.5 (0.1,1.5)
	<b>Male</b>	6.2 (6,7)	15.3 (13,17)	13.5 (12,15)	p: 0.83 (0.53,1.00)

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## 687 **S5. 'Threshold model' for partial migration**

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689 The 'threshold model' of quantitative genetics proposes that discrete phenotypes, such as  
690 residence versus migration, are expressed as a function of a continuous underlying 'liability',  
691 which is best viewed as a compound latent trait that is influenced by some combination of  
692 genetic and permanent and/or temporary environmental effects [16]. Different phenotypes  
693 are expressed when liability values are above versus below some threshold(s). The existence  
694 of variation in liability within a population (whether genetic and/or environmental) then  
695 generates phenotypic variation. In the current context, variation in liability for seasonal  
696 migration can generate partial migration [17].

697

698 The threshold model can rationalise the occurrence of different annual 'migratory strategies',  
699 such as early migration, late migration and residence, and hence within-year phenotypic  
700 plasticity. Conceptually, early migrants comprise individuals whose liabilities exceed the  
701 migration threshold in early autumn, late migrants comprise individuals whose liabilities  
702 exceed the threshold later in autumn, and residents comprise individuals whose liabilities  
703 never exceed the threshold (Figure S5A). Such among-individual variation could arise, for  
704 example, because different individuals have different physiological responses to changing  
705 daylength, or to seasonally changing environmental conditions.

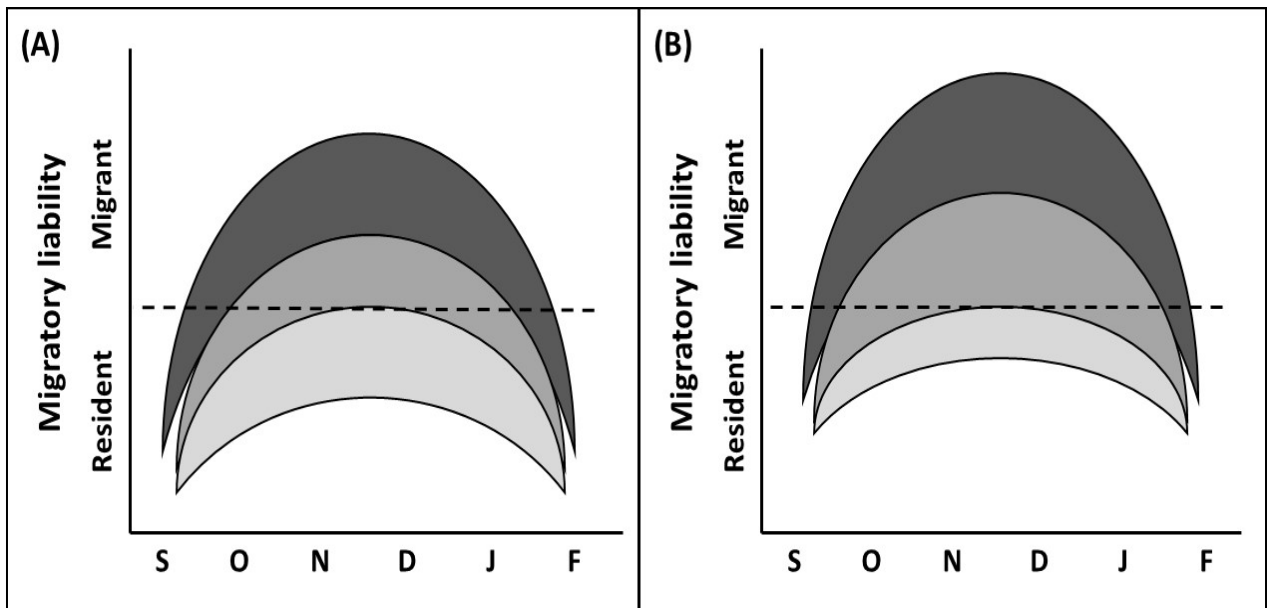
706

707 Further, the threshold model can rationalise how the relative frequencies of different  
708 migratory strategies could change between years (i.e. the form of between-year phenotypic  
709 plasticity). For example, poorer local environmental conditions in one year compared to the  
710 previous year could increase liability values across all or most population members. This

711 would generate increased proportions of early and late migrants and a decreased proportion  
712 of residents (Figure S5). Moreover, if there are permanent individual effects on liability (either  
713 genetic or environmental, the latter representing developmental plasticity and/or  
714 subsequent phenotypic canalisation), individual changes would be directional, such that  
715 residents become late migrants and late migrants become early migrants, but early migrants  
716 do not become residents. These changes qualitatively match those observed in the European  
717 shag system.

718

719 **Figure S5.** Illustration of hypothetical forms of variation in individual liability for seasonal  
720 migration versus residence ('migratory liability') given (A) relatively good and (B) relatively  
721 poor local (i.e. breeding area) environmental conditions. Dark grey, mid grey and light grey  
722 bands illustrate potential patterns of within-winter temporal variation in migratory liability  
723 spanning September-February (sequential months abbreviated S, O, N, D, J and F) in relation  
724 to a threshold (dashed line). Individuals whose liability values exceed the threshold at  
725 different times become early (dark grey) or late (mid grey) migrants, while individuals whose  
726 liability values remain less than the threshold stay resident (light grey). Given poorer local  
727 environmental conditions all liabilities are increased, yielding increased proportions of early  
728 and late migrants and a decreased proportion of residents in B compared to A (illustrated by  
729 wider dark and mid grey bands, and a narrower light grey band). Note that the direction of  
730 liability that leads to migration is arbitrary, and among-year variation could be similarly  
731 conceptualised as a change in threshold rather than a change in liability. The depicted  
732 liabilities are hypothetical and designed to illustrate a general concept; in reality they could  
733 be different shapes, and are not necessarily symmetrical.



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