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1 **Reproductive performance of resident and migrant males,**
2 **females and pairs in a partially migratory bird**

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20 *Running headline: Male & female partial migration & reproduction*

21 **Summary**

- 22 1. Quantifying among-individual variation in life-history strategies, and associated
23 variation in reproductive performance and resulting demographic structure, is key to
24 understanding and predicting population dynamics and life-history evolution. Partial
25 migration, where populations comprise a mixture of resident and seasonally-migrant
26 individuals, constitutes a dimension of life-history variation that could be associated
27 with substantial variation in reproductive performance. However, such variation has
28 rarely been quantified due to the challenge of measuring reproduction and migration
29 across a sufficient number of seasonally-mobile males and females.
- 30 2. We used intensive winter (non-breeding season) resightings of colour-ringed adult
31 European shags (*Phalacrocorax aristotelis*) from a known breeding colony to
32 identify resident and migrant individuals. We tested whether two aspects of annual
33 reproductive performance, brood hatch date and breeding success, differed between
34 resident and migrant males, females and breeding pairs observed across three
35 consecutive winters and breeding seasons.
- 36 3. The sex ratios of observed resident and migrant shags did not significantly differ
37 from each other or from 1:1, suggesting that both sexes are partially migratory and
38 that migration was not sex-biased across surveyed areas.
- 39 4. Individual resident males and females hatched their broods 6 days earlier and fledged
40 0.2 more chicks per year than migrant males and females on average. Resident
41 individuals of both sexes therefore had higher breeding success than migrants.
- 42 5. Hatch date and breeding success also varied with a pair's joint migratory strategy
43 such that resident-resident pairs hatched their broods 12 days earlier than migrant-
44 migrant pairs, and fledged 0.7 more chicks per year on average. However, there was
45 no evidence of assortative pairing with respect to migratory strategy: observed

46 frequencies of migrant-migrant and resident-resident pairs did not differ from those
47 expected given random pairing.

48 6. These data demonstrate substantial variation in two key aspects of reproductive
49 performance associated with the migratory strategies of males, females and breeding
50 pairs within a partially migratory population. These patterns could reflect direct
51 and/or indirect mechanisms, but imply that individual variation in migratory
52 strategy, and variation in pairing among residents and migrants, could influence
53 selection on migration and drive complex population and evolutionary dynamics.

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67 **Key-words:** Carry-over effects; European shag; demography; fitness; phenology;
68 population structure; seabird.

69 **Introduction**

70 Quantifying variation in life-history strategies among different categories of individuals
71 within any population, and associated variation in individual fitness and population-
72 level demographic structure, is key to understanding and predicting population and
73 evolutionary dynamics (Vindenes, Engen & Sæther 2008; Gillis *et al.* 2008; Reid *et al.*
74 2010). Partial migration, where some individuals within a population migrate between
75 locations across seasons while other individuals from the same population remain
76 resident at a single location, constitutes a major form of life-history variation that occurs
77 widely, including in many species of fish, amphibians, mammals and birds (e.g. Boyle
78 2008; Brodersen *et al.* 2008; Grayson & Wilbur 2009; Chapman *et al.* 2011;
79 Hebblewhite & Merrill 2011; Hegemann, Marra & Tieleman 2015). Such among-
80 individual variation in ‘migratory strategy’, most simply defined as migrant versus
81 resident (e.g. Gillis *et al.* 2008; Bai, Severinghaus & Philippart 2012), results in
82 individuals that co-exist during either the breeding or non-breeding season experiencing
83 geographically and ecologically disparate environments during the other season (Boyle
84 2008; Grayson & McLeod 2009; Chapman *et al.* 2011). Among-individual variation in
85 migratory strategy might therefore be associated with among-individual variation in
86 key fitness components (i.e. survival and/or reproductive performance), creating
87 substantial structured variation in demography (Kokko 2011; Gillis *et al.* 2008).

88 Such demographic structure could directly affect population dynamics, and also
89 create selection on migration. If migratory strategy were to some degree repeatable
90 within individuals across years and associated with differences in survival, selection
91 could cause the frequencies of migrants and residents to change across years and age-
92 classes within generations (i.e. ‘selective disappearance’, e.g. van de Pol & Verhulst
93 2006). Furthermore, if migratory strategy were heritable, selection would drive

94 evolutionary change across generations (Lundberg 1987; Kaitala, Kaitala & Lundberg
95 1993; Pulido 2007; Boyle 2008). Selection and the resulting demographic and
96 evolutionary responses could be direct if migratory strategy itself affects fitness
97 components, or indirect if individual migratory strategy and fitness components are
98 both intrinsically affected by some other temporary or permanent individual trait or
99 state. Resulting structured changes in the frequencies of migrants versus residents
100 across years and generations could then affect population-wide reproduction, survival
101 and spatial structure (Adriaensen & Dhondt 1990; Sanz-Aguilar *et al.* 2012), thereby
102 further altering overall population growth rate and spatio-temporal dynamics.

103 In sexually reproducing species, such population dynamic and evolutionary
104 consequences of partial migration will also depend on the degree to which females
105 versus males migrate or remain resident, and on the degree to which relationships
106 between migratory strategy and key fitness components are consistent or different in
107 the two sexes. Partial migration can be substantially sex-biased with one sex being
108 much more likely to migrate than the other, as observed in newts (Bloch & Grayson
109 2010; Grayson & McLeod 2009) and some birds (Boyle 2008; Bai, Severinghaus &
110 Philippart 2012; Table S1). In other systems, including some birds and mammals, both
111 sexes are partially migratory to similar degrees (Warriner *et al.* 1986; Hebblewhite &
112 Merrill 2011; Table S1). However, relationships between fitness components and
113 migratory strategy could still be sex-specific in such systems, for example stemming
114 from sexual dimorphism in body size and associated tolerance to environmental
115 harshness, or from sex-specific determinants of reproductive success that might depend
116 on migration, such as territory acquisition or body condition (Jahn *et al.* 2010; Chapman
117 *et al.* 2011; Bai, Severinghaus & Philippart 2012).

118 Furthermore, in populations where both sexes are partially migratory,
119 reproductive performance might vary with the combined migratory strategy of a
120 breeding pair, rather than with the strategies of females and males independently (e.g.
121 Brommer *et al.* 2015). A key assumption of many models of partial migration is that
122 individuals that remain resident in breeding areas can pre-emptively occupy high
123 quality territories before migrant individuals return, and consequently attain higher
124 reproductive success (Griswold, Taylor & Norris 2010; Kokko 2011). However, the
125 potential reproductive advantage that one pair member attains by remaining resident
126 might be reduced if its mate is a migrant and returns late. Resident-resident pairs may
127 therefore have substantially higher reproductive success than migrant-migrant pairs or
128 pairs with mixed migratory strategies, depending on system- and sex-specific costs,
129 benefits and underlying causes of migration. Assortative pairing with respect to
130 migratory strategy might also arise. In particular, frequencies of resident-resident and
131 migrant-migrant pairs might exceed those expected given random pairing if individuals
132 are more likely to form pairs with those that arrive at similar times (e.g. Gunnarsson *et*
133 *al.* 2004; Anderson *et al.* 2015). Such assortative pairing could increase the population-
134 wide variance in reproductive success, increase selection on migration (Pulido 2007),
135 and even facilitate sympatric reproductive isolation (Bearhop *et al.* 2005; Rolshausen
136 *et al.* 2013).

137 Understanding the population dynamic and evolutionary consequences of
138 partial migration therefore requires studies that quantify relationships between
139 individual male, female and pair migratory strategies and reproductive performance.
140 However, collecting sufficient data is challenging, requiring numerous individuals of
141 both sexes to be tracked across different seasons and geographical locations in order to
142 record migratory strategy and reproductive performance. To date, relatively few studies

143 have related aspects of reproductive performance to individual migratory strategy in
144 partially migratory systems, and these studies report mixed results (Table S1).
145 Residents can show better reproductive performance than migrants (Warriner *et al.*
146 1986; Adriansen & Dhondt 1990; Anderson *et al.* 2015), as commonly assumed by
147 evolutionary models of partial migration (Kaitala, Kaitala & Lundberg 1993; Kokko
148 2011). However, this pattern is not consistent across all systems or aspects of
149 reproductive performance, such as breeding probability and timing, number of
150 offspring, offspring condition and juvenile survival (e.g. Grayson & McLeod 2009;
151 Hebblewhite & Merrill 2011; Table S1).

152 The few studies that have investigated relationships between individual
153 migratory strategy and reproductive performance in both sexes within a single
154 population show that effects can be sex-specific (Table S1). For example, resident
155 males paired earlier than migrant males in snowy plovers (*Charadrius nivosus*) but
156 there was no such relationship for females (Warriner *et al.* 1986). Conversely, resident
157 female Lanyu scops owls (*Otus elegans*) were more likely to nest successfully than
158 migrant females but there was no such relationship for males (Bai, Severinghaus &
159 Philippart 2012). Only one study has quantified relationships between pair (rather than
160 individual) migratory strategy and reproductive performance in a partially migratory
161 population. Warkentin, James & Oliphant (1990) showed that the annual breeding
162 success of ‘resident male, migrant female’ merlin (*Falco columbarius*) pairs exceeded
163 that of ‘resident female, migrant male’ pairs ($4.8 \pm 0.1SE$ versus $4.3 \pm 0.2SE$ chicks), and
164 was substantially higher than ‘migrant-migrant’ pairs ($4.0 \pm 0.1SE$ chicks). However, the
165 small sample sizes available for ‘resident-resident’ pairs precluded rigorous statistical
166 comparison. Therefore, to understand the potential consequences of within-population
167 variation in migratory strategy and associated variation in reproductive performance for

168 population dynamics and evolution, we require studies that quantify relationships
169 between migratory strategy and reproductive performance in males and females
170 separately, and across combined breeding pairs.

171 We used intensive nest monitoring and winter colour-ring resightings from
172 partially migratory European shags (*Phalacrocorax aristotelis*; hereafter “shag”) to
173 quantify variation in key aspects of reproductive performance, hatch date and breeding
174 success, in relation to migratory strategies of individual males and females, and of
175 breeding pairs. First, across individuals that were resighted in winter and hence
176 classified as resident or migrant, we estimated the degree of partial migration in each
177 sex across the surveyed areas and tested whether males or females were more likely to
178 be migratory. Second, we tested whether hatch date or breeding success varied with
179 migratory strategy in males and females separately. Third, we tested whether these
180 aspects of reproductive performance varied with pair migratory strategy. Finally, we
181 tested whether pairing was assortative with respect to migratory strategy. We thereby
182 quantified key relationships between male and female migratory strategy and
183 reproductive performance, and discuss the possible causes of these relationships and
184 their consequences for the dynamics of partially migratory populations and associated
185 life-history evolution.

186

187 **Materials and methods**

188 **Study system**

189 European shags are large, diving seabirds that inhabit rocky coastlines in western
190 Europe (Wanless & Harris 1997). Shags provide a useful system to relate reproductive
191 performance to migratory strategy because they breed in large colonies where aspects
192 of reproduction such as hatch date and breeding success can be readily recorded.

193 Furthermore, adult shags breeding at a single colony can occupy a range of non-
194 breeding (winter) locations, including the breeding colony, and are therefore partially
195 migratory (Sponza, Cosol & Kralj 2013; Grist *et al.* 2014).

196 A breeding colony of shags on the Isle of May National Nature Reserve, Firth
197 of Forth, Scotland (56°11' N, 2°33' W) has been the focus of an intensive long-term
198 demographic study (Harris *et al.* 1994; Aebischer, Potts & Coulson 1995; Daunt *et al.*
199 1999; Frederiksen *et al.* 2008). During 1997-2012, chicks hatched across the colony
200 were ringed with a British Trust for Ornithology (BTO) metal ring and a coloured
201 plastic ring engraved with a unique three letter code. Previously unringed or BTO-
202 ringed adults were captured at their nests and colour-ringed. Colour-rings can be read
203 from up to 150m through a telescope or digital camera, allowing ringed individuals to
204 be identified from field resightings without recapture (Grist *et al.* 2014).

205 Clutches are typically laid during April to June, and pairs rear 0-4 chicks per
206 year in a single brood (Wanless & Harris 1997). There is therefore considerable
207 within-year variation in hatch date and breeding success, with higher breeding success
208 associated with earlier breeding (Aebischer 1993, Daunt *et al.* 1999). Ring resighting
209 and recovery data show that shags typically first breed aged three years (Aebischer,
210 Potts & Coulson 1995), and that annual adult survival probability is typically ≥ 0.85
211 (excluding 'wreck' winters with high mortality, Frederiksen *et al.* 2008). Adults
212 therefore generally survive to breed in multiple years. On average, ca. 50% of
213 surviving adults change mates between years (Aebischer, Potts & Coulson 1995), but
214 breeding dispersal among colonies is rare (Barlow *et al.* 2013). Adults' reproductive
215 timing and success can therefore be directly recorded with little error and few missing
216 data (see *Statistical analyses*).

217

218 **Winter location**

219 Shags have a partially wettable plumage and must return to land every day, restricting
220 their year-round distribution to suitable coastal habitat (Rijke 1968; Grémillet, Tuschy
221 & Kierspel 1998). Colour-ringed shags can therefore be observed in winter, both at
222 night roosts where individuals congregate at dusk (typically on cliffs and islands), and
223 at day roosts where individuals periodically rest between diving bouts (including on
224 rocks and harbour walls).

225 To identify winter locations of shags that breed on the Isle of May and hence
226 identify samples of migrant and resident individuals, extensive colour-ring resighting
227 surveys were undertaken during three winters (2009-2010, 2010-2011 and 2011-
228 2012). Full survey methods are described in Grist *et al.* (2014). For current analyses,
229 both night and day roosts that are known to be used by Isle of May shags were
230 surveyed approximately every 1-2 weeks through each winter (September-February).
231 The surveyed areas comprised the Isle of May night roost and its adjacent day roosts,
232 and roosts across north-east Scotland (Fig. 1). During each survey, experienced
233 observers identified colour-ringed shags using a 60x magnification telescope (Grist *et*
234 *al.* 2014). Surveys were strategically timed to maximise expected site-specific
235 resighting efficiency as influenced by weather, time of day, tide and sea state, and
236 lasted 30-300 minutes depending on viewing conditions and the number and turnover
237 of shags present. These surveys were designed to identify samples of resident
238 individuals that remained at the Isle of May year-round and samples of migrant
239 individuals that wintered at key sites elsewhere (Fig. 1), but not to explicitly estimate
240 the overall population-wide proportions of residents versus migrants across all winter
241 locations. Since colour-ringed individuals can only be resighted when they are on
242 land, the probability of resighting any individual that is present in an area during any

243 single survey is relatively low, particularly during mid-winter when individuals can
244 spend over 90% of daylight hours foraging (Daunt *et al.* 2006; 2014; Lewis *et al.*
245 2015). However, the repeated surveys undertaken throughout the winter increased the
246 probability that individuals that were present would be resighted on one or multiple
247 occasions (Appendix I).

248 Previous analyses of these data established that the distances from the Isle of
249 May at which individual shags were resighted were highly repeatable across sightings
250 within winters (mid-winter repeatability >0.88 , Grist *et al.* 2014), showing that
251 individuals typically remain in a single area throughout winter. Consequently, for
252 current analyses, individuals were classified as resident or migrant based on
253 resightings spanning 6th October-10th February within each winter (hereafter “winter
254 period”). This period encompasses the time for which most migrants were away from
255 the Isle of May (Grist *et al.* 2014). However, despite this restriction, some individuals
256 could still have been resighted on the Isle of May before migrating or after returning,
257 causing individuals that had migrated to unsurveyed locations to be misclassified as
258 residents. To minimise any such misclassification, only individuals that were
259 resighted at least twice on the Isle of May or associated day roosts at least seven days
260 apart within the focal winter period were classified as residents, and all individuals
261 that were resighted at least once away from the Isle of May area were classified as
262 migrants. Any remaining misclassification of migrants as residents is therefore likely
263 to be minimal, and would render any estimated difference in reproductive
264 performance conservative. Furthermore, across all three focal winters there were only
265 14 observed transitions of individuals between the Isle of May and focal migrant areas
266 within winters, resulting from seven observed mid-winter return movements (as
267 distinct from individuals’ early-winter outward and late-winter return migration

268 movements). The mid-winter transitions involved seven out of the total of 295 (2.4%)
269 assigned migrant individuals, and 14 out of the total of 1620 (<1%) potential
270 transitions between consecutive resightings of an individual. These data confirm that
271 individuals can be categorised as residents or migrants within any focal winter with
272 little uncertainty (Appendix I, see also Grist *et al.* 2014).

273 Previous analyses also showed that individual adult shags are resighted at
274 highly repeatable distances from the Isle of May across different winters as well as
275 within winters (across-year mid-winter repeatability ≥ 0.73 , Grist *et al.* 2014). These
276 data show that most individual adults are consistently resident or migrant across
277 winters, as further evidenced by data collected up to 2015 (see *Discussion*). However,
278 in case individuals did switch strategy between our focal winters, current analyses
279 were restricted to observations of reproductive performance of individual adults that
280 bred on the Isle of May in at least one summer during 2010-2012 that had been
281 resighted and classified as resident or migrant during the immediately preceding
282 winter (i.e. utilising data from adjacent winter-summer periods only). The spatio-
283 temporal distribution of survey effort varied among the three winters, due to variation
284 in environmental conditions and observer availability (Appendix I). In particular,
285 there were fewer mid-winter surveys of the Isle of May in winter 2009-2010.
286 Consequently, among-winter variation in the numbers and proportions of shags that
287 were classified as residents and migrants probably predominantly reflects variation in
288 survey effort rather than in shag migration ecology. Such variation does not impede
289 our current aim of comparing reproductive performance between samples of resident
290 and migrant males and females.

291

292

293 **Reproductive performance**

294 To quantify reproductive performance, almost all shag nest sites on the Isle of May
295 were monitored intensively during March-August 2010, 2011 and 2012. The nest
296 locations of all colour-ringed breeding adults were recorded, and males were
297 distinguished from females by larger body size and croaking call (Snow 1963). A
298 breeding attempt was defined as occurring when a fully-built nest, eggs or chicks were
299 observed.

300 All chicks that survived to approximately 20 days post-hatch were ringed and
301 wing lengths measured. The hatch date of each brood was recorded directly during
302 routine nest site monitoring, or back-calculated from measured chick wing lengths
303 using a previously derived relationship (Daunt 2000). To further validate this
304 calculation, hatch date was both recorded directly and back-calculated for 283 broods
305 hatched during 2010-2012. The mean difference in estimated hatch date was $1.6 \pm$
306 $2.4SD$ days, demonstrating that the two methods give consistent results. Breeding
307 success was recorded as the number of chicks fledged per nest recorded through
308 frequent systematic nest checks throughout the season. Sample sizes for hatch date are
309 smaller than for breeding success because hatch date was not observed or accurately
310 estimable for some broods that failed before ringing.

311 Shags sometimes attempt to breed aged two years, but then typically have later
312 hatch dates and lower breeding success than birds aged at least three years (Potts,
313 Coulson & Deans 1980; Aebischer 1993; Daunt *et al.* 1999). Subsequently,
314 reproductive performance varies relatively little with age within adults (Daunt *et al.*
315 1999). Since sample sizes of breeding two year-olds were small and our current aim
316 was not to quantify early-life variation in reproduction or migration, current analyses
317 were restricted to full adults (birds aged 3 years or older), thereby minimising age-

318 specific variation in reproductive performance. Further consideration of age-specific
319 variation across our focal sample is provided in Appendix II.

320

321 **Statistical analyses**

322 Mark-recapture models fitted to the long-term Isle of May resighting data show that
323 the probability of resighting a breeding adult during 2010-2012 was 0.98 (Burthe *et*
324 *al.*, unpublished data). Further multi-event models provided no evidence of non-
325 breeding by experienced adults in these years (breeding probability >0.99 , Lee *et al.*,
326 unpublished data.). The small amount of breeding season observation failure was
327 primarily attributable to a few pairs that bred in inaccessible locations rather than to
328 any specific life-history strategy. Mark-recapture models also showed that apparent
329 adult annual survival probabilities spanning winters 2009-2012 were unusually high
330 (≥ 0.97), reflecting benign winter conditions. Since resighting, breeding and survival
331 probabilities were all so high (≥ 0.97), and individuals were very rarely observed to
332 switch between resident and migrant locations within winters, further mark-recapture
333 models were not necessary to estimate relationships between sex, migratory strategy
334 and reproductive performance across individuals observed in our focal years and
335 winter areas.

336 Consequently, we first fitted generalised linear mixed models to test whether
337 observed male or female shags were more likely to be classified as migrant or resident
338 in each winter, and hence test for sex-biased migration across the surveyed areas.
339 Migratory strategy (i.e. resident or migrant) was modelled as a binary dependent
340 variable, with additive and interacting fixed effects of winter and sex, and random
341 individual effects to account for non-independent observations of individuals that

342 were resighted and bred in multiple years and hence appeared multiple times in the
343 dataset.

344 We then fitted two further sets of generalised linear mixed models to test
345 whether hatch date or breeding success differed between migrants and residents, with
346 hatch date (number of days from 1st April, with Gaussian error structure and identity
347 link) or breeding success (number of chicks fledged, with Poisson error structure and
348 log link) as dependent variables. Models were fitted to data for all three winter-
349 summer periods combined with additive and interacting fixed effects of winter and
350 migratory strategy, and random individual effects to account for multiple observations
351 of individuals (additional models for each year separately are shown in Appendix III).

352 The above models were fitted to data for males and females separately because
353 migratory strategies were not always observed for both individuals in a breeding pair.
354 However, since shags are socially monogamous within breeding seasons, hatch date
355 and breeding success presumably partly reflect the properties of male-female pairs
356 rather than either individual entirely independently (e.g. Brommer *et al.* 2015). To
357 quantify relationships between a pair's reproductive performance and its joint
358 migratory strategy, we fitted further general linear mixed models to data from
359 breeding attempts made by pairs where both individuals were classified as resident or
360 migrant. Random pair effects were fitted to account for multiple observations, along
361 with fixed effects of year and pair strategy, with strategies defined as 'resident male,
362 migrant female', 'resident female, migrant male', 'resident-resident', or 'migrant-
363 migrant'. Sample sizes were insufficient to test for pair strategy by year interactions.

364 Likelihood ratio tests between models that did and did not contain effects of
365 migratory strategy were used to test whether estimated effects on reproductive
366 performance differed significantly from zero. Hatch date was not included in models

367 explaining variation in breeding success, thereby testing whether relationships
368 between breeding success and migratory strategy were statistically explained by hatch
369 date, because breeding attempts where hatch date was unknown were biased towards
370 those that failed.

371 Finally, chi-squared tests were used to test whether the frequencies of the four
372 pair strategies differed from those expected given random pairing, thereby testing for
373 non-random pairing with respect to migratory strategy. Expected frequencies were
374 computed from the observed numbers of migratory and resident individuals across all
375 classified males and females.

376 Analyses were implemented in R 2.15.0 (R Development Core Team 2008),
377 utilising package lme4 (Bates *et al.* 2014).

378

379 **Results**

380 **Data structure**

381 Overall, 439 individual shags that were observed breeding on the Isle of May in
382 summers 2010-2012 had been resighted and hence classified as migrant or resident
383 during the preceding winter, comprising 211 females, 224 males and 4 individuals of
384 unknown sex that were removed from the dataset. The sex ratio of the remaining 435
385 individuals therefore did not differ from 50:50 (51% males, 49% females, $\chi_1^2 = 0.39$, p
386 $= 0.53$). Furthermore, of all individuals that were observed breeding but not resighted
387 during the preceding winter, 51% were male and 49% were female. Together, these
388 data imply that our winter resighting dataset is not sex-biased.

389 Of the 435 known-sex individuals, 278 (64%), 110 (25%) and 47 (11%) were
390 resighted and bred in one, two or three winter-summer periods respectively. Of 207
391 cases where an individual was resighted in two consecutive winters (involving 157

392 individuals) there were only 12 cases of apparent migratory strategy switching (6
393 migrant to resident switches and 6 resident to migrant switches, involving 7 males and
394 5 females). Strategy-switching was therefore rare, and was not directional or sex-
395 biased.

396

397 **Male & female migratory strategy**

398 Across all three years, 243 of the 435 known-sex individuals were classified as
399 resident, and 192 were classified as migrant. Of these individuals, 124 (52%) residents
400 were male, and 119 (52%) migrants were male. Individuals that were classified as
401 migrants were not significantly more likely to be male than female ($\beta = 0.42$, $p =$
402 0.43), and the interactive effect of sex and year on migratory strategy was not
403 significant (estimated effect -0.13 , $p = 0.56$, Appendix III). Both sexes were therefore
404 partially migratory, and there was no evidence of substantial or consistent sex-bias in
405 migratory strategy across the surveyed areas.

406

407 **Male & female migratory strategy and hatch date**

408 There were 380 known-sex individuals whose hatch date was observed or estimated in
409 one or more summers during 2010-2012 and that were classified as resident or
410 migrant in the preceding winter, providing 560 observations of hatch date in total.
411 Mean hatch dates ($\pm 1SD$) were 19 May ± 6.0 days, 12 May ± 9.5 days and 12 May \pm
412 11.4 days in summers 2010, 2011 and 2012 respectively.

413 Overall, resident males and females hatched their broods significantly earlier
414 than migrant males and females, with estimated mean differences of approximately 6
415 days in both sexes (Table 1). The year by migratory strategy interactions were not
416 significant (estimated effects: males, $\beta = 0.89$, $p = 0.56$; females $\beta = 0.44$, $p = 0.82$),

417 showing that the difference in hatch date between residents and migrants was
418 consistent across the three years (see also Appendix III).

419

420 **Male & female migratory strategy and breeding success**

421 There were 435 known-sex individuals whose breeding success was recorded in one
422 or more summers during 2010-2012 and that were classified as resident or migrant in
423 the preceding winter, providing 651 observations of breeding success in total.
424 Individual breeding success varied from 0-4 chicks fledged (Appendix III). Mean
425 ($\pm 1SD$) breeding success was 2.3 ± 1.1 , 2.1 ± 1.1 and 1.6 ± 1.1 chicks in 2010, 2011 and
426 2012 respectively, implying that environmental conditions for reproduction varied
427 among the three focal years.

428 Overall, resident males and females fledged significantly more chicks per year
429 than migrant males and females, with estimated mean differences of approximately
430 0.2 chicks per year for both sexes (Table 1). The year by migratory strategy
431 interactions were not significant (estimated effects: males, $\beta = -0.08$, $p = 0.59$;
432 females $\beta = -0.08$, $p = 0.52$), again showing that the difference in breeding success
433 between residents and migrants was broadly consistent across the three years (see also
434 Appendix III).

435

436 **Pair migratory strategy and reproductive performance**

437 There were 75 breeding attempts where both the male and female were classified as
438 resident or migrant based on resightings during the immediately preceding winter, and
439 all four possible 'pair migratory strategies' were recorded (Table 2; Appendix IV).
440 The observed frequencies of pair migratory strategy did not differ from those
441 expected given random pairing ($\chi^2_3 = 6.1$, $p = 0.11$; Table 2; Appendix IV). Resident

442 and migrant shags were therefore not significantly more or less likely to pair with
443 resident or migrant mates than expected by chance.

444 Hatch date was recorded for 64 of 75 breeding attempts where pair migratory
445 strategy was known. ‘Resident-resident’ pairs hatched broods 12 days earlier than
446 ‘migrant-migrant’ pairs on average (Table 2; Fig. 2), with mean hatch dates of 6th
447 May and 18th May respectively. There were also differences between pairs with
448 mixed migratory strategies: ‘resident female, migrant male’ pairs hatched broods 7
449 days earlier than ‘resident male, migrant female’ pairs on average (Table 2; Fig. 2).

450 Across all 75 pairs, ‘resident-resident’ pairs also had substantially higher
451 breeding success than pairs where one or both individuals were migrant. Specifically,
452 resident-resident pairs fledged a mean of 2.3 chicks compared to approximately 1.6
453 chicks for all other pair migratory strategies (Table 2; Fig. 3).

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460 **Discussion**

461 Quantifying the degree to which reproductive performance differs between resident and
462 migrant males, females and breeding pairs within any population is central to
463 understanding the ongoing evolution of migratory strategy, and to understanding the
464 potential consequences of partial migration for demographic structure and population
465 dynamics (Pulido 2007; Gillis *et al.* 2008; Chapman *et al.* 2011). We show that, in
466 European shags, both sexes are partially migratory and that resident males and females
467 hatched their broods earlier and fledged more chicks per year than migrant males and
468 females. Moreover, these aspects of reproductive performance varied with the joint
469 migratory strategy of a pair, such that resident-resident pairs hatched their broods
470 earlier, and had higher breeding success than pairs comprising one or two migrants.

471

472 **Individual migratory strategy and reproductive performance**

473 Resident individual male and female shags fledged ~0.2 more chicks per year than
474 migrant individuals on average, a difference that equates to ~10% of the grand mean
475 breeding success during 2010-2012 of ~2 chicks. Moreover, resident males and females
476 hatched their broods ~6 days earlier than migrant individuals on average. This
477 difference in timing could increase the difference in the contributions of residents
478 versus migrants to population growth rate beyond that expected solely from their
479 relative breeding success. Chick survival from ringing to recruitment is negatively
480 correlated with hatch date in shags, as in many other bird species (e.g. Lindholm,
481 Gauthier & Desrochers 1994; Arnold, Hatch & Nisbet 2006). Specifically, shag chicks
482 have a 0.01 increase in recruitment probability for every week's advance in hatch date,
483 and this increase has been attributed primarily to higher post-fledging survival (Harris

484 *et al.* 1994). Overall, resident male and female shags will therefore contribute more
485 recruits to the population per year per capita than migrant males and females.

486 Some previous studies on other systems also showed that residents can have
487 better reproductive performance than migrants (e.g. American dippers, *Cinclus*
488 *mexicanus*, Gillis *et al.* 2008; American kestrels, *Falco sparverius*, Anderson *et al.* 2015;
489 Table S1). Such evidence is consistent with an assumption of evolutionary models of
490 partial migration that residence can be associated with higher reproductive success
491 (Griswold, Taylor & Norris 2010; Kokko 2011). However, studies of other species did
492 not find such patterns (e.g. Elk, *Cervus canadensis*, Hebblewhite & Merrill 2011;
493 Skylark, *Alauda arvensis*, Hegemann, Marra & Tieleman 2015; Table S1).
494 Furthermore, the few studies that quantified associations between reproductive
495 performance and migratory strategy in both males and females have often found sex-
496 specific effects (e.g. Snowy plovers, Warriner *et al.* 1986; Lanyu scops owls, Bai,
497 Severinghaus & Philippart 2012; Table S1). Therefore, in showing that the reproductive
498 performance of resident shags exceeded that of migrants to similar degrees in both
499 sexes, our study adds to the diversity of observed patterns of sex-specific variation in
500 reproductive performance with migratory strategy, implying that such patterns cannot
501 yet be generalised and likely depend on system-specific ecology and mechanisms.

502

503 **Pair migratory strategy and reproductive performance**

504 Across shag breeding attempts where both the male and female were classified as
505 resident or migrant, reproductive performance varied with the pair's combined
506 migratory strategy. Specifically, 'resident-resident' shag pairs hatched their broods 12
507 days earlier than 'migrant-migrant' pairs on average, exceeding the difference of 6
508 days estimated between resident and migrant individuals of each sex independently.

509 In addition, the greatest difference in breeding success was between ‘resident-
510 resident’ pairs and all other pairings; ‘resident-resident’ pairs produced an average of
511 0.7 chicks per year more than pairs that contained one or two migrants, representing a
512 substantial proportional increase.

513 Evolutionary and population dynamic models of partial migration often
514 consider single-sex populations to facilitate model tractability (e.g. Kokko 2011;
515 Vélez-Espino, McLaughlin & Robillard 2013). However, the assumption that the
516 reproductive performance of resident and migrant individuals of one sex does not vary
517 with the migratory strategies of their mates may be frequently violated in natural
518 systems, particularly in populations with socially-persistent breeding pairs. Our study
519 illustrates that an individual’s reproductive performance is not necessarily
520 independent of the migratory strategy of its mate. Variation in reproductive
521 performance could therefore be over- or under-estimated in empirical and theoretical
522 studies that consider each sex separately. Quantifying variation in reproductive
523 performance in relation to pair migratory strategies in diverse species and breeding
524 systems may therefore be an important step in understanding the evolutionary
525 maintenance of mixed migratory strategies and resulting population dynamics.

526 To our knowledge, only one previous study explicitly quantified relationships
527 between reproductive performance and pair migratory strategy. Warkentin *et al.*
528 (1990) found that merlin pairs containing at least one resident individual hatched
529 broods up to four days earlier than ‘migrant-migrant’ pairs. However, merlins and
530 shags showed opposite patterns of reproductive performance in mixed strategy pairs:
531 in contrast to shags, ‘resident male, migrant female’ merlin pairs fledged more chicks
532 than ‘resident female, migrant male’ pairs. This indicates that pair reproductive
533 performance varies more with male migratory strategy than with female strategy in

534 merlins, possibly due to the male's primary contribution to prey capture (Espie *et al.*
535 2000). While the shag and merlin studies therefore both indicate that 'resident-
536 resident' pairs have highest reproductive success, they highlight that the directions of
537 mixed pair effects may vary among systems, perhaps reflecting species- or
538 population-specific variation in sex roles and ecology.

539 Dependence of reproductive performance on pair migratory strategy could also
540 potentially drive mate choice among residents and migrants, and create intrinsic
541 frequency-dependence in the fitness consequences of individual migration versus
542 residence. However, perhaps surprisingly, there was no evidence of assortative pairing
543 with respect to migratory strategy in shags; residents and migrants were no more or
544 less likely to pair with residents or migrants than expected by chance. This indicates
545 that there is no sympatric reproductive isolation between residents and migrants, and
546 therefore no evidence of underlying genetic structure (e.g. Pulido 2007; Anderson *et*
547 *al.* 2015). The lack of assortative pairing also means that many paired males and
548 females that bred together cannot over-winter together. Divergent winter conditions
549 occurring in different areas might mean that mates experience different conditions,
550 potentially decoupling reproductive timing the following spring and driving divorce
551 (Gunnarsson *et al.* 2004). Indeed, shags are much less mate-faithful across years than
552 many seabirds (Aebischer, Potts & Coulson 1995). However, since 'resident-resident'
553 shag pairs had the highest breeding success and pairs with a resident female bred
554 earlier, choice for resident mates might be expected. Future analyses could therefore
555 test whether patterns of divorce and re-pairing are non-random with respect to male or
556 female migratory strategy.

557

558 **Mechanisms and implications**

559 Ultimately, the population dynamic and evolutionary consequences of observed
560 relationships between migratory strategy and aspects of reproductive performance
561 such as hatch date and breeding success will depend on the underlying mechanisms.
562 Relationships could potentially be direct and causal, such that an individual's
563 migratory strategy affects its reproductive performance through one or more non-
564 exclusive mechanisms. First, time or energy costs of migration movements
565 themselves could directly constrain breeding date or success. However, while the 200-
566 300km distance between the Isle of May and the surveyed migrant wintering areas is
567 sufficient to constitute a definitive seasonal movement (Fig. 1, Grist *et al.* 2014),
568 shags breeding on the Isle of May typically have a breeding season foraging range of
569 8-11km and make 1-4 feeding trips per day (Bogdanova *et al.* 2014). It therefore
570 seems unlikely that a 200-300km seasonal migration imposes sufficient energetic cost
571 to directly impact reproductive performance. Moreover, tracking data show that shags
572 can accomplish 200-300km migratory movements within 1-2 days (Wanless,
573 *unpublished data*), which is substantially less than the observed delay in migrants'
574 hatch dates.

575 Second, direct effects of migratory strategy on reproductive performance
576 could arise because residents can pre-emptively occupy high quality nest sites while
577 migrants are away (e.g. Kokko 2011). Indeed, studies of other shag populations have
578 shown that nest sites associated with higher breeding success are occupied first
579 (Velando & Freire 2003), although the characteristics that determine these "higher
580 quality" sites vary between colonies (Potts, Coulson & Deans 1980; Aebischer 1985;
581 Velando & Freire 2001). However, any such effects might be expected to be stronger
582 in male shags, since males are primarily responsible for nest defence (Snow 1960),

583 and therefore seem unlikely to explain the higher breeding success of resident
584 females.

585 Third, the relationships between migratory strategy and reproductive
586 performance observed in both sexes might reflect “carry-over” effects, where
587 residents might utilise higher quality winter foraging habitat than migrants, and
588 consequently start the breeding season in better condition and/or reach breeding
589 condition earlier (e.g. Harrison *et al.* 2011). Such mechanisms might explain earlier
590 breeding by resident females, and why mixed strategy ‘resident female, migrant male’
591 pairs hatched their broods earlier than ‘resident male, migrant female’ pairs, since the
592 timing of breeding in shags has been suggested to predominantly reflect female
593 foraging efficiency and associated condition (Daunt *et al.* 2006).

594 Alternatively, there might be little or no direct effect of individual migratory
595 strategy on reproductive performance. Instead, the observed associations could arise
596 from, or be exacerbated by, correlated consequences of variation in some underlying
597 trait or state, often conceptualised as ‘individual quality’. For example, Adriaensen
598 and Dhondt (1990) suggested that migrant robins have lower reproductive
599 performance and survival than residents because less competitive individuals were
600 forced to migrate. However, individual migratory strategy appears not to be a highly
601 flexible condition-dependent or age-dependent strategy in individual shags. Individual
602 adults are very highly repeatable in their migratory strategy and winter location across
603 winters (Grist *et al.* 2014), and even though individual and population-wide breeding
604 success varied within and across our three study years, individuals rarely switched
605 migratory strategy. Any state-dependence underlying observed associations between
606 migratory strategy and breeding success is therefore very unlikely to stem from
607 reverse causality such that breeding failure causes facultative migration (as observed

608 in black-legged kittiwakes, *Rissa tridactyla*, Bogdanova *et al.* 2011). Further, mark-
609 recapture models fitted to winter sighting data collected during 2009-2015 and
610 spanning diverse winter conditions show that between-winter transition probabilities
611 between different wintering areas, and hence between migratory strategies, are
612 generally low for both sub-adult and adult shags (Sturgeon, Burthe, *et al.*, unpublished
613 data). Individuals' migratory strategies therefore appear to be set early and largely
614 remain fixed through life, implying that the observed relationships between adult
615 migratory strategy and reproductive performance cannot be attributable to correlated
616 effects of age (Appendix IV). However, the observed relationships might reflect
617 indirect effects of an underlying fixed state variable that permanently affects both
618 individual migratory strategy and mean reproductive performance. This situation
619 could potentially generate indirect selection on migratory strategy, and generate
620 strong and persistent structured covariation in migratory strategy and reproductive
621 performance at both individual and cohort levels, influencing spatio-temporal
622 population dynamics (e.g. Lindström & Kokko 2002; Vindenes, Engen & Sæther
623 2008).

624 Lifelong longitudinal data on individual migratory strategy, reproductive
625 performance and survival are ultimately required to evaluate the overall fitness
626 consequences of migratory strategy and hence evaluate population dynamic and
627 evolutionary implications; but such data are not yet available for any partially
628 migratory system (Gaillard 2013). During our three study years, winter environmental
629 conditions were consistently good, resulting in high annual survival probabilities for
630 adult shags breeding on the Isle of May (0.97–0.98). Consequently, survival
631 probability did not differ between residents and migrants across these winters (Burthe
632 *et al.*, unpublished data). Over longer timescales spanning harsher winter conditions,

633 the relatively high breeding success of residents could potentially be balanced by
634 decreased survival, facilitating evolutionary maintenance of mixed migration
635 strategies (Sanz-Aguilar *et al.* 2012). Indeed, resident American dippers had higher
636 breeding success than migrants but lower over-winter survival (Gillis *et al.* 2008).
637 Furthermore, our analyses only included migrants that wintered in specific surveyed
638 areas (Fig. 1), and migrants that wintered elsewhere might have had higher or lower
639 breeding success. However, the surveyed migrant areas hold relatively large numbers
640 of migrant Isle of May breeders, and hatch date and breeding success did not differ
641 markedly or systematically among migrants observed at different roosts within the
642 surveyed areas (Appendix V). These data imply that reproductive performance may
643 differ more between residents and migrants than between sets of migrants that move
644 to different destinations. However, estimates of survival and breeding success of
645 migrant and resident individuals over a greater range of environmental and weather
646 conditions and more extensive spatial scales will ultimately be required to understand
647 the associations with overall fitness and the underlying mechanisms, and in particular
648 how mixed strategies are maintained within a single population (Chapman *et al.* 2011;
649 Gaillard 2013).
650

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663 **Data accessibility**

664 The data are available from the Dryad Digital Repository: doi:10.5061/dryad.532j0.

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668 **Author contributions**

669 HG, FD, SW, SJB, MAN, MPH and JMR collected the data; HG analysed the data;
670 HG with FD, SW and JMR wrote the manuscript. All authors contributed critically to
671 the drafts and gave final approval for publication.

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880 **Table 1.** Summary statistics and modelled relationships between aspects of
 881 reproductive performance (brood hatch date or breeding success) and migratory
 882 strategy across male (M) and female (F) shags that bred in one or more summers
 883 during 2010, 2011 and 2012 combined. Raw mean (± 1 standard deviation) hatch date
 884 (days since April 1st) and breeding success (number of chicks fledged) of migrant and
 885 resident males and females are shown. β is the model-estimated effect size for
 886 migrants versus residents (with 95% confidence intervals), and p is the probability
 887 that the estimated effect could be observed by chance. N_I values are the total numbers
 888 of individual residents and migrants (not the total number of observations).

889

	Sex	N_I residents	N_I migrants	Resident raw mean $\pm 1SD$	Migrant raw mean $\pm 1SD$	β [95%CI]	p
Hatch	M	116	88	40.8 \pm 11.7	47.0 \pm 10.2	5.6 [3.3, 7.9]	<0.01
date	F	104	72	40.4 \pm 9.6	46.9 \pm 11.0	5.5 [2.6, 8.5]	<0.01
Breeding	M	119	92	2.1 \pm 1.1	1.8 \pm 1.1	-0.20 [-0.35, -0.04]	0.01
success	F	124	100	2.0 \pm 1.0	1.7 \pm 1.1	-0.17 [-0.35, -0.01]	0.05

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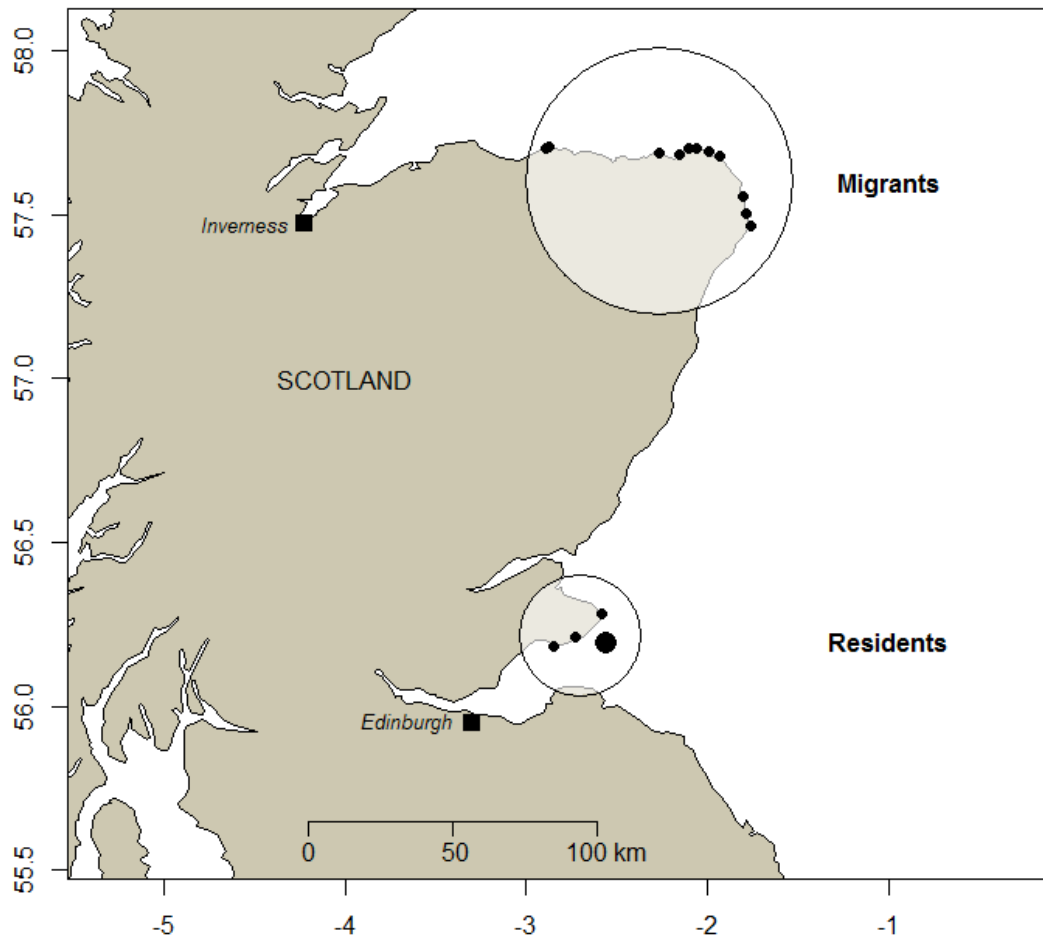
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899 **Table 2.** Summary statistics and modelled relationships between brood hatch date and
 900 breeding success and pair migratory strategy across shag pairs where both the female
 901 and male were classified as resident or migrant. The expected numbers of attempts are
 902 the frequencies of pair migratory strategies given random pairing. Raw mean (± 1
 903 standard deviation) hatch date and breeding success of pairs comprising migrant or
 904 resident males and females are shown. β is the model-estimated effect size for pair
 905 migratory strategy, with 95% confidence intervals. Models that included pair migratory
 906 strategy as an explanatory factor fitted significantly better than models without this
 907 factor (Hatch date, LRT, $\chi^2= 147.0$, $p<0.01$; Breeding success, LRT, $\chi^2= 10.7$, $p=0.05$).
 908

Male strategy	Female strategy	No. of attempts	Expected no. of attempts	Hatch date		Breeding success	
				Raw mean $\pm 1SD$	β [95% CI]	Raw mean $\pm 1SD$	β [95% CI]
Resident	Resident	35	30	36.6 \pm 7.5	37.2 [34.0, 40.6]	2.3 \pm 1.0	0.8 [0.62, 1.05]
Resident	Migrant	14	19	48.4 \pm 14.5	48.6 [42.7, 54.5]	1.6 \pm 1.1	0.5 [0.07, 0.87]
Migrant	Resident	11	16	41.0 \pm 8.5	41.0 [34.8, 47.2]	1.6 \pm 1.1	0.5 [0.03, 0.95]
Migrant	Migrant	15	10	45.5 \pm 9.0	45.6 [40.4, 50.7]	1.6 \pm 1.0	0.5 [0.03, 0.87]

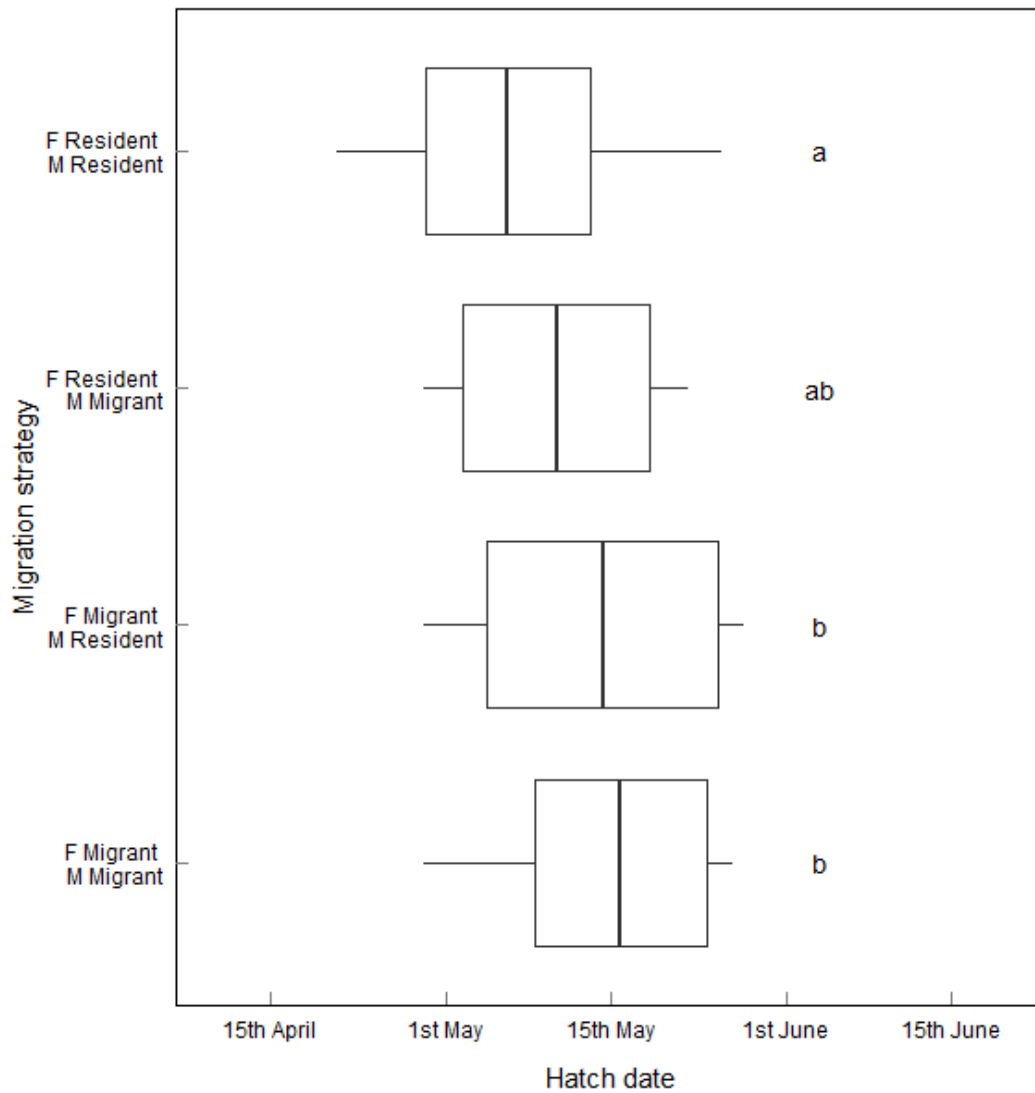
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918 **Figure 1.** Locations of resighting surveys for colour-ringed shags during winters
 919 2009-2012. Circles identify migrant and resident wintering areas, and points are
 920 known roost locations within each area. The larger point marks the Isle of May
 921 breeding colony.

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925 **Figure 2.** Distributions of hatch dates of breeding attempts made by shag pairs where

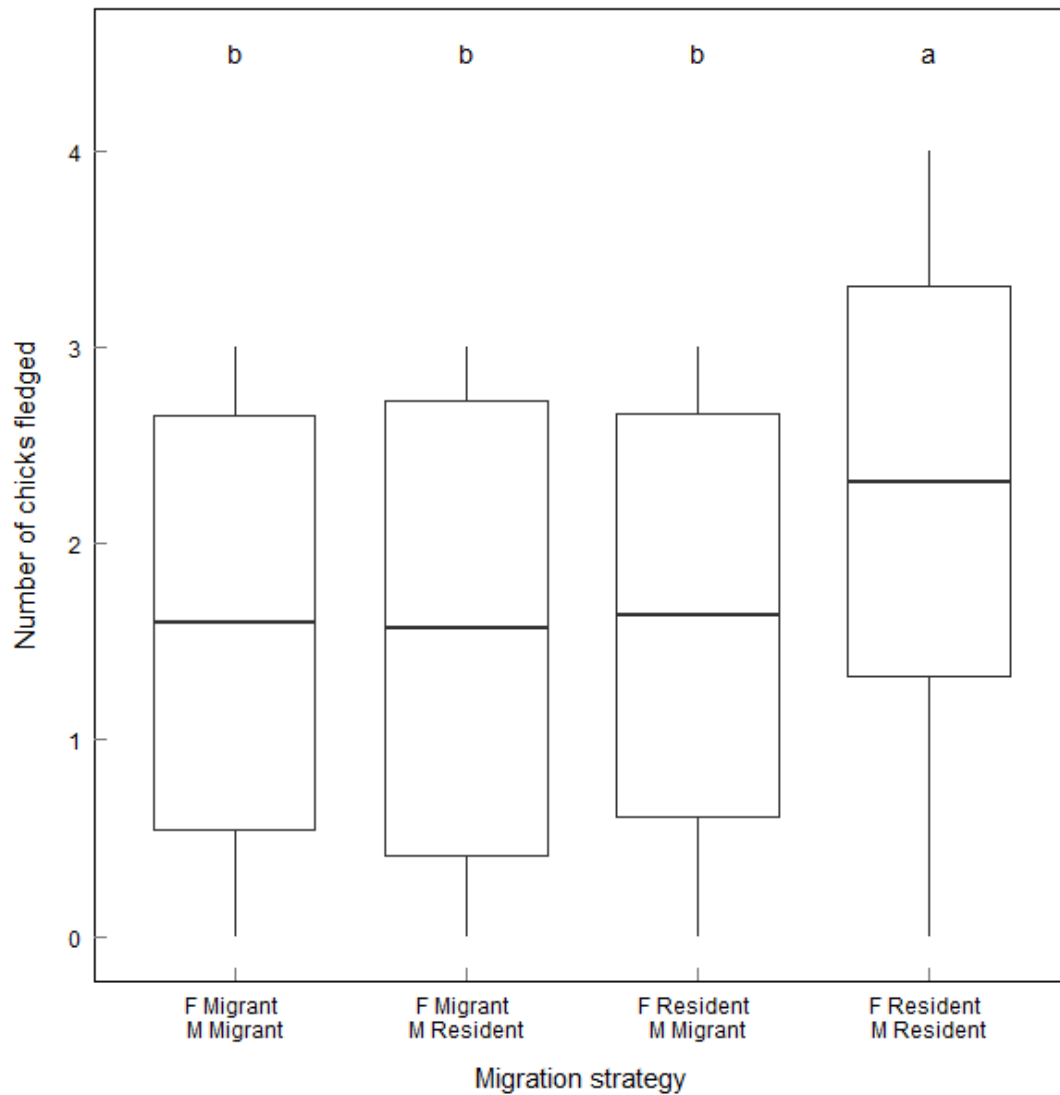
926 both the male (M) and female (F) were classified as resident or migrant. Thick bars

927 and boxes show raw mean breeding success \pm 1 standard deviation, and whiskers

928 demarcate the full range. Lowercase letters indicate significantly different modelled

929 groups.

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933 **Figure 3.** Distributions of breeding success of shag pairs where both the male (M) and
 934 female (F) were classified as resident or migrant. Thick bars and boxes show raw mean
 935 breeding success \pm 1 standard deviation, and whiskers demarcate the full range.
 936 Lowercase letters indicate significantly different modelled groups.

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942 **Table S1.** Studies that related measures of reproductive performance to migratory strategy in partially migratory populations. N is the largest
 943 number of individuals (i.e. sample size) analysed within each study. ‘Sex bias’ states which sex is more likely to migrate, or ‘equal’ if both sexes
 944 are equally partially migratory. ‘Sex analysed’ states the sexes for which data were analysed. ‘Measure(s)’ states the metrics of reproductive
 945 performance considered.

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Species	N	Sex bias	Sex analysed	Measure(s)	Results	References
American dipper (<i>Cinclus mexicanus</i>)	342	Equal	Males and females	Hatching date; brood size; nestling condition; fledgling survival	In this ‘breeding season partial migrant’ where residents and migrants breed in different areas, residents bred earlier, had larger broods and were more likely to have second broods than migrants. Chicks produced by residents had better nestling condition and post-fledging survival than chicks produced by migrants.	Mackas <i>et al.</i> (2010); Morrissey <i>et al.</i> (2004); Gillis <i>et al.</i> (2008)
American kestrels (<i>Falco sparverius</i>)	210	Equal	Males and females	Laying date	Resident males and females laid eggs earlier in two of the three winters analysed. A female’s migratory strategy predicted her mate’s migratory strategy, i.e. residents were likely to breed with residents.	Anderson <i>et al.</i> (2015)

Elk (<i>Cervus canadensis</i>)	150	Equal	Females only	Pregnancy rates; calf weights	Resident females had lower pregnancy rates and calf weights than migrant females.	Hebblewhite & Merrill (2011)
European robin (<i>Erithacus rubecula</i>)	76	Female	Males and females in separate studies	Proportion of individuals paired; pairing date	A higher proportion of resident males than migrant males were paired. Resident females paired earlier than migrant females.	Adriaensen & Dhondt (1990); Harper (1985)
Giant tortoise (<i>Testudo gigantea</i>)	39	Equal	Females only	Number of pre-ovulatory follicles	Migrant females had more follicles than resident females.	Swingland <i>et al.</i> (1979)
Lanyu scops owl (<i>Otus elegans botelensis</i>)	129	Female	Males and females	Probability of breeding; nesting success; brood size	Resident males were more likely to breed than migrant males, but there was no difference in nesting success or brood size. Resident females were no more likely to breed or have larger brood sizes than migrant females, but had higher nesting success.	Bai, Severinghaus & Philippart (2012)
Merlin (<i>Falco columbarius</i>)	118	Equal	Males and females	Hatch date; brood size	Pairs with >1 resident hatched chicks earlier than migrant-migrant pairs. Pairs with a resident male had higher brood sizes than all other pair combinations.	Warkentin <i>et al.</i> (1990)

Red-spotted newt <i>(Notophthalmus viridescens viridescens)</i>	110	Female	Males and females in separate studies	Tail fin height; lay date; number of eggs; larval size	Resident males developed tail fins earlier than migrant males. Resident females produced larger larvae than migrant females, but did not lay earlier or produce more eggs.	Bloch & Grayson (2010); Grayson & McLeod (2009)
Skylark (<i>Alauda arvensis</i>)	107	Equal	Males and females	Number of nestlings, fledglings and recruits	Numbers of nestlings, fledglings and recruits did not differ between residents and migrants.	Hegemann, Marra & Tieleman (2015)
Snowy plover <i>(Charadrius nivosus)</i>	43	Equal	Males and females	Pairing date	Resident males paired earlier than migrant males, but pairing date did not differ between resident and migrant females.	Warriner <i>et al.</i> (1986)
Spruce grouse <i>(Canachites canadensis)</i>	118	Female	Females only	Proportion of females breeding	The proportions of migrant and resident females breeding did not differ.	Herzog & Keppie (1980)
White-ruffed manakin <i>(Corapipo altera)</i>	117	Equal	Males only	Attracting females	Resident males attract females to lek sites more frequently and for longer durations than migrant males.	Boyle <i>et al.</i> (2011)

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992 **Appendix I: Details of winter surveys for colour-ringed shags conducted during winters 2009-2010, 2010-2011 and**
 993 **2011-2012.**

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995 **Table A1.2.** The frequency of resightings of individual adult colour-ringed shags across all surveyed areas in winters 2009-2010, 2010-2011 and 2011-2012.

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Winter	Number of times resighted										Total no. of individuals
	1	2	3	4	5	6	7	8	9	=>10	
2009-2010	115	44	23	13	6	2	3	1	1	3	211
2010-2011	210	140	60	32	3	4	5	5	1	14	474
2011-2012	248	139	70	45	16	21	1	4	5	17	566

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999 **Table A1.3.** The number of resightings of adult colour-ringed shags during October to February in winters 2009-2010, 2010-2011 and 2011-2012 across the surveyed
 1000 migrant and resident areas (see Fig. 1).

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Winter	Migrant area			Resident area					Total no. of resightings		
	Oct	Nov	Dec	Jan	Feb	Oct	Nov	Dec		Jan	Feb
2009-2010	65	28	42	66	39	84	85	6	11	4	430
2010-2011	132	54	70	105	78	160	20	114	25	358	1116
2011-2012	187	95	151	149	79	207	201	62	293	49	1473

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1005 **Table A1.3.** The number of positive survey days per month across 2009-2010, 2010-2011 and 2011-2012. Positive survey days are dates on which ≥ 1 colour-ringed adult
 1006 shag was resighted in a resident and/or migrant area.

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Winter	Area	Number of positive survey days					Total
		Oct	Nov	Dec	Jan	Feb	
2009-2010	Resident	8	7	2	4	1	22
	Migrant	12	8	8	9	9	46
2010-2011	Resident	10	4	8	5	5	32
	Migrant	19	11	13	18	9	70
2011-2012	Resident	8	13	6	12	6	45
	Migrant	16	14	17	17	9	73

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Appendix II: Analysis of variation in reproductive performance with age, cohort and migratory strategy

In general, indirect associations between individual reproductive performance (i.e. hatch date and breeding success) and migratory strategy (i.e. resident versus migrant) could potentially arise if both reproductive performance and migratory strategy vary concordantly, but independently, with age (or some other state variable). For example, older individuals might both show better reproductive performance and be more likely to be resident. Such indirect mechanisms would not necessarily alter the conclusion that there is, ultimately, selection on migratory strategy but would alter the form of direct versus indirect selection and hence alter expected evolutionary and population dynamic outcomes.

Indirect associations between reproductive performance and migratory strategy stemming from age effects can, in principle, be accounted for by modelling effects of age on reproductive performance alongside effects of migratory strategy. However, in practice, distinguishing the effects of age on any phenotype from confounding effects of survival selection (i.e. selective disappearance) is problematic given cross-sectional data on different individuals of diverse ages observed over a short period (rather than longitudinal data on the same individuals observed across different ages, e.g. Lande & Arnold 1983; van de Pol & Verhulst 2006). For example, in the current context, if migrants were more likely to survive any year than residents, then migrants would on average be older than residents at any time of observation and represent older cohorts. If reproductive performance in fact varied with migratory strategy but not directly with age or cohort, then modelling effects of age or cohort would likely capture some of the variance in reproductive performance that is directly due to migratory strategy and indicate spurious effects of age or cohort. Such analyses should

consequently be formulated and interpreted cautiously, and in the light of known attributes of the biology of any focal system.

In our study system, previous analyses showed that two year-old shags that attempt to breed have later hatch dates and lower breeding success than older shags, but that there is little age-specific variation in reproductive performance thereafter (Potts, Coulson & Deans 1980; Daunt *et al.* 1999). Consequently, by excluding data from shags that bred aged two years (see main Methods) we minimised the degree to which any associations between migratory strategy and reproductive performance could stem from covariances with age. Furthermore, there is no evidence that migratory strategy varies markedly with individual age. Individual shags are highly repeatable in their migratory strategy across years (see main text and Grist *et al.* 2014), and typically acquire their strategy soon after fledging (i.e. before commencing reproduction, Sturgeon *et al.* unpublished data). It is therefore unlikely that observed associations between reproductive performance and migratory strategy could result primarily from covariation with age in our system. However, we undertook further analyses to examine such effects.

A substantial proportion of the individual shags included in our main analyses were first caught and ringed as breeding adults, meaning that their age (and cohort) were unknown. Therefore to quantify whether age or cohort effects may explain the observed difference in reproductive performance between residents and migrants, the dataset was restricted to individuals ringed as chicks and hence of known cohort and age at observation during our focal study years (2010-2012). We first fitted the same models relating hatch date or breeding success to migratory strategy as were fitted to the full dataset (see main manuscript) to the reduced dataset, thereby verifying whether the same patterns detected across the full dataset

were also evident in the reduced known-age dataset. We then fitted further generalised linear (mixed) models to the reduced datasets, with hatch date (number of days from 1st April with Gaussian error structure) or breeding success (number of chicks fledged with Poisson error structure) as dependent variables, and that included age or natal cohort as additional fixed effects (alongside observation year). Age was measured as the number of years between hatching and the observed breeding event and modelled as a continuous variable with linear and quadratic effects. Cohort (i.e. hatch year) was modelled as a categorical fixed effect. Likelihood ratio tests between models that did or did not contain cohort were used to test whether estimated effects differed significantly from zero.

Data

Overall, of the 435 known-sex individuals of known migratory strategy that were subsequently recorded breeding in summers 2010-2012, 272 (63%) were ringed as chicks and were therefore of known age and cohort (comprising 144 males and 128 females).

Four cohorts that were represented by fewer than five observed individuals were additionally excluded from the cohort analyses, leaving 13 remaining cohorts. The earliest included cohort was 1996, and the latest 2009.

The age of individuals retained in the dataset ranged from 3 to 21 years for males, and 3 to 18 years for females.

Hatch date

A total of 330 hatch dates were observed or estimated during summers 2010-2012 across 236 individuals that were both classified as resident or migrant and ringed as chicks (comprising 134 males and 102 females).

Across this reduced dataset, resident males hatched their broods on average five days earlier than migrant males ($\beta= 5.2$ [95% CI 2.0, 8.3], $p <0.01$), and resident females hatched their broods on average five days earlier than migrant females ($\beta= 5.4$ [95% CI 1.9, 8.8], $p <0.01$). These estimated effects are very similar to those estimated across the full dataset that included individuals ringed as adults (main text, Table 1).

When cohort was included in the hatch date analysis, resident males still hatched their broods four days earlier than migrant males ($\beta= 3.7$, $p=0.03$), and there was also a significant effect of cohort on hatch date ($\chi^2= 21.3$, $p=0.05$). Resident females also hatched their broods four days earlier than migrant females ($\beta= 3.9$ $p =0.03$), and there was a significant effect of cohort on hatch date ($\chi^2= 39.2$, $p<0.01$).

When age was included in the hatch date analysis, resident males still hatched their broods four days earlier than migrant males ($\beta= 3.6$, $p=0.02$), and older males hatched their broods earlier than younger males ($\beta = -2.1$, $p=0.01$; the quadratic age term was not significant, $\beta= 0.07$, $p =0.08$). Resident females also hatched their broods four days earlier than migrant females ($\beta= 4.0$, $p =0.01$), and older females hatched their broods earlier than younger females ($\beta = -4.3$, $p<0.01$). The quadratic age term was also significant for females ($\beta= 0.2$, $p <0.01$), suggesting that the cross-sectional relationship between hatch date and age is non-linear in female shags.

Breeding success

A total of 399 observations of breeding success across 272 individuals ringed as chicks were recorded during 2010-2012. Across the reduced dataset, both resident males and females tended to fledge more chicks than migrant males ($\beta= -0.16$, $p =0.09$), and females ($\beta= -0.22$, $p =0.05$) respectively. This difference was not significant for males, and only marginally significant for females. However, the estimated effects were similar to those estimated across the full dataset; slightly smaller for males and slightly larger for females (main text, Table 3).

The non-significant effect in males therefore primarily reflects reduced statistical power resulting from excluding observed individuals that had been ringed as adults rather than any substantively different biological effect.

When cohort was included in the breeding success analysis, resident males and females still tended to fledge slightly more chicks than migrant males ($\beta = -0.17$, $p=0.12$), and females ($\beta = -0.12$, $p=0.33$) although the effects were again not significant. However, the cohort effects were also non-significant for both males ($\chi^2 = 7.7$, $p=0.80$) and females ($\chi^2 = 14.7$, $p=0.20$).

When age was included in the breeding success analysis, resident males and females again tended to fledge slightly more chicks than migrant males ($\beta = -0.17$, $p=0.10$), and females ($\beta = -0.17$, $p=0.14$); the estimated effects were similar to those estimated across the full dataset (main text table 1), but again not significant due to the reduced statistical power. The linear and quadratic effects of age were also not significant for males (age: $\beta = 0.09$, $p=0.10$, age²: $\beta = 0.01$, $p=0.10$), but significant for females (age: $\beta = 0.21$, $p=0.01$, age²: $\beta = -0.01$, $p=0.02$).

Conclusions

Overall, our analyses of reduced datasets comprising individual shags that had been ringed as chicks showed that including age or cohort in the models did not substantially alter the size or direction of the estimated effects of migratory strategy on hatch date or breeding success. Further, any covariance attributed to age or cohort in these analyses must be interpreted with caution given that our data are cross-sectional, and that individual shags are rarely observed to switch migratory strategy between years. The estimated age and cohort effects could consequently be spurious consequences of selective disappearance. It is therefore unlikely that the relationships between reproductive performance and migratory strategy described in the main text are substantively caused by age or cohort effects (see also the ‘Mechanisms and implications’ section in the main manuscript Discussion).

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Appendix III: Relationship between migratory strategy and reproductive performance in shags across individual years 2009-2012.

The analyses relating migratory strategy to sex and reproductive performance presented in the main text utilised all data from the full study period 2009-2012. Here, we provide more detailed descriptive statistics and analyses for each consecutive winter-summer period 2009-2010, 2010-2011 and 2011-2012 separately.

Data structure in each year

Overall, 825, 1010 and 1200 individual colour-ringed shags were observed breeding on the Isle of May in summers 2010, 2011 and 2012 respectively. Totals of 305, 808 and 1025 resightings of these adults were recorded across the winter survey areas (main text, Fig. 1) during the winter immediately preceding each summer (i.e. 2009-2010, 2010-2011 and 2011-2012 respectively). These resightings allowed totals of 112, 254 and 285 individuals to be classified as migrant or resident in the three winters following the strict criteria, comprising 14%, 25% and 24% of all individuals observed breeding in the subsequent summer.

Of the individuals retained in the dataset, 39 (35%), 153 (60%) and 161 (56%) were classified as residents in winters 2009-2010, 2010-2011 and 2011-2012 respectively (Table A3.1). This among-year variation in the proportions of individuals that were classified as residents rather than migrants reflects among-year variation in the spatio-temporal distribution of resighting surveys, not necessarily among-year variation in population-wide migratory strategy (Appendix I).

Male & female migratory strategy in each year

Of the known-sex individuals that were classified as resident or migrant, 75 (68%), 129 (51%) and 149 (53%) were males in the three winters respectively (Table A3.1).

In total, 71%, 47% and 54% of known-sex residents were male in the three winters respectively, and 65%, 57% and 52% of known-sex migrants were male (Table A3.1).

Individuals that were classified as migrants were not significantly more likely to be male than female in any single winter (Table A3.1).

Table A3.1. Numbers of individual adult male (M) and female (F) shags classified as resident or migrant in winters 2009-2010, 2010-2011 and 2011-2012. ‘% residents’ gives the percentage of individuals of each sex that was classified as resident. ‘% male’, ‘% residents male’ and ‘% migrants male’ respectively give the percentages of all known-sex individuals, and of known-sex individuals classified as residents and migrants, that were male. Individuals of unknown sex comprised 1 migrant in 2009-2010, 2 residents in 2010-2011 and 1 resident in 2011-2012. β is the binomial model estimate for the effect of sex on migratory strategy (± 1 standard error) and p is the probability that the estimated effect could be observed by chance.

Winter	Sex	No. of residents	No. of migrants	Total	% residents	% male	% residents male	% migrants male	$\beta \pm 1SE$	p
2009-2010	M	28	47	75	37	68	71	65	-0.30 \pm 0.43	0.48
	F	11	25	36	31					
2010-2011	M	71	58	129	55	51	47	57	0.41 \pm 0.26	0.11
	F	80	43	123	65					
2011-2012	M	86	63	149	58	53	54	52	-0.08 \pm 0.24	0.73
	F	74	59	133	56					

Male & female migratory strategy and hatch date

There were 100, 217 and 243 known sex individuals that were classified as resident or migrant in winters 2009-2010, 2010-2011 and 2011-2012 whose hatch date was observed or estimated in summers 2010, 2011 and 2012 respectively. Mean hatch dates ($\pm 1SD$) were 19 May ± 6.0 days, 12 May ± 9.5 days and 12 May ± 11.4 days in summers 2010, 2011 and 2012 respectively.

Table A3.2. Summary statistics and modelled relationships between brood hatch date and migratory strategy of male (M) and female (F) shags that bred in summers 2010, 2011 and 2012. Raw mean (± 1 standard deviation) hatch dates of broods produced by migrant and resident males and females are expressed as days since 1st April. β is the model-estimated effect size for migrants versus residents (with 95% confidence intervals), and p is the probability that the estimated effect could be observed by chance.

Summer	Sex	No. of residents	No. of migrants	Resident	Migrant	β [95%CI]	p
				raw mean $\pm 1SD$	raw mean $\pm 1SD$		
2010	M	26	40	47.2 \pm 5.9	50.3 \pm 6.0	3.1 [0.2, 6.0]	0.04
	F	10	23	47.3 \pm 6.4	48.2 \pm 6.4	0.9 [-3.8, 5.6]	0.73
2011	M	63	47	39.9 \pm 8.6	44.9 \pm 9.2	4.9 [2.0, 7.9]	<0.01
	F	69	26	37.8 \pm 11.8	44.6 \pm 11.7	6.8 [1.4, 12.2]	0.01
2012	M	74	48	41.1 \pm 11.2	46.6 \pm 14.1	5.5 [1.4, 9.7]	0.01
	F	61	41	38.7 \pm 11.4	46.8 \pm 10.2	8.1 [3.0, 13.2]	<0.01

Resident male shags hatched chicks significantly earlier than migrant males in all three years, with mean differences of approximately 5 days in 2011 and 2012 and 3 days in 2010 (Table A3.2). Similarly, resident female shags hatched chicks significantly earlier than migrant females in 2011 and 2012, with mean differences of approximately 6 and 8 days respectively (Table A3.2). Hatch date did not differ between resident and migrant females in 2010, but sample sizes were small (Table A3.2).

Male & female migratory strategy and breeding success

There were 112, 254 and 285 known-sex individuals that were classified as resident or migrant in winters 2009-2010, 2010-2011 and 2011-2012, and whose breeding success was recorded in summers 2010, 2011 and 2012 respectively. Mean ($\pm 1SD$) breeding success was 2.3 ± 1.1 , 2.1 ± 1.1 and 1.6 ± 1.1 chicks in 2010, 2011 and 2012 respectively, and individual breeding success ranged from 0-4 chicks fledged across all three years (Table A3.3).

Table A3.3. Raw breeding success of individual shags across summers 2010-2012. Breeding success is the number of chicks fledged.

Summer	Breeding success				
	0	1	2	3	4
2010	9	15	28	56	4
2011	32	34	77	107	4
2012	55	70	98	61	1

In general, resident male and female shags tended to fledge slightly more chicks than migrant males and females in each of the three years. The estimated differences spanned approximately 0.1-0.3 chicks per year, and were significantly greater than zero for males in 2012 (Table A3.4). The only exception was that resident females tended to fledge fewer chicks than migrant females in 2010, but sample sizes were small and the estimated effect did not differ significantly from zero (Table A3.4).

Table A3.4. Summary statistics and modelled relationships between breeding success and migratory strategy of male (M) and female (F) shags that bred in summers 2010, 2011 and 2012. Raw mean (± 1 standard deviation) breeding success of migrant and resident males and females are shown. β is the model-estimated effect size for migrants versus residents (with 95% confidence intervals), and p is the probability that the estimated effect could be observed by chance.

Summer	Sex	No. residents	No. migrants	Resident raw mean ± 1 SD	Migrant raw mean ± 1 SD	β [95%CI]	p
2010	M	28	47	2.4 \pm 1.1	2.2 \pm 1.0	-0.11 [-0.42, 0.20]	0.47
	F	11	25	2.1 \pm 0.9	2.4 \pm 1.0	0.12 [-0.35, 0.62]	0.62
2011	M	71	58	2.2 \pm 1.1	1.8 \pm 1.1	-0.17 [-0.42, 0.08]	0.18
	F	80	43	2.3 \pm 1.0	1.8 \pm 1.1	-0.22 [-0.49, -0.04]	0.10
2012	M	86	63	1.9 \pm 1.0	1.4 \pm 1.0	-0.28 [-0.55, -0.03]	0.03
	F	74	59	1.6 \pm 1.0	1.3 \pm 1.0	-0.22 [-0.51, 0.07]	0.14

Appendix IV: Details of estimates of assortative pairing between male and female colour-ringed shags with different migratory strategies.

There were 112, 254 and 285 known sex adult colour-ringed shags that were classified as resident or migrant in winters 2009-2010, 2010-2011 and 2011-2012 respectively, whose brood hatch date was observed or estimated on the Isle of May in summers 2010, 2011 and 2012 respectively. Of these individuals, there were 75 breeding attempts where both the male and female were classified as resident or migrant based on resightings during the immediately preceding winter: 7, 31 and 37 in 2010, 2011 and 2012 respectively (Table A4.1).

These attempts involved 66 individual females and 65 individual males, of which 57 females and 55 males bred in one year, and 9 females and 10 males bred in two years. They included 50 attempts made by 50 discrete female-male pairs that bred with each other once during the focal study years, 10 attempts made by 5 discrete pairs that bred with each other twice, and 15 attempts made by pairs where one or both individuals also bred with a different mate within the dataset.

A chi-squared test was used to test whether the frequency of pair migratory strategies differed from that expected by chance. Data were pooled across years because sample sizes were insufficient to consider each year separately. The expected values were calculated by dividing the total number of individuals of each sex observed by the number of that sex observed of each migratory strategy, and then multiplying the probabilities for the relevant male and female strategies. For example, the expected number of migrant-migrant pairs was calculated by dividing the total number of males observed by the total number of male migrants observed, dividing the total number of females observed by the total number of female migrants observed, and multiplying these two values together.

The observed frequencies of pair migratory status did not differ from those expected given random pairing ($\chi^2_3 = 6.1$, $p = 0.11$). Resident and migrant shags were therefore no more or less likely to pair with resident or migrant mates than expected by chance.

Table A4.1 The number of each type of migratory pairing (‘migrant-migrant’, ‘resident male, migrant female’, ‘resident female, migrant male’, ‘resident resident’) of colour-ringed shags observed breeding on the Isle of May during summers 2010, 2011 and 2012. ‘F’ and ‘M’ denote female and male respectively.

Summer	F Migrant	F Resident	F Migrant	F Resident	Total
	M Migrant	M Migrant	M Resident	M Resident	
2010	4	0	1	2	7
2011	3	7	5	16	31
2012	8	4	8	17	37
All years	15	11	14	35	75

Appendix V: Analysis of variation in hatch date and breeding success between four focal wintering areas of colour-ringed shags.

Our primary aim was to test whether reproductive performance differed between individuals that remained resident at the focal breeding colony and individuals that migrated to focal winter areas located ca. 200-300km north. However, to further investigate whether reproductive performance differed between shags that wintered in different geographical areas within the overall focal areas, four wintering areas were defined (Fig. A5.1). Since individual shags make small-scale movements between day and night roosts within a restricted geographical range, a wintering area was defined as a group of known roost sites within <15km (Fig. A5.1).

To quantify variation in reproductive performance between wintering areas, separate analyses were conducted with hatch date and breeding success as dependent variables. All years were pooled using a mixed effects model, with fixed effects of wintering area (areas 1-4, Fig. A5.1) and year, and random individual effects. The overall significance of the relationship between hatch date or breeding success and wintering area was calculated by comparing models with or without wintering area as an explanatory factor using likelihood ratio tests. The significance of differences between wintering areas was calculated using a Tukey post-hoc test.

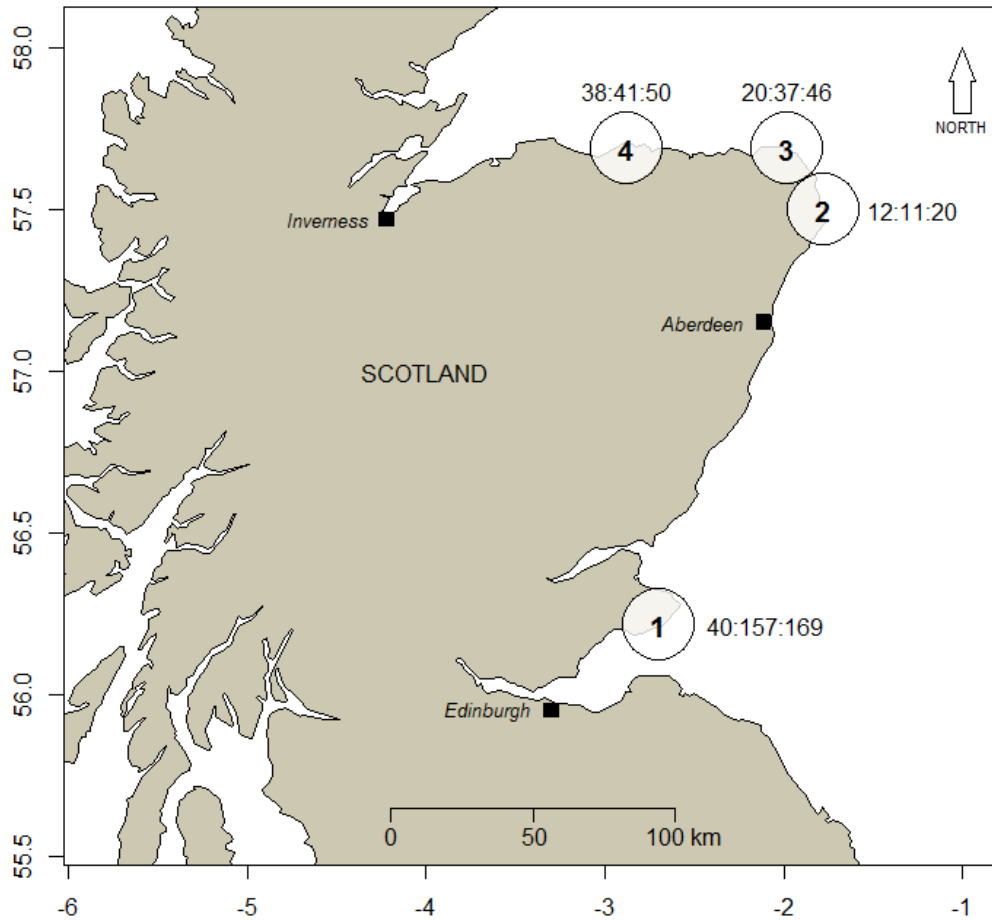


Figure A5.1. Wintering areas of colour-ringed shags breeding on the Isle of May in summers 2010, 2011 and 2012. Figures show the total number of individual shags (of both sexes) that were assigned to each wintering area (1-4) during winters 2009-2010, 2010-2011 and 2011-2012 respectively, that were recorded breeding on the Isle of May in the subsequent summer. Area 1 encompasses the Isle of May, and hence holds resident shags.

1.1.1 Sex-specific wintering area and hatch date

Overall, mean hatch date varied significantly among individuals wintering in different areas in both males (LRT: $\chi^2= 28.3$, $p<0.01$, Fig A5.2) and females ($\chi^2= 18.1$, $p<0.01$; Fig A5.2) Males and females wintering in Area 1 (i.e. residents) hatched broods a mean of 3-7 days and 4-9 days earlier than males and females wintering in the other three areas (i.e. migrants, Fig

A5.1; Fig A5.2; Table A5.1). There was no pattern of later hatch date with increasing distance of wintering area from the Isle of May (e.g. from areas 2-4, Fig. A5.1).

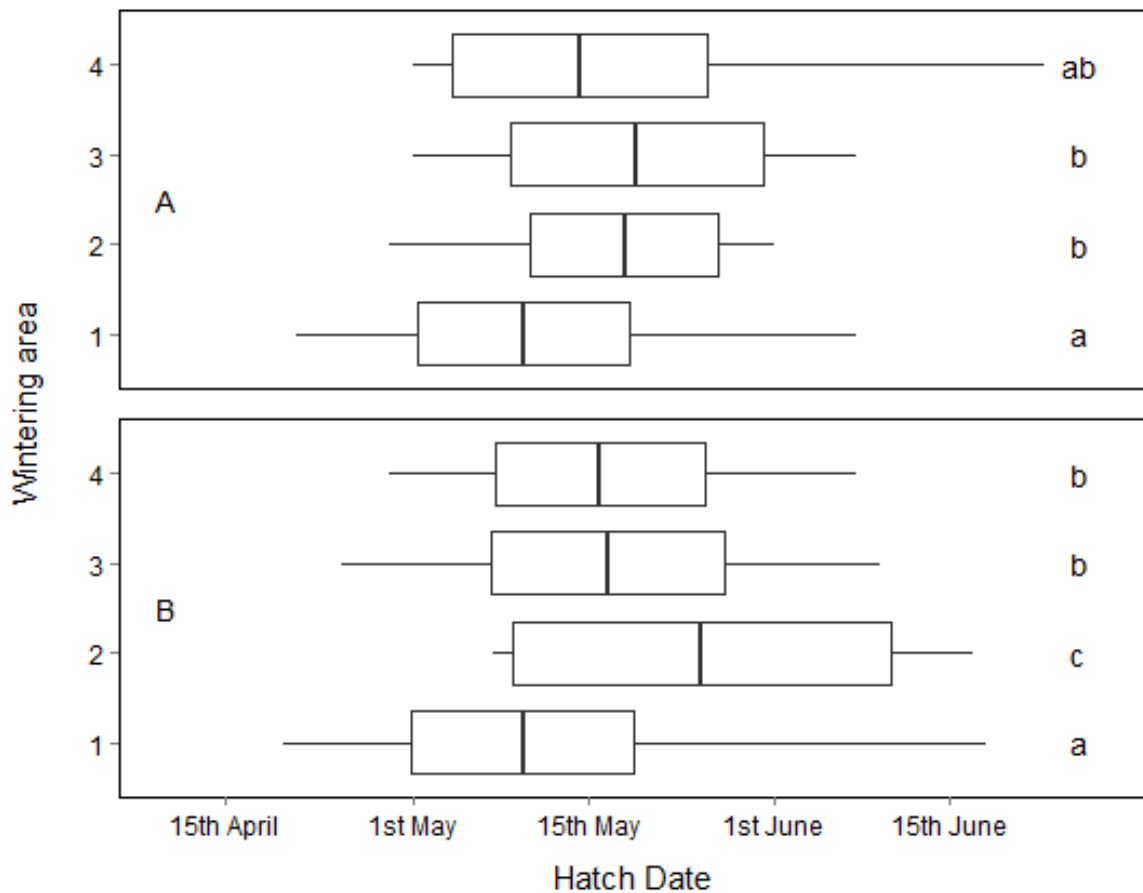


Figure A5.2. Hatch date of broods produced on the Isle of May in summers 2010-2012 by (A) female and (B) male colour-ringed shags that wintered in different areas. Individuals wintering in area 1 are resident, and individuals wintering in areas 2-4 are migrant. Areas are numbered with increasing distance from the breeding colony on Isle of May. Thick bars and boxes show raw mean hatch date \pm 1 standard deviation, and whiskers demarcate the full range. Lowercase letters indicate significantly different modelled groups.

Table A5.1. Summary statistics and modelled relationships between brood hatch date and wintering area of male (M) and female (F) shags that bred in summers 2010-2012. Raw mean hatch dates of broods are expressed as days since 1st April. β is the model-estimated effect size relative to zero (with 95% confidence intervals). Individuals wintering in area 1 are resident, and individuals wintering in areas 2-4 are migrant.

Wintering area	Sex	No. individuals	No. breeding attempts	Raw mean hatch date	β [95% CI]
1	M	122	167	40	46.4 [43.6, 49.3]
	F	111	142	40	44.1 [39.8, 48.3]
2	M	5	7	56	62.8 [54.5, 71.0]
	F	21	28	49	51.3 [46.1, 56.5]
3	M	41	60	47	52.1 [48.7, 55.6]
	F	18	19	50	53.1 [47.0, 59.0]
4	M	40	59	46	51.2 [47.9, 54.5]
	F	26	36	45	47.6 [43.1, 52.2]

1.1.2 Sex-specific wintering area and breeding success

The mean number of chicks fledged differed significantly among individuals that wintered in different areas for both males (LRT: $\chi^2= 14.3$, $p<0.01$, Fig. A5.3, Table A5.2) and females ($\chi^2= 10.2$, $p=0.02$; Fig. A5.3, Table A5.2). Males and females that wintered in the Isle of May area (Fig. A5.1) fledged the most chicks (Fig. A5.3). Breeding success did not differ between males and females that migrated to different areas, and there was no consistent pattern of decreasing breeding success with increasing distance from the Isle of May (i.e. between areas 2-4; Fig. A5.1).

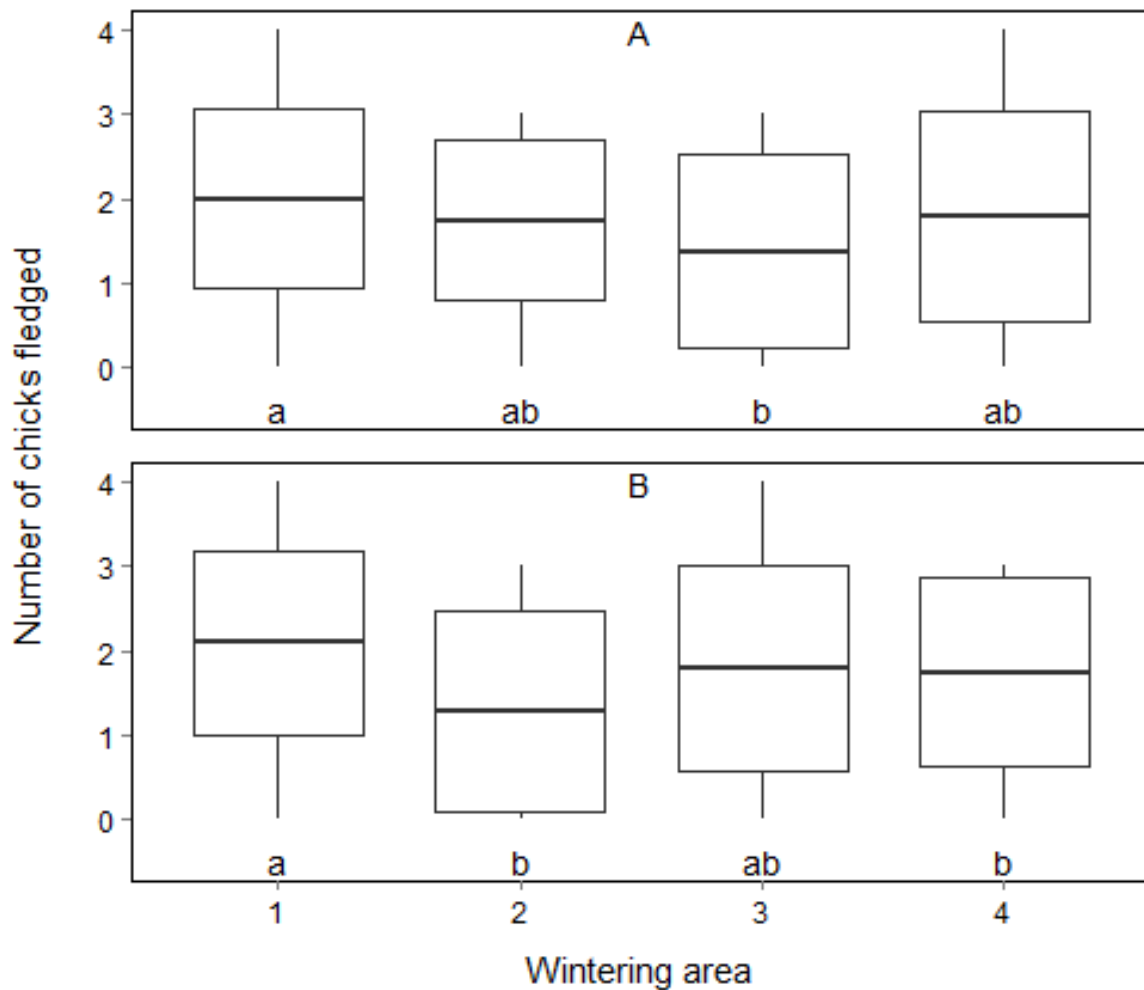


Figure A5.3. Breeding success (i.e. number of chicks fledged) on the Isle of May in summers 2010 - 2012 of (A) female and (B) male colour-ringed shags that wintered in different areas. Individuals wintering in area 1 are resident, and individuals wintering in areas 2-4 are migrant (Fig. A5.1). Thick bars and boxes show raw mean hatch date \pm 1 standard deviation, and whiskers demarcate the full range. Lowercase letters indicate significantly different modelled groups.

Table A5.2. Summary statistics and modelled relationships between breeding success and wintering area of male (M) and female (F) shags that bred in summers 2010-2012. Raw mean breeding success is expressed as the number of chicks fledged successfully. β is the model-estimated effect size (with 95% confidence intervals). Individuals wintering in area 1 are resident, and individuals wintering in areas 2-4 are migrant.

Wintering area	Sex	No. individuals	No. breeding attempts	Raw mean breeding success	β [95% CI]
1	M	137	195	2.1	0.94 [0.76, 1.11]
	F	128	168	2.0	0.96 [0.71, 1.21]
2	M	8	11	1.3	0.39 [-0.14, 0.92]
	F	23	32	1.8	0.8 [0.48, 1.11]
3	M	46	76	1.8	0.76 [0.54, 0.97]
	F	25	27	1.4	0.60 [0.21, 0.99]
4	M	47	77	1.7	0.71 [0.51, 0.92]
	F	36	49	1.8	0.79 [0.53, 1.05]

Conclusions

These analyses confirm that in both sexes residents hatched their broods consistently earlier than migrants and had higher breeding success. However, we found no consistent variation in reproductive performance between migrants that moved to different wintering areas. Sample sizes for Areas 2-4 were small and thus our power to detect differences in reproductive performance between the three migrant areas is fairly low. Future analyses of larger datasets might consequently reveal differences which we cannot currently detect.