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

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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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Abstract

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

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

1. Introduction

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

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

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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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2. Methods

(a) Overall approach

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

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

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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 ≥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 ≥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 1st–Feb 28th)

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. ≥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 1st–Feb 18th through each winter. This is the maximum number (i.e.

191   shortest duration) of equal-duration occasions for which there was ≥1 local positive survey

192   day within each occasion in both winters. Later (≥Feb 19th) 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 (ΔAICc≥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 (ϕ_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 ≥ 0.96 respectively, and hence $\phi_I \geq 0.995$ and ≥ 0.998 for

222   each inter-occasion interval ($\phi_I = \phi_A^{1/18}$ given 19 occasions and 18 intervals, assuming time-

223   independent mortality). Consequently, we fitted constant ϕ_I 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 χ^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 χ^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 χ^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 χ^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 (χ^2_{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 χ^2_{Rand}. The statistic $\chi^2_{Diff}=\chi^2_{Obs}-\chi^2_{Rand}$ 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 ($P(\chi^2_{Diff}<0)$) 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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3. Results

(a) Migratory strategies

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

339   migrants and early migrants were 0.42±0.05, 0.26±0.04 and 0.32±0.06 respectively in 2017-

340   2018, and 0.22±0.04, 0.39±0.05 and 0.39±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 χ^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 χ^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 (±1SD) across all observed focal individuals was 1.1±1.1 and

364   1.0±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).

386

387

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.

404

405

(a) Migratory strategy

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

Our analyses also demonstrate substantial within-individual variation in non-breeding season location within years, and in defined migratory strategy between years. Defining 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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Table 1. Frequencies of inferred two-year migratory strategies for 103 European shags included in analyses for both focal years, given (A) mixture model-assigned strategies for both years, and (B) model-assigned strategy for 2017-2018 and a randomly resampled strategy for 2018-2019 (full details, Supplementary Material S3). Rows and columns index strategies in 2017-2018 and 2018-2019 respectively, showing the mean frequency and 95% confidence interval across 10000 realisations. In (A), dark grey shading (leading diagonal) identifies individuals assigned to the same strategy in both years. Light grey and white identify individuals that became more and less migratory in 2018-2019 respectively. In (B), dark and light grey indicate two-year strategies that occurred more and less frequently than expected respectively (compared to frequencies in A). White indicates strategies whose frequencies did not differ from overall expectation, but occurred more frequently than expected conditional on change (Supplementary Material S3). In addition, 17 new individuals entered the dataset in 2018-2019 (and hence do not contribute to estimates of between-year individual 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
(A) 2019	**R → LM**	19.0	1.32	1.01		
		(17,21)	(1.21,1.42)	(0.95,1.08)	154.4	0.71
	LM → LM	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) 2018	**R → R**	19.3	1.74	0.88		
		(18,21)	(1.65,1.80)	(0.86,0.96)	144.7	0.36
	R → LM	18.2	1.35	1.21	(123.0,166.5)	(0.11,0.74)
		(16,20)	(1.21,1.50)	(1.15,1.26)		
	LM → LM	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 ≥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**

2

3   **Among-individual and within-individual variation in seasonal migration**

4   **covaries with subsequent reproductive success in a partially-migratory bird**

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6   Jane M. Reid, Moray Souter, Sarah R. Fenn, Paul Acker, Ana Payo-Payo, Sarah J. Burthe, Sarah

7   Wanless & Francis Daunt

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9   **Proceedings of the Royal Society B**

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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].

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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.

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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.

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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.

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79   **(A)**

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81   **(B)**

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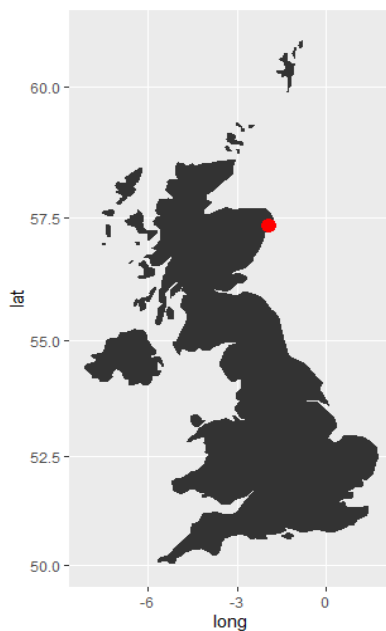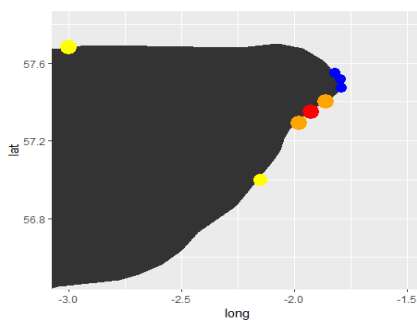
Figure S2. Frequency distributions of the number of times that an adult colour-ringed shag

was resighted at Bullers of Buchan during the breeding season in (A) 2017, (B) 2018 and (C)

2019. Y-axes show the numbers of individuals. Mean numbers of resightings per individual

were 4.1, 4.7 and 5.6 in 2017-2019 respectively, and variances were 4.1, 4.4 and 5.8

respectively. Consequently, there was therefore little or no overdispersion compared to

expectation given a Poisson distribution of resightings.
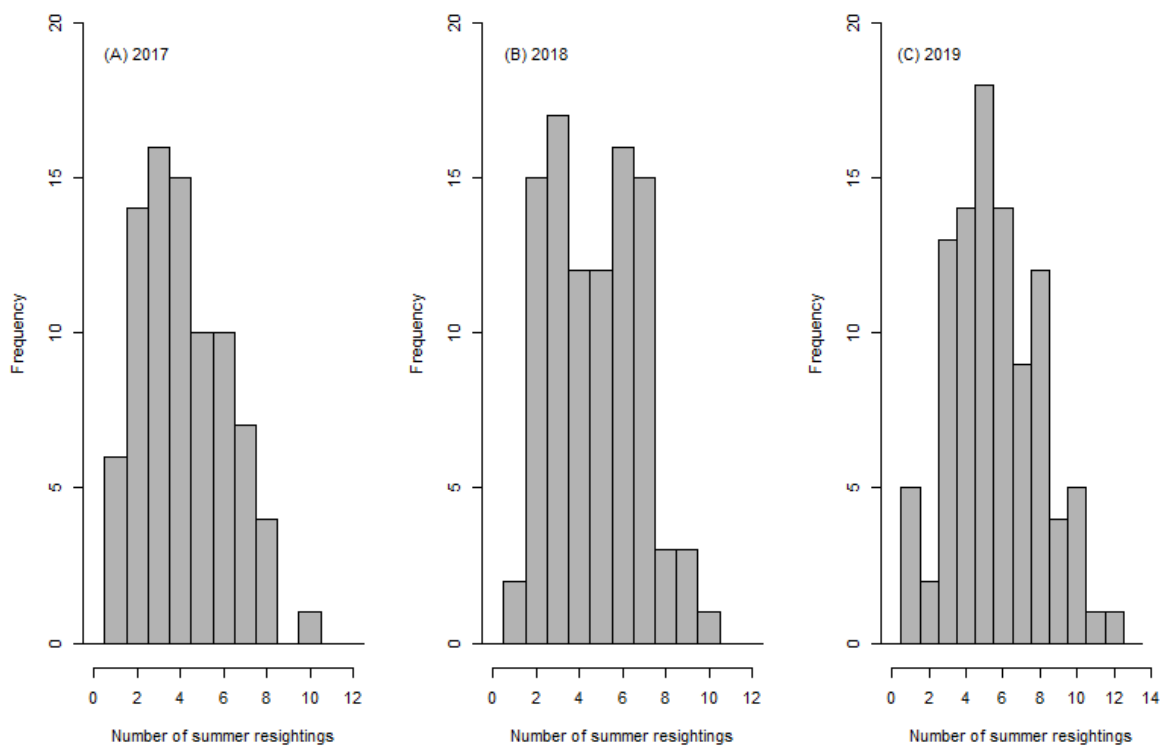
96   Winter surveys for colour-ringed shags were also carried out at numerous other sites along

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.
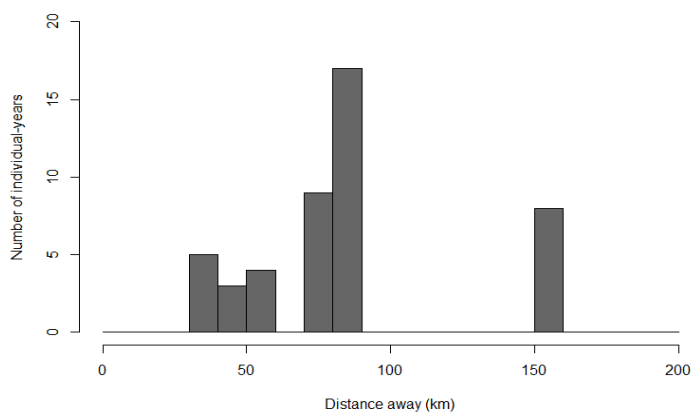
114

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 (± 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 ≥ 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.

	2017-2018	**2018-2019**
(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±0.05, 95%CI: 0.33,0.52 LM: 0.26±0.04, 95%CI: 0.19,0.35 EM: 0.32±0.05, 95%CI: 0.22,0.41	R: 0.22±0.04, 95%CI: 0.16,0.30 LM: 0.39±0.05, 95%CI: 0.30,0.50 EM: 0.39±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

S2. Details of capture-mark-recapture mixture models

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

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

		2017-2018				2018-2019			
		Deviance	Par.	AICc	ΔAICc	Deviance	Par.	AICc	ΔAICc
(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)	**Model i**	**1871.3**	**31**	**1935.4**	**-**	**1776.4**	**31**	**1840.9**	**-**
	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

11

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.	S₁	W₁	W₂	W₃	W₄	W₅	W₆	W₇	W₈	W₉	W₁₀	W₁₁	W₁₂	W₁₃	W₁₄	W₁₅	W₁₆	W₁₇	S₂
R	1	r_1	r_2	r_3	r_4	r_5	r_6	r_7	r_8	r_9	r_{10}	r_{11}	r_{12}	r_{13}	r_{14}	r_{15}	r_{16}	r_{17}	s_2
LM	1	r_1	r_2	r_3	l_4	l_5	l_6	l_7	l_8	l_9	l_9	l_9	l_9	l_9	l_9	l_{15}	l_{15}	l_{15}	s_2
EM	1	e_1	e_1	e_1	e_4	e_4	e_4	e_4	e_4	e_4	e_4	e_4	e_4	e_4	e_4	e_{15}	e_{15}	e_{15}	s_2

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 19th–28th) 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 (ΔAICc>>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 ϕ_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 ϕ_l was slightly overestimated and S_2 slightly underestimated. These

264　small biases probably arose because ϕ_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 ϕ_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 (≥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 ϕ_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 ĉ 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) ĉ.

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 ĉ	14.3	13.3
	Mean simulated ĉ	12.8	11.6
	Observed / mean simulated ĉ	1.12	1.15
(B)	Median ĉ	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:

π	π	*

350

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

Ψ	_	_	*
_	ψ	_	*
_	_	ψ	*
_	_	_	*

352

353 Event probabilities:

*	β
*	β
*	β
*	_

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
	10000000000000000011	0.000	0.002	0.998	10000000000000000011	0.000	0.003	0.997	0.000	0.001	0.001
	10010000000000000001	0.000	0.014	0.986	10010000000000000001	0.000	0.017	0.983	0.000	0.003	0.003
	10010100000000000001	0.000	0.821	0.179	10010100000000000001	0.000	0.824	0.176	0.000	0.003	0.003
	10100000000000000001	0.000	0.001	0.999	10100000000000000001	0.000	0.006	0.994	0.000	0.005	0.005
	11000000000000000001	0.000	0.005	0.995	11000000000000000001	0.000	0.003	0.997	0.000	0.002	0.002
	11010000000000000001	0.000	0.134	0.866	11010000000000000001	0.000	0.044	0.956	0.000	0.090	0.090
	11010100000000000001	0.000	0.980	0.020	11010100000000000001	0.000	0.923	0.077	0.000	0.057	0.057
	11011011100000000001	0.000	1.000	0.000	11011011100000000001	0.001	0.999	0.000	0.000	0.000	0.000
	11111110000000000001	0.000	1.000	0.000	11111110000000000001	0.000	1.000	0.000	0.000	0.000	0.000
(B)	11111111111110011001	1.000	0.000	0.000	11111111110110101111	1.000	0.000	0.000	0.000	0.000	0.000
	11111111111101010111	1.000	0.000	0.000	11111111111101001011	1.000	0.000	0.000	0.000	0.000	0.000
	11111110011101111001	1.000	0.000	0.000	11111111110100101011	1.000	0.000	0.000	0.000	0.000	0.000
	11111101101101110111	1.000	0.000	0.000	11111111110100111011	1.000	0.000	0.000	0.000	0.000	0.000
	11011111101000111001	0.980	0.020	0.000	11011111011000101011	0.999	0.001	0.000	0.019	0.019	0.000

It would in principle be possible to fit a single CMR mixture model to individuals' two-year encounter histories. By allowing class (i.e. state) transitions in the middle summer, the probability of changing class between years could then be estimated (at the population level). However, such two-year models would not necessarily define the same biologically interpretable mixture classes as the single-year models, and individual class assignment probabilities cannot be so easily estimated when individuals can change class. Such additional analyses therefore provide no major benefit given our current aims. Indeed, since no parameter values are shared between the two years and most individuals were assigned to one class in each year with very high probability, the frequencies of individual class transitions can be estimated *post hoc*, while propagating the small remaining uncertainty (see main text). However, CMR mixture models that directly consider multiple years may be appropriate for 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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S3. Details of class assignments

Figure S4 summarises the probabilities with which individual shags were assigned to the three

mixture model classes interpreted as residents, late migrants and early migrants in 2017-2018

and 2018-2019, further illustrating that individuals could be assigned to any of the three

strategies with high probabilities. Table S6 provides examples of individual encounter

histories that were assigned to each class with high probability, and with lower probability.

All encounter histories are provided in the supporting datafiles.

Figure S4. Frequencies of the probabilities with which individuals were assigned to the

mixture model classes interpreted as (A and D) resident (R), (B and E) late migrant (LM) or (C

and F) early migrant (EM) in (A-C) 2017-2018 and (D-F) 2018-2019.
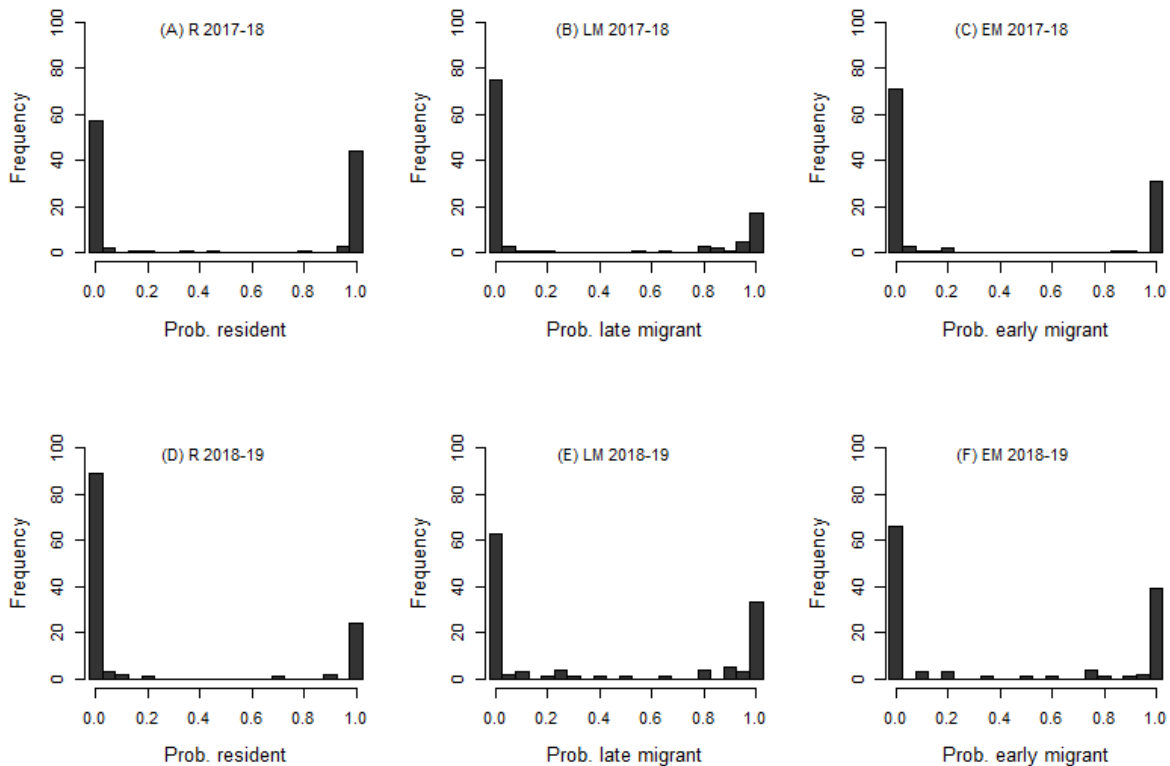
Table S6. Illustrative examples of individual encounter histories (*i-xi*) from 2017-2018 assigned with high probability (P$_A$≈1) to the mixture classes interpreted as (A) resident (R), (B) late migrant (LM) and (C) early migrant (EM), or (D) assigned with lower probability. For each of the 19 occasions (S$_1$, W$_1$-W$_{17}$ and S$_2$, representing the 17 winter occasions and the preceding and subsequent summers), 1 (grey shading) and 0 respectively denote that an individual was or was not locally resighted. Assignment probabilities (P$_A$) are shown, where 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*	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	*ii*	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
	iii	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)	*iv*	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	*v*	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
	vi	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)	*vii*	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	*viii*	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
	ix	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)	*x*	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
	xi	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

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

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 χ^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)	-

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(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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S4. Details of reproductive success analyses

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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
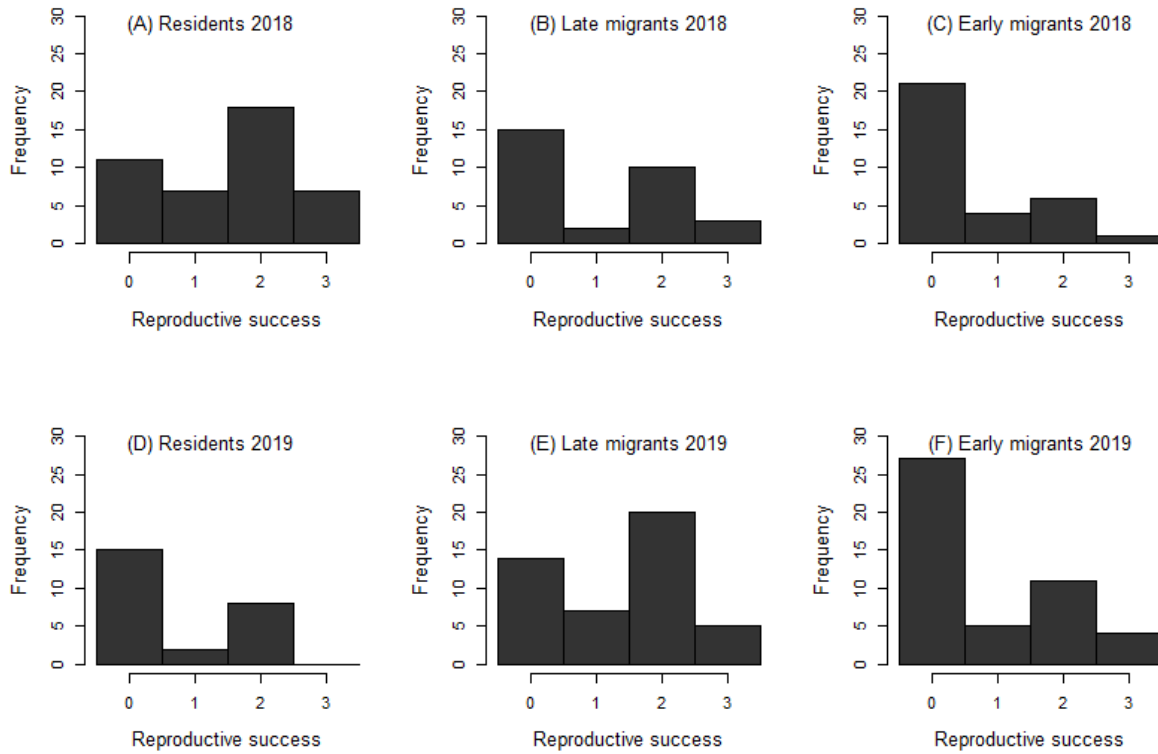
562 in Table S9.

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Figure S5. Frequency distributions of reproductive success of shags classified as (A and D)

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. χ^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. χ^2_{Diff} is

586   the difference in χ^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. $P(\chi^2_{Diff}<0)$ is the proportion of realisations

589   where χ^2_{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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(A) 2018	Estimate	SE	p
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)
χ^2	13.6 (10.5,16.3)		0.0025 (0.0005,0.0087)
χ^2_{Diff}	11.5 (5.3,15.4)		P(χ^2_{Diff} < 0): 0.002
(B) 2019			
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)
χ^2	9.3 (5.9,13.0)		0.019 (0.0021,0.065)
χ^2_{Diff}	7.0 (0.45,11.9)		P(χ^2_{Diff} < 0): 0.020
(C) Both years			
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)
χ^2	10.5 (8.1,13.2)		0.009 (0.002,0.024)
χ^2_{Diff}	8.3 (2.2,12.2)		P(χ^2_{Diff} < 0): 0.009

Table S9. Expected mean reproductive success (±1SE) for two-year migratory strategies

comprising combinations of resident (R), late migrant (LM) and early migrant (EM) for (A)

young (aged 3-4 years) adults and (B) older (aged 5+ years) adults. Rows and columns identify

strategies in 2017-2018 and 2018-2019 respectively. Expectations are simply calculated as the

means of predicted strategy-specific reproductive success in 2017-2018 and 2018-2019 and

are consequently cross-sectional rather than individual-based. Standard errors are calculated

using the Delta method. Darker colours highlight strategies with higher expected reproductive

success. Thick borders highlight the most frequently observed two-year strategies (Table 1).

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

Age and sex effects

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

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

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).

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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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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 χ^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.

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

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S5. 'Threshold model' for partial migration

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

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

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

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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.

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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.
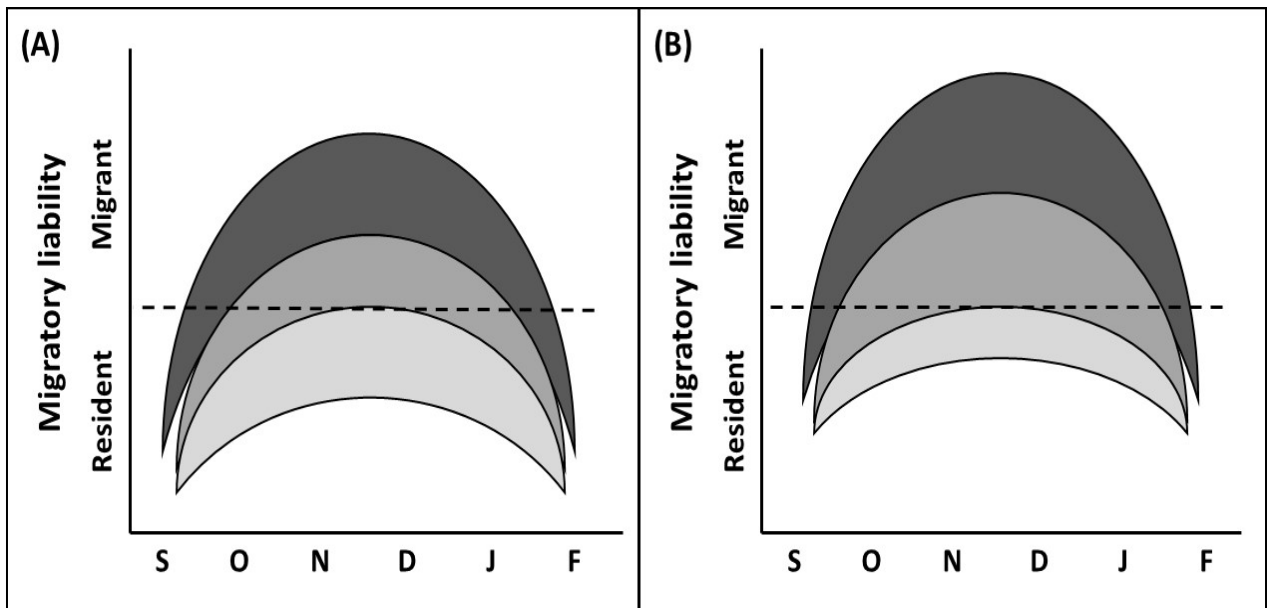
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