Strong survival selection on seasonal migration versus residence induced by extreme climatic events

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ABSTRACT

1. Elucidating the full eco-evolutionary consequences of climate change requires quantifying the impact of extreme climatic events (ECEs) on selective landscapes of key phenotypic traits that mediate responses to changing environments. Episodes of strong ECE-induced selection could directly alter population composition, and potentially drive micro-evolution. However, to date, few studies have quantified ECE-induced selection on key traits, meaning that immediate and longer-term eco-evolutionary implications cannot yet be considered.

2. One widely-expressed trait that allows individuals to respond to changing seasonal environments, and directly shapes spatio-seasonal population dynamics, is seasonal migration versus residence. Many populations show considerable among-individual phenotypic variation, resulting in 'partial migration'. However, variation in the magnitude of direct survival selection on migration versus residence has not been rigorously quantified, and empirical evidence of whether seasonal ECEs induce, intensify, weaken or reverse such selection is lacking.

3. We designed full-annual-cycle multi-state capture-recapture models that allow estimation of seasonal survival probabilities of migrants and residents from spatio-temporally heterogeneous individual resightings. We fitted these models to nine years of geographically extensive year-round resighting data from partially migratory European shags (*Phalacrocorax aristotelis*). We thereby quantified seasonal and annual survival selection on migration versus residence across benign and historically extreme non-breeding season (winter) conditions, and tested whether selection differed between females and males.

4. We show that two of four observed ECEs, defined as severe winter storms causing overall low survival, were associated with very strong seasonal survival selection against residence. These episodes dwarfed the weak selection or neutrality evident otherwise, and hence caused selection through overall annual survival. The ECE that caused highest overall mortality and

strongest selection also caused sex-biased mortality, but there was little overall evidence of sex-biased selection on migration versus residence.

5. Our results imply that seasonal ECEs and associated mortality can substantially shape the landscape of survival selection on migration versus residence. Such ECE-induced phenotypic selection will directly alter migrant and resident frequencies, and thereby alter immediate spatio-seasonal population dynamics. Given underlying additive genetic variation, such ECEs could potentially cause micro-evolutionary changes in seasonal migration, and thereby cause complex eco-evolutionary population responses to changing seasonal environments.

KEY-WORDS

INTRODUCTION

Major aims in contemporary biology are to quantify interacting ecological and evolutionary processes that shape population responses to environmental change (Chevin, Lande, & Mace, 2010; Hoffmann & Sgrò 2011; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Moritz & Agudo, 2013). Among ongoing global changes, climate change is predicted to cause increasing frequencies and intensities of extreme climatic events ("ECEs"; e.g. storms, droughts, floods) that drastically alter environmental quality (Easterling et al., 2000; Coumou & Rahmstorf 2012; Ummenhofer & Meehl 2017). Such ECEs can clearly cause severe mortality or reproductive failure, thereby directly reducing population sizes and threatening population persistence (Brown & Bomberger Brown 1998; Parmesan et al., 2000; Welbergen, Klose, Markus, & Eby, 2007; van de Pol et al., 2010; Niu et al., 2014; but see Hansen et al.,

2019). However, beyond these primary demographic impacts, ECEs could also cause

episodes of strong direct phenotypic selection, defined as differential mortality or

reproduction with respect to key phenotypic traits that mediate responses to climate-induced

environmental variation (Grant & Grant 1995; Brown & Bomberger Brown 1998; Marrot,

Garant, & Charmantier, 2017). Given underlying additive genetic variance, such ECEs could

then drive rapid microevolution of key climate-sensitive traits, and hence exert long-lasting

effects on population ecology and dynamics (Grant et al., 2017). Quantifying the form,

magnitude and variability of ECE-induced selection on such traits is thus one central

component of understanding and forecasting eco-evolutionary consequences of climate

change. However, very few such studies currently exist (Bailey & van de Pol 2016; Marrot et

al., 2017; Maxwell et al., 2019).

One taxonomically widespread trait that allows many animals to overcome climatic and

environmental variation is seasonal migration (hereafter "migration"), defined as reversible

individual movements between locations across seasons (Dingle 1996; Newton 2008).

Migration allows individuals to exploit spatially-restricted seasonal resource peaks while

avoiding seasonally hostile environments, thereby enhancing survival and/or reproduction

and directly causing spatio-seasonal population dynamics (e.g. Skov et al., 2013; Avgar,

Street, & Fryxell 2013; Zúñiga et al., 2017; Reid et al., 2018). Further, many populations are

"partially migratory", where some individuals remain resident in their breeding location year-

round while other individuals are seasonal migrants (Lundberg 1988; Chapman, Brönmark,

Nilsson, & Hansson, 2011; Hsiung, Boyle, Cooper, & Chandler, 2018). Because partial

migration can cause sympatric-breeding individuals to be spatially segregated in non-

breeding seasons, partially-migratory populations could potentially experience episodes of

extremely strong direct survival selection on migration versus residence caused by localised

non-breeding season ECEs (Reid et al., 2018). For example, residents could experience high

mortality during an ECE while migrants that moved to unaffected locations survive (or conversely, migrants could be impacted). By definition, such strong survival selection would cause an immediate shift in the current proportion of residents versus migrants within a population, and hence in seasonal population distributions and dynamics. Further, given underlying additive genetic variance, such events could cause micro-evolutionary change in migration propensity (Pulido 2007, 2011). This could potentially generate a form of 'evolutionary rescue' (e.g. Gonzalez, Ronce, Ferriere, & Hochberg, 2013) of populations facing increasing risk of localised seasonal ECEs, which would profoundly alter spatio-seasonal ecology (Reid et al., 2018). To understand the potential for such outcomes, we first need to quantify the magnitude and form of ECE-induced selection. However, such selective landscapes of seasonal migration versus residence have not been rigorously quantified in any system (Reid et al., 2018).

In general, the dynamics of any trait will depend on the degree to which ECE-induced selection intensifies or opposes selection occurring under more typical non-extreme conditions, thereby generating strong directional or fluctuating selection overall (Bailey & van de Pol 2016; Grant & Grant 2017). Such outcomes will also depend on any sex difference in mean phenotype, and any associated sex-bias in the magnitude of ECE-induced impacts and resulting sex-biased selection (Kruuk, Slate, & Wilson, 2008). Quantifying these key effects for non-breeding season migration versus residence as the focal trait requires data on survival of large numbers of migrants and residents of both sexes across diverse environmental conditions. This requires recording geographical locations of sympatric-breeding and allopatric-nonbreeding individuals across seasons, at sufficiently fine temporal resolution to pinpoint ECE effects. Further, data encompassing multiple ECEs are ideally needed to assess within-system consistency and facilitate among-system comparisons (Bailey & van de Pol 2016; Altwegg, Visser, Bailey, & Erni 2017).

110   Such quantification of seasonal survival selection is highly data-demanding and

111   technically challenging, and has rarely been achieved for any trait in any system. One

112   approach is to mark individuals with field-readable tags, and undertake year-round large-

113   scale resightings. Such resightings are inevitably restricted and incomplete, to degrees that

114   vary in time and space. Individual phenotypic expression of migration versus residence and

115   associated survival, and hence survival selection, are therefore only partially observable.

116   However, the required parameters can be estimated using advanced capture-recapture

117   analyses that account for resighting failure and resulting uncertainty (Cam 2009).

118   Accordingly, we designed full-annual-cycle multi-state capture-recapture models that

119   allow estimation of survival probabilities of seasonal migrants and residents within and

120   across years, and hence allow estimation of survival selection on migration versus residence.

121   We fitted these models to nine years of year-round resighting data from partially migratory

122   European shags (*Phalacrocorax aristotelis*) experiencing non-extreme and historically

123   extreme non-breeding season conditions. We *a priori* defined four ECEs that occurred during

124   the study period, each comprising a different extreme winter storm event that caused major

125   coastal and marine environment perturbations and widely observed mortality of birds and

126   other marine wildlife (see *Methods*, Appendix S1). We first tested whether these four defined

127   seasonal ECEs were associated with episodes of seasonal survival selection on migration

128   versus residence, and whether these episodes intensified or opposed seasonal selection

129   occurring under non-extreme conditions. We then tested whether the four ECEs were

130   associated with sex-biased mortality and/or sex-biased seasonal selection, and quantified the

131   degree to which episodes of seasonal survival selection scaled up to cause selection at the

132   annual timescale. We thereby illustrate how ECEs can cause episodes of survival selection

133   that directly alter the sex-specific population proportions of migrants versus residents, and

discuss how such selection could potentially drive micro-evolutionary responses to changing

seasonality.

MATERIALS AND METHODS

Study system and data collection

A population of European shags (hereafter "shags") breeding on Isle of May National Nature

Reserve (hereafter "IoM"), Scotland (56°11′N, 2°33′W), provides a valuable opportunity to

quantify survival selection on migration versus residence across diverse environmental

conditions, including ECEs. Shags are colonially-breeding seabirds which, since they have

partially-wettable plumage, must roost onshore every day to dry and thermoregulate

(Grémillet, Tuschy, & Kierspel, 1998; Harris & Swann 2002). Marked individuals can

therefore be visually resighted, and hence locations directly recorded, all year. The focal

population is partially migratory: some individuals remain around IoM all year, while other

individuals migrate up to ~500 km along east coasts of Scotland and northern England (Grist

et al., 2014; Fig. 1). Such migration distances and resulting spatial spread of individuals is

typical of numerous partially migratory species, spanning fish, mammals and birds (e.g.

Chapman et al., 2011; Papastamatiou et al., 2013, Eggeman, Hebblewhite, Bohm,

Whittington, & Merrill, 2016; Zúñiga et al., 2017; Sawyer, Merkle, Middleton, Dwinnell, &

Monteith, 2018). Further, the focal population is known to experience episodes of high

mortality caused by ECEs involving onshore gales and heavy rain that impede foraging and

thermoregulation (Appendix S1; Frederiksen, Daunt, Harris, & Wanless, 2008).

To monitor individual life-histories, since 1997 ~80% of chicks that survived to ~3

weeks post-hatch were captured at the nest (using a crook, or occasionally by hand) and

marked with a uniquely-coded colour ring (field readable at distances up to ~150m with a

telescope) alongside a uniquely-inscribed metal ring (Appendix S1). Adult breeders

158 (typically aged ≥3 years) alive prior to 1997, and subsequent unringed recruits, were similarly

159 caught and ringed as far as feasible. During ten breeding seasons (April–June 2009–2018),

160 ringed breeding adults were systematically identified at their nests (~95% of all breeders;

161 Appendix S1). Further observations at adjacent roost areas allowed identification of ringed

162 non-breeders and early-failed breeders, thereby ensuring very high breeding season adult

163 resighting probability (Barlow, Daunt, Wanless, & Reid, 2013; Grist et al., 2017). Individuals

164 were sexed based on vocalisations and/or genotype (Appendix S1).

165   During the intervening nine non-breeding seasons ("winters", September–February

166 2009-2018) we conducted resighting surveys around IoM and more widely to locate

167 individuals and thereby distinguish residents and migrants. Key roost sites across eastern

168 Scotland, identified during pilot fieldwork in 2008–2009, were surveyed every ~2 weeks

169 (Fig. 1; Appendix S1). Additional known roost sites were surveyed less frequently, and

170 opportunistic resightings from birdwatchers were actively solicited (Fig. 1).

171   The 2009–2018 study period encompassed diverse climatic conditions, from benign to

172 historically extreme. In particular, the eastern Scotland coastline experienced severe storms

173 in December 2012, February 2013, January 2014, and February-March 2018 (Appendix S1).

174 These four events involved different forms of unusually strong and/or protracted onshore

175 winds resulting in extremely rough sea states, coupled with intense precipitation or low

176 temperature (Appendix S1). We therefore expected these events to be biologically-relevant

177 (following Bailey & van de Pol 2016) to our study system by causing low over-winter shag

178 survival, as observed for similar storms in previous decades (Frederiksen et al., 2008) and

179 confirmed by our analyses (see *Results*). We thus defined these four events as ECEs (further

180 details in Appendix S1). Given the complex multidimensional nature and spatial structure of

181 underlying weather conditions (Appendix S1), we had no strong *a priori* prediction on the

182   strength, direction, consistency or sex-specificity of any resulting selection on migration

183   versus residence, including in relation to any selection arising under more typical conditions.

184   **Model design**

185   Quantifying seasonal survival selection on migration versus residence from ring-resighting

186   data requires unbiased estimation of survival probability conditional on winter location, given

187   that location is unknown for unobserved individuals. This can be achieved by jointly

188   modelling the processes of hidden individual state-transition (i.e. movement between

189   residency and migratory area(s), and survival conditional on location) and partial observation

190   of individual states (i.e. resighting efficiency, reflecting observer effort and conditions during

191   resighting surveys). Accordingly, we formulated a discrete-time multi-state capture-recapture

192   model (Lebreton & Pradel 2002) that represents full-annual-cycle dynamics of partial

193   migration and the overlaid observational design. We modelled multiple migrant areas to

194   account for spatial heterogeneity in resighting efficiency, therefore controlling for potential

195   biases in observed movements and hence in estimates of survival for residents and migrants.

196   We defined three types of observation event: 'resighted at the residency area' (i.e. IoM

197   area), 'resighted at a migratory area' (i.e. away from IoM, divided into multiple areas; Fig. 1)

198   and 'not resighted'. We defined three types of underlying individual state: 'resident',

199   'migrant in a given area' and 'dead'. For current analyses we considered five possible

200   migratory areas (Fig. 1): three regularly-monitored areas where winter resighting effort was

201   typically high, one geographically-broad area representing all locations where resighting

202   effort was low but non-zero, and one "ghost area" where resighting probability was zero

203   (Schaub, Gimenez, Schmidt, & Pradel, 2004) representing unmonitored migrant locations

204   that presumably exist on remote coasts. Accordingly, we modelled five migrant states (i.e.

205   four observed migratory areas, plus the "ghost area" unobservable state) and four migrant

206   observation events (referring to each observable migrant state).
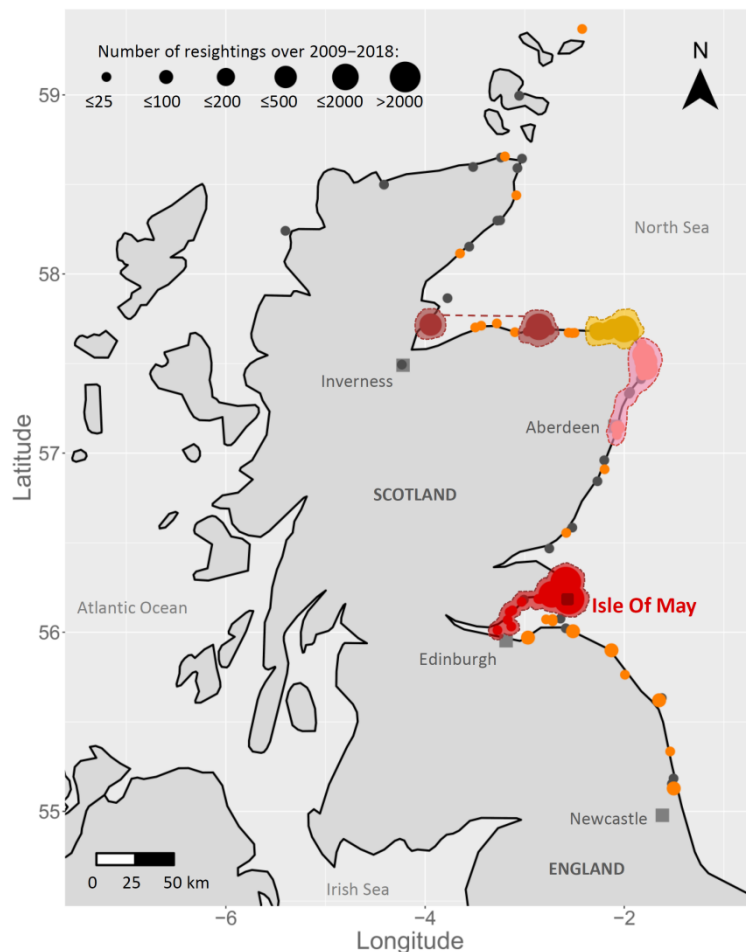
Figure 1. Locations of resightings of ringed adult shags that bred on IoM during 2009−2018. Shaded zones outline four systematically surveyed areas, comprising the residency area (red, IoM and nearby regularly visited day-roosts), and three main defined migratory areas (brown, yellow, pink). In one case, data from two locations (brown, linked by a dashed line) were pooled into a single area to provide sufficient sample sizes for current analyses. Orange points denote locations of unstructured or opportunistic resightings pooled into one low-resighting-effort "area". Dark grey points indicate additional locations of resightings that were not included in current analyses (e.g. from previous years, or of sub-adults), and are shown to indicate possible locations of unobserved individuals. A small number of locations further south are not shown.

We divided each year into five capture-resighting occasions, comprising the breeding season and four winter occasions (Fig 2a). We defined occasion time windows to capture

220 fine-scale temporal variations in survival and movement probabilities (Appendix S1), and

221 thereby isolate episodes of ECE-induced selection. The overall model structure therefore

222 generates three timeframes: years (y, one breeding season to the next), occasions within years

223 (o), and the full temporal sequence of occasions across years (t; Fig 2).

224   In each breeding season (occasion 1 within each year), new individuals enter the dataset

225 and all alive individuals are located in the residency area (i.e. the resident state; Fig. 2a). In

226 each winter occasion (occasions 2–5 within each year), alive individuals can be located in the

227 residency area or in a migratory area (i.e. the corresponding migrant state; Fig. 2a).

228 Individuals can move between residency and migratory areas between winter occasions

229 within a year (Fig. 2a). However, between each occasion 5 and subsequent occasion 1

230 individuals can only move to or remain in the residency area, and between each occasion 1

231 and subsequent occasion 2 individuals can only move from or remain in the residency area

232 (Fig. 2a). The movement process is parameterised as dependent on the state and occasion at

233 the start of each time step. Movements of current residents are described by the probabilities

234 of departing (ε), and of moving to a specific migrant area conditional on departure (δ; Fig.

235 2b). Movements of current migrants are described by the probabilities of returning to the

236 residency area (ω), and of switching between migratory areas conditional on not returning (σ;

237 Fig. 2b). Mortality occurs between occasions according to occasion-dependent and

238 migration-dependent (i.e. migrants vs. residents) survival probability (ϕ), and dead

239 individuals cannot be resighted (Fig. 2b). At each occasion, alive individuals can be resighted

240 where they are located or not resighted, according to occasion- and state-dependent

241 resighting probability (p, which is zero in the "ghost area"; Fig. 2b).

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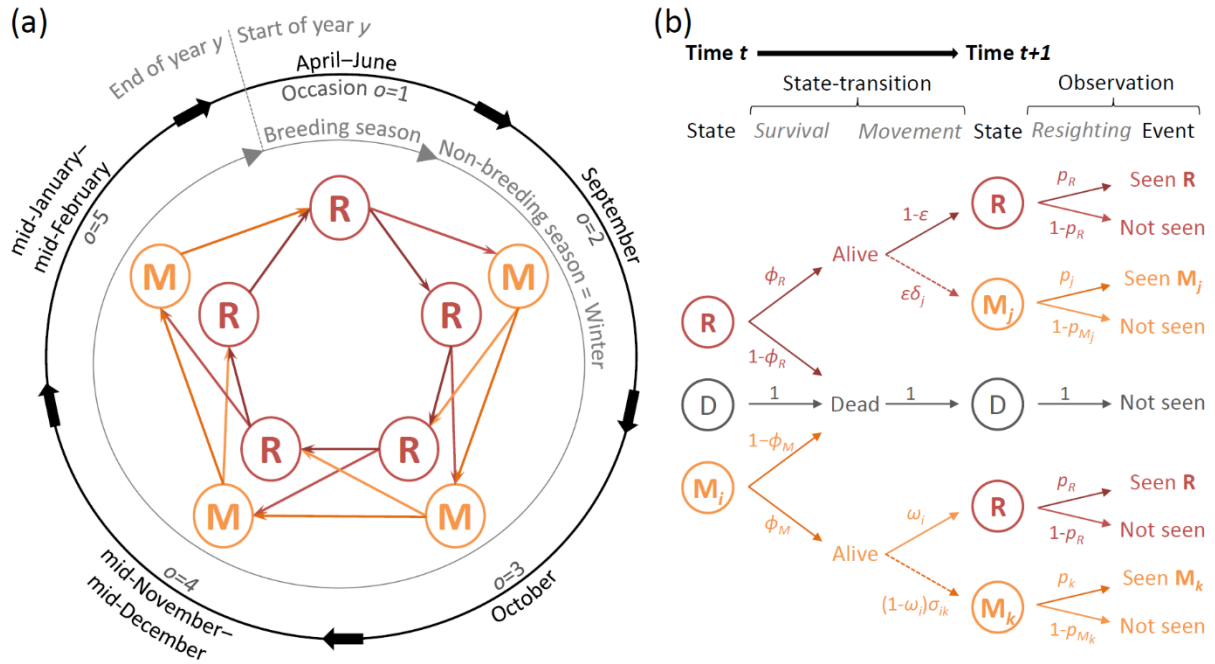
Figure 2. Structure of the multi-state capture-recapture model. Panel (a) illustrates the full-annual-cycle of partial migration, indicating possible transitions of surviving individuals between the 'resident' state (R) and 'migrant' states (M) between five consecutive defined occasions within a year. Panel (b) illustrates the fate of residents (R), migrants in area i (M_i; $i \in [\![1,5]\!]$) and dead individuals (D) from time t to $t+1$. Time goes across occasions ('o') over years ('y'), from $t=1$ ({$o=1,y=1$}: breeding season 2009) to $t=46$ ({$o=1,y=10$}: breeding season 2018); e.g. time $t=18$ is {$o=3,y=4$}: October 2012. Arrows indicate possible paths in the state-transition and observation steps, with corresponding probabilities as arrows' indices; dashed arrows symbolise multifurcations. Parameters are elementary probabilities: ϕ_R and ϕ_M for survival of residents and migrants at t, ε for departure (from the residency area), δ_j for moving to migratory area j ($j \in [\![1,5]\!]$) conditional on departure ($\Sigma(\delta_j)=1$), ω_i for return to residency (from area i), σ_{ik} for switching from migratory area i to migratory area k ($k \in [\![1,5]\!]$) conditional on not returning (i can be equal to k, and $\Sigma(\sigma_{ik})=1$; if σ is constant across space, then for $k \neq i$: $\sigma_{ik} = \frac{1-\sigma_{ii}}{4}$), p_R and p_{M_j} for resighting of residents and migrants (in area j) at $t+1$ ($p_j=0$ if j is the "ghost area"). These parameters can be occasion- and/or time-dependent (i.e. occasion×year-dependent). Between {$o=5,y$} and {$o=1,y+1$}, residents remain in the

12

259 residency and migrants return there to breed (i.e. $\varepsilon=0$, $\omega_i=1$, and δ_j, σ_{ik} are undefined), and

260 then ($o=1$) all alive individuals are residents (i.e. p_j and subsequent ϕ_M, ω_i, σ_{ik} are undefined).

261 To fit this model, we compiled individual capture-resighting histories (i.e. sequences of

262 observation events) for all adult shags known to have bred on IoM during 2009–2017,

263 starting from their first observed breeding attempt during that period. We utilised 43214

264 sightings of 2274 eligible individual adults (including 2147 individuals of known sex) and

265 collapsed multiple resightings of focal individuals in each occasion into a unique event

266 (Appendix S1). Since previous studies and recent resightings show virtually no breeding

267 dispersal from IoM (Aebischer 1995; Barlow et al., 2013; Appendix S1), estimated survival

268 probabilities primarily represent true survival with little or no confounding permanent

269 emigration.

Model analyses

271 We fitted and analysed our model with the current primary objective of estimating occasion-

272 specific survival probabilities of residents and migrants in each year, and hence quantifying

273 ECE-induced survival selection on migration versus residence across time. We built and

274 analysed the model using Stan, a probabilistic programming language for Bayesian inference

275 using Hamiltonian Monte Carlo, via package *rstan* (Carpenter et al., 2017) in R (R core team

276 2019). We formulated a general code, thereby providing tools for capture-recapture analysis

277 of other partially-migratory populations (Appendix S2). We used objective ("uninformative")

278 uniform priors for all parameters (Appendix S2). Details of posterior sampling procedures

279 and diagnostics are in Appendix S5.

280 We first analysed a main model that included interacting migration-, occasion- and year-

281 dependence (i.e. migration×time-dependence) in survival probability ϕ (Table 1). This model

282 also included interacting area-, occasion- and year-dependence (i.e. state×time-dependence)

in movement probabilities ε, δ and ω, and resighting probability p (Fig. 2b, Table 1). Because switching between migratory areas between winter occasions was rarely observed (Appendix S1), the corresponding movement probability σ was set constant across space and time (Fig. 2b, Table 1). Before drawing inference from the shag data, we fitted this model to analogous simulated data to evaluate parameter identifiability and likely capability of our model and dataset to infer survival probabilities of residents versus migrants. These analyses suggested that all focal parameters were effectively identifiable and estimable with no obvious major bias or computational problems, and that all key survival probabilities should be estimable with reasonably high precision (including for the last time step; Appendix S3). We then fitted this model to the shag data, comprising capture-resighting histories of all 2274 individuals. We evaluated model fit through posterior predictive checks (Gelman et al., 1996) devised to assess discrepancies between capture-resighting data and their posterior predictions (Appendix S4). These checks indicated good overall model fit regarding current objectives (Appendix S4).

We then tested for sex-dependence of key parameters, and hence for sex-biased migration, survival, and survival selection on migration versus residence. We extended the main model to include interacting sex-dependent variation in survival (ϕ), departure (ε), return (ω) and resighting (p) probabilities, i.e. sex×migration×time-dependence for ϕ and sex×state×time-dependence for ε, ω, and p (Table 1). We did not include sex-dependence in δ or σ (Table 1), because previous analyses revealed no major sex biases in migrants' destinations (Grist et al., 2014; Appendix S1). This model was fitted to capture-resighting histories of 2147 known-sex adults, and posterior predictive checks again indicated good overall fit.

Table 1. Summary of multi-state capture-recapture model parameterisations for current analyses.

Model	Survival	Movement				Resighting
		From the residency area		From a migratory area		
		Departing	Moving to migratory area	Returning	Switching migratory area	
	(ϕ)	(ε)	(δ)	(ω)	(σ)	(p)
Main sex-independent model	M×O×Y	O×Y	A_{to}×O×Y	A_{from}×O×Y	·	A×O×Y
Sex-dependent model	M×O×Y×S	O×Y×S	A_{to}×O×Y	A_{from}×O×Y×S	·	A×O×Y×S

'M' indicates migration-dependence (i.e. migrant wherever located vs. resident), 'O' indicates occasion-dependence, 'Y' indicates year-dependence, 'A' indicates area-dependence with index '*from*' or '*to*' when it refers respectively to the area *from* or *to* which the movement occurs (if relevant), 'S' indicates sex-dependence, '×' indicates interactions, and '·' indicates a single constant parameter.

In principle, non-causal relationships between survival and migration versus residence could arise if individuals of different ages have different migration propensities and also (independently) different survival probabilities. In our study population, there is previous evidence of actuarial senescence, with adult survival declining from age 14 years (Harris, Buckland, Russell, & Wanless, 1994). However, there were too few old individuals in our current dataset to explain substantial overall variation in survival, or for age-dependent movement and survival parameters to be estimated with useful precision (Appendix S1). Inspection of observed year-to-year changes in age distributions (Appendix S1), and goodness of fit assessments (Appendix S3), provided no indications that age effects could have substantially affected current inferences.

From both models (Table 1), we derived posterior distributions for quantities of biological interest that are not elementary parameters, thereby synthesising compound effects

325   while retaining associated uncertainties. Key quantities are the probabilities of annual

326   survival, and of being a migrant (yielding the "migratory fraction"). Annual survival

327   probability given different possible paths through the partial-migration cycle (Fig. 2a) was

328   computed as the product of corresponding survival probabilities across successive occasions

329   (Appendix S2). For purposes of concise illustration, we mainly focus on two stereotypical

330   paths that were most likely to be realised (Appendix S5): full-winter migration (i.e. leaving

331   residency area by September and returning next breeding season: phenotypic sequence 'R-M-

332   M-M-M' through the annual cycle, Fig. 2a) and full-winter residence (i.e. phenotypic

333   sequence 'R-R-R-R-R', Fig. 2a). Details of estimates for other paths are in Appendix S5.

334   These derived annual survival probabilities utilise cross-sectional estimates of seasonal

335   survival conditional on migration. Consequently, they do not directly quantify fates of

336   individuals undertaking particular full-winter strategies or consider any potential carry-over

337   effects among occasions. The migratory fraction in each occasion was computed as the

338   product of appropriate seasonal survival and movement probabilities (Appendix S2).

339   To explicitly test for differences in survival probability between residents and migrants,

340   or between males and females, we computed posterior distributions of such differences ("Δ").

341   We assessed support for the sign of each difference through the posterior probability that it

342   was positive ("Pr(Δ>0)"). Pr(Δ>0) values close to 1 or 0 provide substantial support for

343   positive or negative differences respectively, while values close to 0.5 indicate similar

344   support for both (i.e. no clear evidence for either). We summarised parameter estimates and

345   derived quantities as posterior means with 95% credible intervals ('95%CRI'; further details

346   in Appendix S5).

RESULTS

Survival and movement probabilities

The main model (Table 1) revealed the decade-long pattern of temporal variation in seasonal

survival probability (Fig. 3). There were four episodes of notably low adult survival,

following occasion 4 (mid-winter) in 2012-13, and occasion 5 (late-winter) in 2012-13, 2013-

14 and 2017-18. These episodes coincide with the four *a priori* defined ECEs (December

2012, February 2013, January 2014, and February-March 2018).

Further, these ECEs were associated with two episodes of strong selection against

residents, in late-winter 2012-13 and 2017-18 (Fig. 3). Here, survival probabilities were ~0.3

higher for migrants than residents (posterior mean [95%CRI] differences, Δ: 0.31 [0.20,0.41]

in 2013 and 0.26 [0.17,0.33] in 2018, Pr(Δ>0): 1.00 for both). In contrast, there was no clear

evidence for higher or lower survival probability in migrants than residents in mid-winter

2012-13 (Δ: 0.02 [-0.11,0.16], Pr(Δ>0): 0.65) or late-winter 2013-14 (Δ: -0.03 [-0.11,0.04],

Pr(Δ>0): 0.20).

Across all other time steps (that contained no *a priori* defined ECEs) survival

probabilities were very high (Fig. 3). Differences between migrants and residents were

correspondingly small (posterior means of Δ ranged -0.05–0.06), with no consistent

directionality (grand mean 0.00; Appendix S5) indicating overall neutrality. Nonetheless,

there was evidence for higher survival of migrants than residents following occasion 4 (mid-

winter) 2015-16 (Δ: 0.05 [0.01,0.09], Pr(Δ>0): 0.99) and following occasion 3 (October)

2016-17 (Δ:0.05 [-0.01,0.11], Pr(Δ>0): 0.94), and for lower survival of migrants than

residents following occasion 2 (September) 2017-18 (Δ:-0.05 [-0.12,0.00], Pr(Δ>0): 0.04).

The magnitudes of these differences (~0.05 in adult survival) are not biologically trivial,

providing some evidence of fluctuations in selection in non-ECE years. However, any such

selection is dwarfed by the two episodes of notably strong selection against residence

372   associated with two ECEs (Fig. 3).
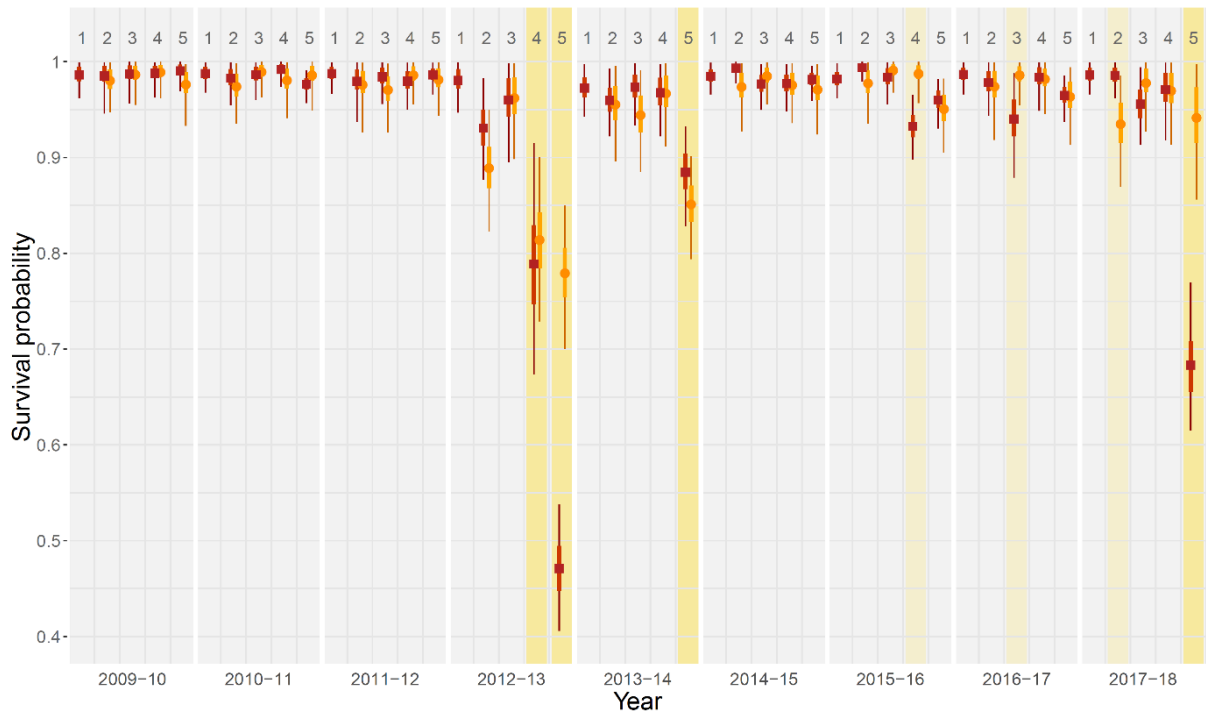
Figure 3. Seasonal survival probabilities of adult shags that bred on IoM, conditional on

   presence in the residency area (red squares) or a migratory area (orange circles) on each

   occasion. Point estimates are posterior means, inner and outer line segments indicate 50%

   and 95% credible intervals. Survival time steps span consecutive occasions within each year

   (numbered 1–5, see Fig. 2). In the breeding season, all individuals are in the residency area,

   hence there is no migrant survival probability following occasion 1. Episodes of specific

   interest are highlighted in yellow: darker bands indicate ECEs, and lighter bands indicate

   non-ECE episodes with strong support for a difference in survival probability between

   migrants and residents (i.e. selection). Note that quantitative comparison of estimates

   between occasions should account for differences in the length of interval between occasions,

   and of occasions themselves.

   Derived estimates of annual survival probabilities showed that the ECE-induced

   selection events in late winter 2012-13 and 2017-18 (Fig. 3) translated into strong selection at

the annual scale (Fig. 4; Appendix S5). Survival probabilities were ~0.2 higher for full-winter migration than for full-winter residence (Δ: 0.21 [0.12,0.29] in 2012-13 and 0.21 [0.11,0.30] in 2017-2018, Pr(Δ>0): 1.00 for both). In contrast, in the second ECE winter (2013-14), there was weak evidence for slightly lower annual survival probability for full-winter migration than for full-winter residence (Δ: -0.06 [-0.15,0.04], Pr(Δ>0): 0.12). There was no clear evidence for differences in annual survival probability between full-winter migration and full-winter residence across the six non-ECE winters (Fig. 4; Appendix S5).
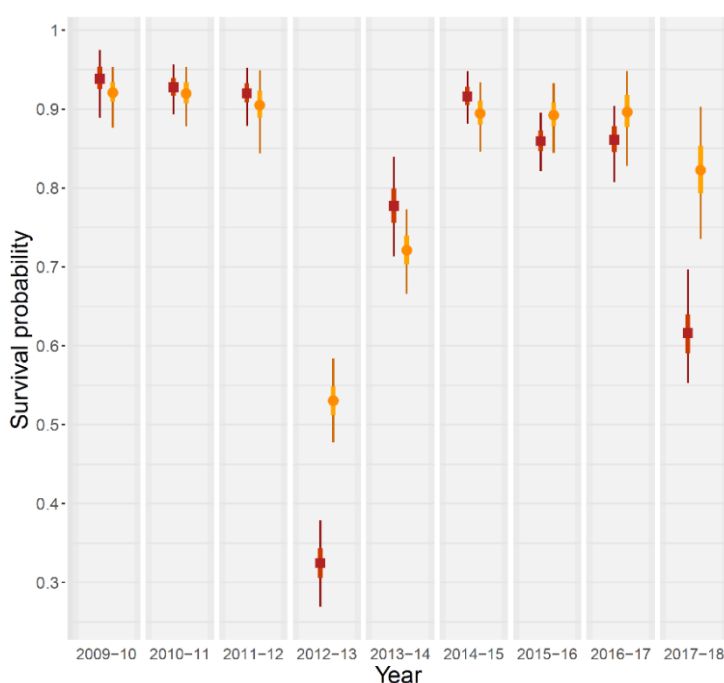
Figure 4. Annual survival probabilities of adult shags that bred on IoM, derived for full-winter residence (red squares) and full-winter migration (orange circles). Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. See Appendix S5 for other possible paths through the annual cycle.

More generally, in 2012-13 and 2017-18, there was clear evidence for differences in annual survival probabilities between the set of paths through the annual cycle (Fig. 2a) that ended as migrant in late winter versus the set of paths that ended as resident (Δ≈0.2; Appendix S5). There was no clear evidence for differences in annual survival probability

among the possible paths within each of these two sets (Appendix S5). This implies that late-winter ECE-induced selection against residents was the main driver of annual survival selection in these two years. In all other years, there was typically no strong evidence for differences in annual survival probability among the different possible paths through the annual cycle (Appendix S5).

Movement probabilities varied strongly among occasions and years (Appendix S5). However, the derived migratory fraction for the winter occasions was typically ~0.3−0.6 (posterior means ranged 0.21–0.76, grand mean 0.44; Appendix S5). This shows that, at any time in winter, the population contained substantial proportions of both residents and migrants. Specifically, immediately preceding the selective ECEs (i.e. in occasion 5 2012-13 and 2017-18), the estimated migratory fractions were 0.54 [0.44,0.66] and 0.26 [0.20,0.34] respectively. The ECE-induced selection events would therefore directly translate into marked reductions in the number and proportion of residents (see *Discussion*).

The model also confirmed that breeding season resighting probability was consistently very high (posterior means ranged 0.90–0.98, grand mean 0.95; Appendix S5). Winter resighting probability varied substantially, reflecting spatio-temporal heterogeneity in observation effort and efficiency (Appendix S5). However, it was usually reasonable and often high in the residency area (posterior means ranged 0.02–0.89, grand mean 0.47), typically high in regularly surveyed migratory areas (posterior means ranged 0.13–0.94, grand mean 0.66), and typically lower in the pooled migratory area with opportunistic resightings (posterior means ranged 0.03–0.74, grand mean 0.34). This high year-round resighting success facilitates relatively precise estimation of survival and movement probabilities.

Sex-specific probabilities

The sex-dependent model (Table 1) provided clear evidence of major sex-dependence in

survival probability during the ECE that most severely reduced overall survival (late-winter 2012-13). Survival probability was much lower in females than males in both migrants (Δ: -0.28 [-0.41,-0.14], Pr(Δ>0): 0.00) and residents (Δ: -0.14 [-0.27,-0.01], Pr(Δ>0): 0.01; Fig. 5a). Further, there was some evidence for a sex-specific difference in survival between migrants and residents, and hence for sex-biased selection. Specifically, there was some evidence for a greater difference in survival probability between migrants and residents in males than females (Δ: 0.13 [-0.05,0.32], Pr(Δ>0): 0.92), implying stronger selection against residence in males.

Across other occasions, there was no clear evidence for substantial sex-dependence in seasonal survival, or hence of sex-biased selection, although there were some small differences (posterior means of Δ ranged -0.05–0.1 in migrants and -0.14–0.07 in residents, grand means 0.00 and -0.01 respectively; Appendix S5). In addition, there was no evidence of consistent sex differences in movement probabilities or the resulting migratory fraction, except for a slightly larger proportion of September migrants in males (indicating earlier migration in males; Appendix S5).

Derived estimates of sex-specific annual survival probabilities showed a major sex difference associated with the ECEs in 2012-13 (Fig. 5b; Appendix S5). The differences in survival between females and males through this year were -0.19 [-0.30,-0.08] for full-winter migrants and -0.13 [-0.23,-0.04] for full-winter residents, (Pr(Δ>0): 0.00 for both). However, there was no evidence of sex-biased selection at the annual level (difference in migrant versus resident survival for males versus females: 0.06 [-0.10,0.22], Pr(Δ>0): 0.76). In addition, slight sex-biases in seasonal survival during 2013-2014 generated lower annual survival probabilities in females (Fig. 5). This was strongly supported for both full-winter migrants (Δ: -0.10 [-0.20,0.01], Pr(Δ>0): 0.03) and full-winter residents (-0.14 [-0.27,-0.02], Pr(Δ>0): 0.01), but again there was no clear evidence of sex-biased selection (Δ: -0.05 [-

0.23,0.14], Pr(Δ>0): 0.31). Otherwise, sex differences in annual survival probability were
smaller, with no clear directionality or consistent occurrence in any annual partial-migration
path, and no clear evidence of sex-biased selection (Fig. 5; Appendix S5).
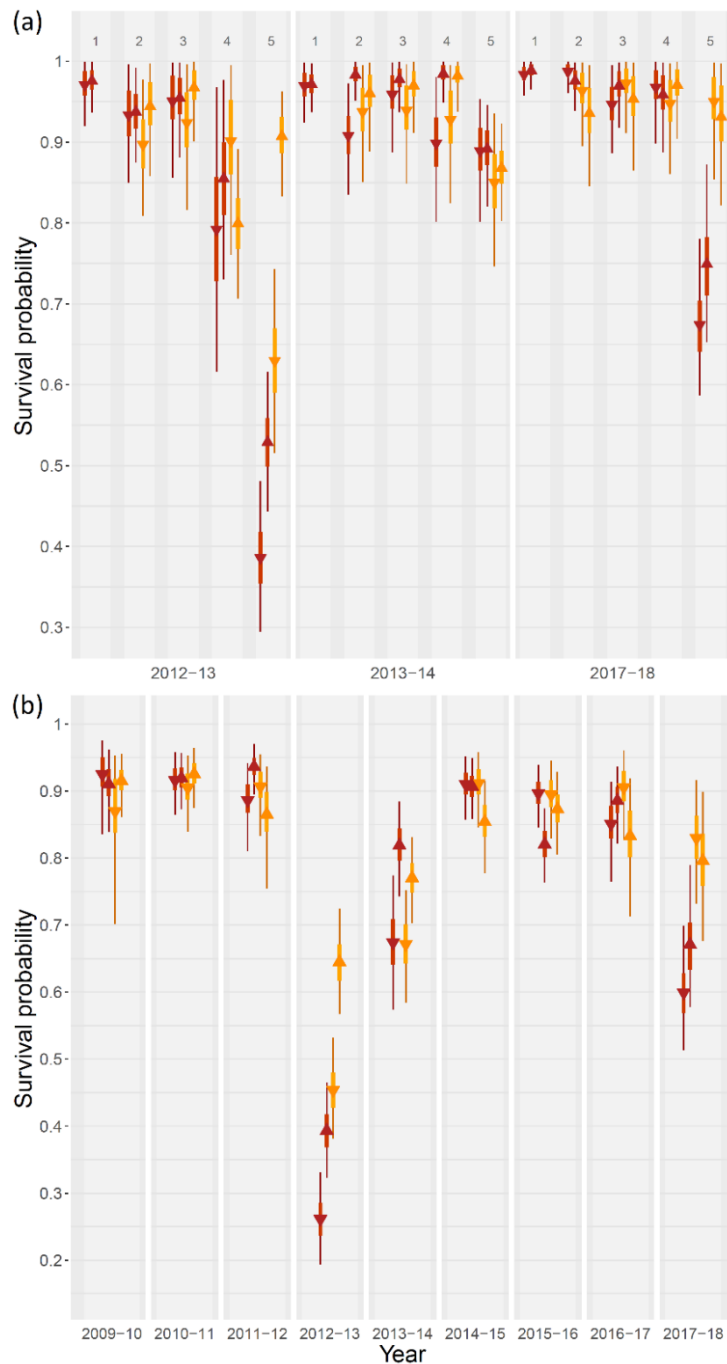
Figure 5. Migration- and sex-dependent survival probabilities of adult shags that bred on
IoM. Panel (a) shows seasonal survival probabilities in the three years containing *a priori*
defined ECEs (see Appendix S5 for other years). Panel (b) shows derived annual survival

460   probabilities in all years for full-winter migration and full-winter residence. Point estimates

461   are posterior means (residents: red, migrants: orange; females: down-triangles, males: up-

462   triangles), inner and outer line segments indicate 50% and 95% credible intervals. On panel

463   (a), the top row indicates initial occasion of the time step.

DISCUSSION

465   Understanding and predicting eco-evolutionary dynamics, including responses to increasing

466   frequencies and/or magnitudes of ECEs caused by climate change, requires quantifying

467   selective landscapes for key traits that mediate population responses to changing

468   environments. Individual expression of migration versus residence is one such trait, that

469   directly shapes spatio-seasonal population dynamics. However, the forms and magnitudes of

470   phenotypic selection on migration versus residence occurring during extreme versus non-

471   extreme climatic conditions have not previously been rigorously quantified. Our full-annual-

472   cycle capture-recapture models applied to extensive resighting data from shags exposed to

473   severe winter storms show that *a priori* defined ECEs that caused high mortality can also

474   induce episodes of very strong selection against residence, dwarfing the weaker selection or

475   neutrality otherwise observed.

476   Estimates of phenotypic selection on binary phenotypes are difficult to standardise and

477   quantitatively compare with selection gradients for continuous traits (Kingsolver et al., 2001;

478   Hereford, Hansen, & Houle, 2004). However, the observed differences between migrants and

479   residents of ~0.3 in adult seasonal survival probability, and ~0.2 in annual survival

480   probability, undoubtedly represent very strong selection. Further, fitness of relatively long-

481   lived iteroparous species with low annual fecundity and delayed recruitment, such as shags,

482   is highly sensitive to variation in adult survival (Sæther & Bakke 2000), which is often

483   strongly canalised (Gaillard &Yoccoz 2003; Péron et al., 2016). Our study therefore implies

that ECEs can induce episodes of selection that are likely to dominate the temporal selective landscape of migration versus residence.

Previous studies on diverse systems have shown that ECEs can cause severe mortality (Welbergen et al., 2007; Moreno & Møller 2011; Bailey & van de Pol 2016). Indeed, ECEs are often defined by such biological impacts (Bailey & van de Pol 2016). However, few studies have explicitly tested whether ECEs cause selection on key phenotypic traits. Seminal studies reported strong ECE-induced selection on morphology (body size traits: O'Donald 1972; Jones 1987; Brown & Bomberger Brown 1998; beak size and shape: Grant & Grant 1995) or phenology (entering diapause: Hairston & Walton 1986; arrival on breeding grounds: Brown & Bomberger Brown 2000; egg-laying: Marrot et al., 2017), or against inbred individuals (Keller, Arcese, Smith, Hochachka, & Stearns, 1994). By demonstrating strong selection for seasonal migration associated with *a priori* defined ECEs, our results highlight one route by which ECEs could directly alter spatio-seasonal population dynamics and distributions.

Surprisingly few previous studies have tested for differential survival of migrants versus residents, or hence quantified survival selection, under any conditions and in any taxa (Reid et al., 2018; Buchan, Gilroy, Catry & Franco, 2019). Recent studies demonstrated higher survival in migrants than residents in blackbirds (*Turdus merula*; Zúñiga et al., 2017) and roach (*Rutilus rutilus*; Skov et al., 2013), but this was not evident in American dippers (*Cinclus mexicanus*; Green, Whitehorne, Middleton, & Morrissey, 2015), and residents had higher survival than migrants in elk (*Cervus canadensis*; Hebblewhite and Merrill 2011) and red-spotted newts (*Notophtalmus viridescens*; Grayson, Bailey, & Wilbur, 2011). However, these studies did not quantify temporal variation in phenotype-dependent survival within or among years, or consider effects of ECEs. Sanz-Aguilar, Béchet, Germain, Johnson, and Pradel (2012) showed a >0.3 decrease in annual survival of adult flamingos (*Phoenicopterus*

roseus) wintering in France during a freezing winter compared with non-extreme winters or other areas. Their results imply strong ECE-induced selection against residence, but they estimated winter-to-winter survival and did not explicitly distinguish residents versus migrants. Consequently, our study unites current interest in seasonal movement and biological impacts of ECEs (van de Pol, Jenouvrier, Cornelissen, & Visser, 2017; Reid et al., 2018), showing that seasonal ECEs can be prominent in the selective landscape of migration. Moreover, by pinpointing the impacts of ECEs at a fine temporal scale, our results suggest a key role of migration timings in shaping ECE-induced differences in annual survival probability. Discrete seasonal ECEs therefore have the potential to generate strong selection on circannual migratory tactic, defined as the sequential path of location through the annual cycle (Fig. 2a).

In the focal shag population, post-breeding migration is typically northerly (Fig. 1; Grist et al., 2014, 2017). The indented destination coastline facing north can provide shelter from (south-)easterly gales that induce rough seas, whereas the IoM provides little protection. Such conditions, especially combined with intense precipitation or low temperature, impede foraging and thermoregulation (Daunt, Afanasyev, Silk, & Wanless, 2006; Daunt et al., 2014; Frederiksen et al., 2008; Appendix S1). Phenotypic variation in migration versus residence, and hence in winter location, can thereby affect survival, constituting direct selection. ECE-induced selection would not occur when ECE characteristics are such that migrant destinations do not provide sufficient shelter, likely explaining why two seasonal ECEs caused notable mortality but no clear selection (Fig. 3, Appendix S1). Such geographical effects also imply that survival probabilities could differ between migrants that move to different destinations, yielding more complex overall selection on migration tactic. Such effects could in future be explicitly estimated using analyses designed to identify and quantify appropriate environmental effects acting on survival at relevant spatio-temporal

534 scales (Appendix S1). However, this is likely to be highly challenging in the IoM shag

535 system, due to the complex and divergent climatic attributes of ECEs (Appendix S1), and

536 because winter locations of some focal shags are unknown (represented by the "ghost area"

537 in our models).

538   In general, eco-evolutionary consequences of ECEs will further depend on magnitudes of

539 sex-biased mortality and selection, but such effects have seldom been quantified for any trait

540 in any system (Frederiksen et al., 2008; Moreno & Møller 2011; Bailey & van de Pol 2016;

541 van de Pol et al., 2017). Our analyses show that adult female shags had substantially lower

542 survival probabilities than males during the most severe ECE in 2012-13. This may reflect

543 their smaller size and lower foraging efficiency in stormy conditions (e.g. Lewis, Phillips,

544 Burthe, Wanless, & Daunt, 2015). However, the strong selection on migration versus

545 residence induced by two ECEs affected both sexes. There was some evidence that selection

546 against residence during the 2012-13 ECE was stronger in males, despite higher overall

547 mortality in females. However, mortality occurring earlier during the 2012-13 winter meant

548 that selection was not sex-biased at the annual level. This concurs with the absence of

549 evidence for consistent sex biases in movement probabilities, and hence for sexual

550 dimorphism in migration, in our system. Nevertheless, substantial sex-biased mortality such

551 as we observed during one ECE would directly alter the adult sex-ratio. This could have

552 multiple consequences in general, potentially including altering mating systems and forms of

553 sexual selection (Widemo & Sæther 1999; Székely, Weissing, & Komdeur, 2014), and

554 further decreasing effective population sizes (Boyce 1992). Such effects could further shape

555 short-term and longer-term eco-evolutionary responses to ECEs (Székely et al., 2014;

556 Haridas, Eager, Rebarber, & Tenhumberg, 2014).

Implications and prospects

557

558 Episodes of strong ECE-induced survival selection on migration versus residence, such as we

559 observed, have potential to affect eco-evolutionary dynamics and resulting spatio-seasonal

560 population dynamics over multiple timescales. By definition, such selection will immediately

561 change the phenotypic distribution (i.e. population proportion of residents versus migrants),

562 and hence change the magnitude of within-year population movement. Based on estimated

563 survival probabilities of migrants and residents through the two selective ECEs (Fig. 1) and

564 the immediately preceding migratory fractions, posterior estimates for the immediate

565 decreases in the proportion of residents are -0.12 [-0.04,-0.19] in 2013 and -0.07 [-0.04,-0.11]

566 in 2018. This shows that strong selection combined with intermediate initial frequencies of

567 migrants and residents generated appreciable short-term phenotypic shifts.

568   The longer-term consequences of such ECEs will depend on the degrees to which direct

569 selection on migration versus residence (i.e. non-breeding season location) arising through

570 adult survival concurs with selection arising through other fitness components (specifically,

571 sub-adult survival, and indirectly through subsequent recruitment and breeding success), and

572 to which net phenotypic shifts propagate across years and generations. Propagation will be

573 determined by combinations of within-individual plasticity and additive genetic variance, and

574 resulting heritability, in migration versus residence (e.g. Charlesworth 1994; Coulson,

575 Tuljapurkar, & Childs, 2010). Our system provides valuable future opportunities to quantify

576 these components, especially with further years of data following the 2018 ECE, although

577 this will require further major technically-challenging analyses.

578   We previously showed that resident shags had higher breeding success than focal sets of

579 migrants following the 2009−2012 winters (Grist et al., 2017). However, these winters were

580 benign with uniformly high survival (Fig. 3), and potential carry-over effects of ECEs on

581 subsequent differential breeding success of residents and migrants remain to be quantified.

582 We also previously showed that locations of adult shags were highly repeatable within and

583 among winters during 2009−2012 (Grist et al., 2014). Across the full winter, repeatabilities

584 of individual resighting distances were 0.72 within winters and 0.59 among winters,

585 increasing to 0.95 and 0.79 respectively across restricted mid-winter periods (Grist et al.

586 2014). These estimates suggest strong canalisation of individual migratory phenotype (see

587 also Appendix S4), allowing for substantial heritability. However, some adult shags do

588 switch between residence and migration within and among winters (Grist et al., 2014), as

589 observed in other partially migratory systems (e.g. brown trout, *Salmo trutta*: Wysujack,

590 Greenberg, Bergman, & Olsson, 2009; skylark, *Alauda arvensis*: Hegemann, Marra, &

591 Tieleman, 2015; elk: Eggeman et al., 2016). Future analyses can test whether individuals

592 surviving ECEs were more likely to subsequently switch between migration and residence.

593   Depending on the degree and form of density- and frequency-dependence in phenotypic

594 expression of migration versus residence (Grayson & Wilburn 2009; Mysterud et al., 2011),

595 such plastic responses could either 'trap' or 'rescue' populations facing increased risk of

596 ECEs that induce substantial mortality and strong phenotypic selection. Alternatively or

597 additionally, depending on the magnitude of additive genetic variance, such selection could

598 potentially drive rapid micro-evolutionary change and resulting 'evolutionary rescue' (Grant

599 et al. 2017). Fully understanding and predicting such eco-evolutionary responses to ECEs

600 will now require studies that can explicitly quantify and integrate all components of selection,

601 genetic variation and plasticity that underlie the occurrence of major phenotypic responses to

602 changing seasonality in key traits such as migration versus residence.

AUTHORS' CONTRIBUTIONS

JMR and FD conceived the overall study; FD, SW, SJB, MAN, MPH, HG, JS, RLS, CG and

JMR collected the data; PA designed the modelling methodology, coded the models,

analysed the data and drafted the manuscript, assisted by JMR. FD, SJB, and APP

contributed to conceptual development and manuscript editing. All authors gave final

approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c2fqz616r

(Acker et al., 2020).

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APPENDIX S1

Additional details of the study system and dataset

Contents:

S1.1 Impacts of extreme weather and ECE characteristics

European shags inhabiting the UK east coast are known to experience episodes of substantial mortality caused by adverse weather (Potts 1969; Aebischer 1993; Harris & Wanless 1996; Frederiksen, Daunt, Harris, & Wanless, 2008). Major "wrecks" (i.e. mass occurrence of dead beached birds) occur, usually concomitant with extreme late-winter storms involving protracted periods of strong easterly onshore winds that cause particularly rough sea states, and intense rainfall (Potts 1969; Harris & Wanless 1996; Frederiksen et al., 2008; Reid & Daunt 2013; Fig. S1). Shags reduce foraging time during strong winds, and stop foraging altogether during the strongest gales (Daunt, Afanasyev, Silk, & Wanless, 2006), probably due to flying difficulties or foraging inefficiency under high water turbidity (Schreiber 2001; Strod, Arad,

Izhaki, & Katzir, 2004). Such weather-induced constraints on foraging can exacerbate constraints resulting from limited daylight foraging time in winter (Daunt et al., 2006). Further, their partially wettable plumage generates major thermogulatory costs under wet and cold conditions, that wind presumably amplifies (Grémillet, Tuschy, & Kierspel, 1998; Grémillet, Chauvin, Wilson, Le Maho, & Wanless, 2005; Frederiksen et al., 2008). Above a threshold of cumulative easterly wind and rainfall in late winter, adult survival probability of shags falls drastically (Frederiksen et al., 2008). During 1965-2005, mean annual adult survival probability was 0.858 (±0.030 SE), but substantial drops in adult survival (notably, below 0.6 in 1965 and 2004, 0.3 in 1992) were associated with periods of extreme winter weather (Frederiksen et al., 2008).

Figure S1. Shags recovered dead in Fraserburgh, Scotland, after a major easterly storm in late December 2012 (Photo credit: Raymond Duncan).

All four defined ECEs that occurred during our current 2009–2018 study period when winter resightings were collected (storms in December 2012, February 2013, January 2014 and the cold wave in February-March 2018) were characterised by strong easterly gales and rough seas (Met Office 2019) which caused major structural damage to coastal infrastructure (e.g. BBC 2012a,b, 2013a) and/or major 'wrecks' of seabirds (e.g. Reid & Daunt 2013; BBC 2013b; CEH 2013) and marine invertebrates (e.g. Alexander 2018). Fieldworkers rapidly perceived major perturbations to shag behavior, including cessation of foraging and daytime roosting in atypical habitats (e.g. harbors, Fig. S2). These qualitative behavioral observations further support the previously identified mechanistic link between easterly gales and low survival (Daunt et al., 2006; Frederiksen et al., 2008).

Figure S2. Shags sheltering from a north-easterly gale in Fraserburgh harbour, Scotland, in December 2012 (Photo credit: Euan Ferguson). Several individuals were found dead at this location following consecutive days when weather conditions precluded foraging (Fig. 1).

However, formally linking particular weather or environmental variables to seasonal survival in residents versus migrants is in fact highly challenging. Such analyses would require biologically-relevant composite values of multiple weather variables (notably comprising onshore wind, precipitation and temperature), and resulting sea state, to be calculated in a

comparable way at multiple coastal locations. Further, rough sea states in coastal areas were sometimes caused by gales centred offshore, meaning that the exact locations of the driving weather events are not always obvious and could be a long distance away from the focal coastal locations. Further, since locations are unknown for shags that wintered outside surveyed sites (represented by the 'ghost area' in our models), the appropriate locations in which to evaluate environmental conditions are not fully known. Progress would ideally require integration and interpolation of datasets from multiple UK onshore and offshore weather stations (which are not always located at biologically relevant locations) and assessment of geographical characteristics of each coastal location that would shape seastate and hence marine and biological impacts. Further, ECEs that occurred during 2009–2018 and caused substantial mortality had clearly different characteristics and timescales (e.g. extreme north-easterly gale and intense rainfall in December 2012, versus a protracted (south-)easterly gale and extreme cold wave in February-March 2018; Met Office 2019). Consequently, simple axes of weather variation cannot be expected to adequately explain spatio-temporal variation in shag survival across our current 10-year dataset. This highlights what are likely to be general challenges in mechanistic modelling of biological impacts of ECEs: such events are by definition infrequent, and may also be highly idiosyncratic (Bailey & van de Pol 2016). This means that, as in our case, sequentially observed ECEs may be highly different from each other and spatially heterogenous, and cannot be easily collapsed into simple axes of variation. With further years of data, the shag system with its relatively regular occurrence of ECEs that cause high mortality (Frederiksen et al., 2008) could provide a valuable opportunity to evaluate the complex multidimensional function capturing the interacting effects of weather and location on shag survival.

Since we do not currently have appropriate climatic data and models to formally quantify the properties of the defined ECEs, we cannot explicitly test whether they fulfilled the

quantitative definition of the IPCC (2001) that ECEs are ″rare as or rarer than the 10th or 90th percentile of a probability density function estimated from observations at a given place and time of year″. Nonetheless, the four defined ECEs heuristically fulfil this criteria, based on their observed characteristics and impacts on wildlife and infrastructure. They certainly fulfil the proposed biological definition of an ECE (Bailey & van de Pol 2016) as conditions that were expected to cause high mortality; and our results confirmed that this was the case for all four defined events.

Observers' perceptions during the two ECEs that caused selection against residence (February 2013 and February-March 2018) were that weather and sea conditions, and related perturbation of shag behavior, were more severe in the residency area surrounding the Isle of May (hereafter "IoM") than in northern migrant areas. Indeed, since swells were predominantly (south-)easterly, key migrant areas would be relatively sheltered (e.g. yellow and brown area on Fig. 1). As a corollary, since the ECEs in December 2012 and January 2014 involved primarily north-easterly swells, the full coastline was likely impacted similarly (see Fig. 1).

Interestingly, and contrasting with the east coast, shag wrecks are not observed on the west coast of Scotland. This is probably because the indented coastline and islands can provide shelter from all wind directions (Swann & Ramsay 1979; Frederiksen et al., 2008), further implying that availability of shelter from winter storms is critically important.

S1.2 Details of the study population and summer sightings

The Isle of May National Nature Reserve is a small island (~2 km long, <0.5 km wide) located ~8 km from the Fife coast. Its shag population is intensively studied through the breeding season.

Annual nest counts undertaken by Scottish Natural Heritage (SNH) at the peak of shag reproductive activities during 2009–2018 estimated breeding population sizes of 322–648 nests (Fig. S3). These nest counts presumably slightly underestimate breeding population size, due

to early nesting failure, late breeding attempts, and undetected nest sites at the time of survey. Nevertheless, these data illustrate the effects of the ECEs in December 2012 and February 2013, and in February-March 2018, in reducing adult survival and hence breeding population size.
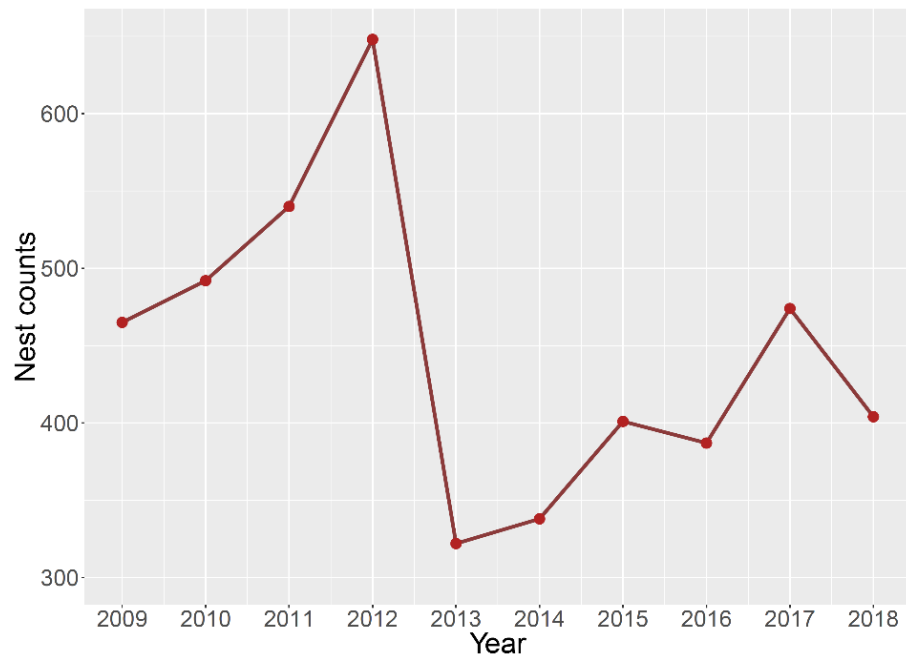

Figure S3. Number of nests counted at the peak of reproductive activities on the Isle of May in each year during 2009-2018.

The proportion of marked breeders, calculated as the number of marked individuals resighted as breeders on the Isle of May divided by twice the SNH nest counts, was: 0.79 in 2009, 0.88 in 2010, 1.02 in 2011, 0.96 in 2012, 0.92 in 2013, 0.99 in 2014, 0.94 in 2015, 1.02 in 2016, 0.96 in 2017, and 1.00 in 2018. Due to the slight underestimation of breeding population size, this proportion of marked breeders is presumably slightly overestimated, which explains why it was slightly >100% in some years.

Systematic observations of all shag nests, and of adjacent roost areas, generate large numbers of shag resightings and ensure the very high breeding-season resighting rate (see Results). For field logistical convenience, breeding season resightings of individuals at nest sites were stored as one record per breeding attempt, attributed to May 1st in the focal year. Of

the total of 43214 "resightings" utilised for the present analyses, almost 60% (25963) were in April–June on the Isle of May, including 8267 that corresponded to breeding attempt records.

Breeding dispersal from the focal population is negligible (<<1%; Aebischer 1995; Barlow, Daunt, Wanless, & Reid, 2013). However, observed natal dispersal rates ranged ~5–10% (Aebischer 1995; Barlow et al., 2013). Accordingly, we focused on individuals from their first observed breeding event during 2009–2017, thereby excluding the pre-breeding life-history phase during which individuals may disperse. Because we analysed capture-resightings histories spanning the 2009−2018 breeding seasons, individuals first recorded breeding in 2018 were not informative regarding survival probabilities across the study period, and were hence excluded from the dataset. In the 2009−2018 resighting data, while the main breeding colonies in north-east UK were monitored and ringed breeders actively searched for, we confirmed only two breeding dispersal events (0.09% of individuals). Resightings off the Isle of May during the breeding season led to suspicion of breeding dispersal for two further individuals. The entire capture-recapture histories of these four individuals were excluded from the dataset. Consequently, we can assume that apparent survival is not confounded with permanent emigration once individuals have recruited to breed on IoM.

S1.3 Age effects and observed changes in age distribution

In principle, relationships between seasonal migration versus residence and survival could potentially arise if individuals of different ages have different propensities to migrate or remain resident, and also have different survival probabilities. Such effects are not straightforward to explicitly quantify, but are very unlikely to explain our current main conclusions. Formal estimation of age effects in our models would require further stratification not only of survival probabilities, but also of the movement parameters that are already characterized by large spatio-temporal variation. Given this complex model structure and substantial spatio-temporal heterogeneity in detection, adding age effects would result in a large loss of precision in the

estimation. This is exacerbated because 615 of 2274 focal individuals were first ringed as adults and hence are of uncertain age. Restricting the analyses to known-age individuals would thus reduce the number of individual encounter histories by 27%.

Previous (cross-sectional) capture-recapture analyses of age-dependence in survival probability of IoM shags found evidence of acturial senescence only from age 14 years. However, individuals aged ≥14 years comprise a small proportion of the current dataset (4–12% across years of known-age individuals). Effects of senescence would therefore be very hard to detect with our current model. By corollary, it is very unlikely that underlying senescence could have substantially affected survival parameters in our models, or could have caused the large difference in survival between residents and migrants during the late-winter ECEs in 2012-13 and 2017-18.

Indeed, visual inspection of year-to-year changes in the age distribution of surviving individuals observed during the breeding season (when recapture probability is very high, see main text), show no indication of change as would result from major age-dependent mortality (Fig. S4). This was even true during the years with ECEs that were associated with strong selection (2012-13 and 2017-18), indicating that apparent ECE-induced selection was not mainly driven by correlated age effects on survival and migration propensity. And indeed, there was no evidence of major lack of fit that could be attributable to age effects in our models (Appendix S4). These conclusions are further supported by additional analyses focusing on known-age individuals resighted in winter 2012-13, 2013-14 and 2017-18, which did not find evidence of age-dependence in survival probability (Burthe et al., in prep.).

Figure S4. Year-to-year changes in the age distribution of known-age surviving adult shags observed on IoM during each breeding season. Each panel shows the age distribution in the initial year *y* (rose), superimposed with the age distribution of individuals that survived to the next year *y+1* (light blue). Common parts of both distributions appear in purple. Differences between distributions (rose and blue areas) are essentially attributable to age-dependent survival variation.

S1.4 Details of sexing

We sexed most individuals from repeated field observations, mainly of vocalisations and occasionally of behavior (Snow 1963). In addition, we used DNA extracted from blood samples to sex 11% of individuals by genotyping the CHD1 gene region (using primers 2550F

and 2757R; Griffiths, Double, Orr, & Dawson, 1998; Fridolfsson & Ellegren 1999). Comparisons in the wider database including all sex assignments since 1997 showed that sexes were typically accurately assigned from observations: field assignments matched genotypic assignments in 98.7% of 1295 cases where both information sources were available (98.2% if considering only the first field observation of each individual). In the few cases where an individual had been assigned as both sexes from field observations, we assumed that the most frequent assignment was correct (only 1.32% of observations conflicted). Sex was assigned as unknown when an individual had no field observations or genetic data (5.10% of the 2274 individuals analysed here, mostly first-time breeders in 2018 and individuals who died early) or when it was evenly assigned to both sexes (0.48% of individuals). The sexed dataset was thus reduced to 2147 individuals. Most unsexed individuals entered the dataset in 2016 or 2017 (29 and 59 respectively, versus 1–15 in each previous year), obviously because there had been more opportunities to sex individuals that entered the dataset earlier.

S1.5 Details of winter sightings

Color-ringed shags can be observed onshore in winter (e.g. Fig. S4), because their partially wettable plumage forces them to return to land every day (Grémillet et al., 1998, 2005; Grist et al., 2014, 2017). Historical dead recoveries of shags ringed on IoM and surrounding colonies were used to define the east coast of Scotland and northern England as the geographical range likely to be relevant to shags migrating away from IoM in winter (Galbraith et al., 1986; Harris & Swan 2002; Grist et al., 2014). Pilot fieldwork in 2008-09 winter confirmed that shags ringed on the IoM could be located and resighted across this geographical range (see Fig. 1). Individuals were observed across surveys spanning 540 km north to 355 km south of the IoM, encompassing night roosts where shags congregate at dusk and day roosts where they rest between foraging trips. These roost sites are typically located on cliffs, rocky islets, and harbor walls. Shags were very seldom resighted inland or along beaches and dunes. Accordingly, their

winter habitat is patchy: migrant sites are not continuously distributed along the coastline (Fig. 1). Shags are uncommon south of the focal range, since the coast is sand or mudflats with few potential roost sites.

Figure S5. Shags with unique individual color-rings 'IAI' and 'LXJ' resighted in winter on the eastern Scottish coast (Photo credit: Bradley Fairclough).

Resighting surveys were undertaken across known accessible sites every winter from early September to the end of February. In addition to sites identified during the pilot fieldwork, additional survey sites were identified by consulting local birdwatchers and bird reports, and by further field exploration. The primary goal was to repeatedly locate individuals wintering across a large geographical range, not to map or infer the complete winter distribution of the entire population. Therefore, winter surveys were designed to ensure that key sites were visited repeatedly, ca. every 1–2 weeks, and visits were planned to coincide with site-specific use by shags, tides or weather conditions to maximise resighting efficiency. Additional sightings from

any location were actively solicited from birdwatchers to maximise the resighting probability of color-ringed shags over their full winter range.

During each survey, at least one observer screened the roost site with a 60× magnification telescope for 30–300 minutes depending on the number and turnover of shags. Each survey lasted until all visible individuals were checked for rings and color-ring codes carefully recorded, or light, tide or weather conditions prevented further resightings. Not all roost areas were accessible for visual resightings, and not all color-rings were always fully visible (e.g. hidden by rocks, plumage, other birds, vegetation, etc.). Accordingly, the probability of resighting an individual present at the survey site was <1 and presumably varied among sites and surveys. Survey effort and efficiency also varied within and among winters due to variation in weather and observer knowledge of roost sites. Day roost occupancy varies markedly with time of day, tide and weather, and decreases in mid-winter as the proportion of daylight hours spent foraging increases (Daunt et al., 2006; Daunt et al., 2014; Lewis, Phillips, Burthe, Wanless, & Daunt, 2015; Grist et al., 2014, 2017). Such variations inevitably generate spatio-temporal heterogeneity of resighting probability, which was taken into account in the models analysed in the present study by parameterising resighting probabilities as location×time-dependence (see Methods). However, the repeated surveys undertaken throughout the winter increased the probability that present individuals would be resighted at least once within the ~1-month time windows of the five capture-resighting occasions defined in the present analyses (see Results; Appendix S5). To provide an indication of resighting effort and resulting spatio-temporal distribution of data collected, Table S1 contains the numbers of sightings and individuals recorded in each occasion and observed area, comprising the total of 43214 sightings of 2274 individuals utilised for the capture-recapture analyses (see Methods; Fig. 1).

Table S1. Number of (re)sightings (and corresponding number of unique individuals) in each area, per occasion ('occ.') across years. R: is the residency area (IoM, red on Fig. 1), or migratory area M1: orange on Fig. 1, M2: brown on Fig. 1, M3: yellow on Fig. 1, and M4: pink on Fig. 1.

Area	Occ.	Year									
		(1) 2009-10	(2) 2010-11	(3) 2011-12	(4) 2012-13	(5) 2013-14	(6) 2014-15	(7) 2015-16	(8) 2016-17	(9) 2017-18	(10) 2018-19
R	1	2171 (723)	3248 (831)	3330 (1033)	3537 (1235)	2692 (665)	2169 (686)	2220 (751)	2000 (792)	2588 (915)	2074 (621)
	2	75 (62)	267 (208)	74 (70)	544 (389)	756 (357)	386 (274)	559 (337)	307 (230)	1181 (553)	
	3	83 (68)	144 (114)	197 (162)	631 (361)	339 (204)	426 (263)	317 (217)	133 (104)	621 (393)	
	4	89 (69)	127 (110)	128 (116)	262 (199)	309 (176)	302 (197)	337 (216)	118 (97)	360 (249)	
	5	7 (6)	384 (280)	301 (227)	363 (229)	204 (144)	224 (184)	387 (240)	253 (193)	521 (325)	
M1	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	12 (11)
	2	15 (12)	11 (8)	31 (22)	70 (43)	85 (40)	29 (14)	34 (23)	36 (20)	20 (15)	
	3	21 (12)	55 (28)	77 (37)	124 (46)	93 (36)	74 (32)	77 (32)	80 (35)	44 (19)	
	4	16 (13)	35 (15)	67 (31)	147 (58)	67 (34)	44 (22)	54 (27)	47 (28)	36 (19)	
	5	9 (7)	71 (28)	104 (41)	139 (48)	158 (73)	70 (21)	135 (49)	40 (20)	61 (26)	
M2	1	0 (0)	0 (0)	0 (0)	0 (0)	4 (4)	0 (0)	0 (0)	1 (1)	0 (0)	20 (17)
	2	4 (4)	6 (6)	4 (4)	12 (10)	8 (5)	18 (10)	4 (4)	11 (6)	18 (10)	
	3	11 (6)	44 (24)	26 (16)	81 (45)	93 (42)	20 (13)	22 (13)	27 (16)	25 (14)	
	4	46 (24)	24 (17)	75 (37)	56 (44)	60 (32)	35 (16)	38 (18)	52 (23)	44 (22)	
	5	66 (34)	39 (18)	63 (30)	113 (63)	67 (41)	25 (13)	47 (31)	54 (21)	62 (30)	
M3	1	0 (0)	0 (0)	1 (1)	1 (1)	1 (1)	2 (2)	0 (0)	2 (2)	2 (2)	0 (0)
	2	1 (1)	7 (5)	0 (0)	34 (31)	18 (12)	20 (14)	3 (3)	5 (5)	22 (19)	
	3	6 (6)	14 (9)	14 (9)	20 (16)	33 (23)	13 (12)	28 (17)	6 (5)	17 (16)	
	4	1 (1)	1 (1)	8 (7)	8 (7)	13 (10)	4 (3)	0 (0)	3 (3)	10 (8)	
	5	5 (3)	4 (2)	13 (8)	6 (5)	0 (0)	1 (1)	2 (2)	7 (7)	4 (3)	
M4	1	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	2	13 (8)	11 (10)	20 (17)	159 (62)	71 (23)	27 (16)	56 (28)	64 (25)	75 (26)	
	3	26 (13)	29 (15)	79 (32)	118 (59)	85 (25)	67 (20)	36 (21)	38 (20)	88 (26)	
	4	6 (5)	3 (3)	11 (10)	50 (37)	29 (14)	8 (8)	21 (16)	30 (19)	83 (25)	
	5	1 (1)	5 (5)	5 (5)	5 (5)	3 (3)	6 (3)	13 (13)	17 (12)	35 (21)	

S1.6 Data checking

We undertook thorough checking and validation of resighting data before compiling encounter histories. We discarded resightings of individuals that were known or highly suspected to have been mistakes in field observation or reporting. We removed resightings reported after an individual was found dead (11 records, <0.02% of the original, unchecked dataset before restriction to occasion time-windows). We examined all isolated records of individuals that

had not previously been resighted for ≥2 years, and were not resighted again subsequently. Quite often, resighting or reporting errors were identified. When there was no indication that the record was mistaken, we kept it in the dataset. These checks led to the removal of 138 resightings (<0.3% of the original dataset). Further, we checked the history of birds that were resighted outside IoM during the breeding season. Indeed, regular resightings in another breeding location, and hence no or rare opportunistic resightings with no breeding record on IoM, would have suggested that they dispersed from IoM.

S1.7 Details of compilation of capture-recapture histories

The exact date limits of the time windows chosen to define the five annual resighting occasions (see Methods) were: 1st April to 30th June for occasion 1, 1st September to 30th September for occasion 2, 1st October to 31st October for occasion 3, 13th November to 18th December for occasion 4, 6th January to 15th February for occasion 5. These time windows represent a pragmatic balance between narrowing the window and hence excluding intervening resightings, and expanding the window and hence violating standard capture-recapture assumptions of no movement or mortality within occasions (O'Brien, Robert, & Tiandry, 2005). In addition, these date limits were chosen given the temporal distribution of resightings. For example, July resightings were not included in occasion 1 because resightings on the residency area in July were redundant with earlier resightings during the peak of shag breeding in April–June. Very few resightings are recorded in August or March. For other occasions, date limits were selected to include many resightings occurring in trips to IoM, which are constrained by winter accessibility.

Collapsing all resightings of each focal individual in each occasion into a unique event was straightforward in 99.65% of cases, because the individual was either not resighted within the focal occasion (74.4%), or was resighted once or several times in the same area (25.3%). Some remaining cases (0.05%) concerned resightings in a migratory area in the breeding

season followed by resighting(s) on IoM, indicating late return from migration. We thus assigned the observation event to the residency area. Other cases (0.3%) concerned resightings in several areas within a winter occasion. Here, we picked the observation event at random from these areas.

Figure S6. Examples of uniquely-coded alphabetic color-rings, and uniquely-coded British Trust for Ornithology metal rings, used to individually mark shags on IoM.(Photo credit: Keith Barrow and Dave Pickering).

During compilation of individual capture-resighting histories, we excluded 7071 resightings (among 50285, i.e. 14%) that occurred outside the defined time windows, meaning that 43214 resightings utilised for the present analyses. Individuals were considered from their first breeding during 2009–2017 up to the 2018 breeding season. Accordingly, individuals that had already bred on IoM before 2009 entered the dataset as already recruited (essentially in 2009), while others entered the dataset as new recruits. The number of new individuals entering the dataset was 723 (32%) in 2009, 163 (7%) in 2010, 271 (12%) in 2011, 318 (14%) in 2012, 147 (6%) in 2013, 169 (7%) in 2014, 117 (5%) in 2015, 135 (6%) in 2016, and 231 (10%) in 2017. Table S2 hereafter provides details of individual observation events across the study period, after compiling individual capture-resighting histories.

Table S2. Summary of observation events over all individuals resighted in each occasion ('occ.') across years. Entries indicate the number of individuals assigned to the corresponding positive observation event (either R: 'resighted in the residency area', or Mi: 'resighted in migratory area i' – on Fig. 1: i=1 for the orange points, i=2 for the brown area, i=3 for the yellow area, and i=4 for the pink area), with their proportion among individuals known to be alive at the focal time point (given later resighting) between parentheses.

Occ.	Event	Year									
		(1) 2009-10	(2) 2010-11	(3) 2011-12	(4) 2012-13	(5) 2013-14	(6) 2014-15	(7) 2015-16	(8) 2016-17	(9) 2017-18	(10) 2018-19
1	R	723 (1)	831 (0.98)	1033 (0.98)	1234 (0.96)	664 (0.93)	685 (0.96)	751 (0.97)	790 (0.97)	915 (0.96)	605
2	R	60 (0.09)	205 (0.25)	68 (0.07)	373 (0.35)	336 (0.51)	260 (0.38)	325 (0.44)	225 (0.29)	548 (0.61)	
	M1	1 (0)	5 (0.01)	0 (0)	31 (0.03)	11 (0.02)	12 (0.02)	3 (0)	5 (0.01)	19 (0.02)	
	M2	4 (0.01)	6 (0.01)	4 (0)	9 (0.01)	5 (0.01)	9 (0.01)	3 (0)	6 (0.01)	9 (0.01)	
	M3	12 (0.02)	7 (0.01)	21 (0.02)	42 (0.04)	40 (0.06)	13 (0.02)	22 (0.03)	18 (0.02)	15 (0.02)	
	M4	8 (0.01)	9 (0.01)	17 (0.02)	52 (0.05)	18 (0.03)	13 (0.02)	25 (0.03)	24 (0.03)	24 (0.03)	
3	R	65 (0.1)	113 (0.14)	156 (0.16)	347 (0.36)	196 (0.32)	249 (0.37)	206 (0.28)	101 (0.13)	391 (0.46)	
	M1	5 (0.01)	9 (0.01)	9 (0.01)	15 (0.02)	21 (0.03)	12 (0.02)	16 (0.02)	5 (0.01)	13 (0.02)	
	M2	5 (0.01)	24 (0.03)	14 (0.01)	42 (0.04)	36 (0.06)	11 (0.02)	13 (0.02)	16 (0.02)	13 (0.02)	
	M3	12 (0.02)	27 (0.03)	36 (0.04)	41 (0.04)	30 (0.05)	31 (0.05)	31 (0.04)	34 (0.05)	17 (0.02)	
	M4	12 (0.02)	13 (0.02)	29 (0.03)	54 (0.06)	22 (0.04)	20 (0.03)	20 (0.03)	19 (0.03)	26 (0.03)	
4	R	65 (0.1)	108 (0.14)	112 (0.11)	192 (0.23)	169 (0.28)	185 (0.28)	208 (0.29)	97 (0.13)	244 (0.31)	
	M1	1 (0)	1 (0)	7 (0.01)	7 (0.01)	10 (0.02)	2 (0)	0 (0)	3 (0)	7 (0.01)	
	M2	24 (0.04)	16 (0.02)	35 (0.04)	44 (0.05)	30 (0.05)	16 (0.02)	17 (0.02)	23 (0.03)	22 (0.03)	
	M3	13 (0.02)	14 (0.02)	29 (0.03)	52 (0.06)	32 (0.05)	22 (0.03)	26 (0.04)	27 (0.04)	19 (0.02)	
	M4	5 (0.01)	3 (0)	10 (0.01)	32 (0.04)	13 (0.02)	8 (0.01)	16 (0.02)	19 (0.03)	25 (0.03)	
5	R	6 (0.01)	275 (0.35)	220 (0.23)	223 (0.31)	128 (0.22)	178 (0.27)	226 (0.33)	191 (0.26)	318 (0.43)	
	M1	3 (0)	1 (0)	8 (0.01)	5 (0.01)	0 (0)	1 (0)	2 (0)	5 (0.01)	3 (0)	
	M2	33 (0.05)	17 (0.02)	28 (0.03)	62 (0.09)	39 (0.07)	12 (0.02)	26 (0.04)	21 (0.03)	28 (0.04)	
	M3	7 (0.01)	27 (0.03)	40 (0.04)	45 (0.06)	64 (0.11)	21 (0.03)	42 (0.06)	20 (0.03)	22 (0.03)	
	M4	1 (0)	3 (0)	5 (0.01)	5 (0.01)	3 (0.01)	3 (0)	8 (0.01)	9 (0.01)	19 (0.03)	

Moreover, individual capture-resighting histories were completed with information regarding observability of the focal individual. Few individuals have worn or missing color rings, that are usually replaced during the breeding season to minimise resighting mistakes and unobservability. Nonetheless, time of mark loss remains uncertain. Although individual identification is ensured by a virtually-unlosable inscribed metal ring, such ring is unreadable given the usual conditions of observations in the non-breeding season (see Fig. S5) but is

readable in the breeding season because shags can be caught or observed at very close-range. Therefore, we considered these individuals (75 individuals, 3.3% of all individuals) as unobservable in non-breeding occasions up to the time of color-ring replacement. This information was added to the individual capture-recapture histories (in the form of "observability sequences") so that their probability of resighting was constrained to be 0 during the winters when they were unobservable (see details in Appendix S2).

Note that we have not included dead recoveries in our analyses, mainly because resighting probabilities were sufficiently high to provide precise estimates of seasonal survival (see Results). Accordingly, the precision that could have been gained by adding dead recoveries was likely to be very low, and unlikely to justify modelling an additional observation process for dead recovery.

S1.8 Details of observed switching between migratory areas in winter

Over the study period, switching between migratory sites was observed for 5.8% of consecutive resightings (i.e. in occasion *o* and occasion *o+1*) of a single migrant individual in winter (out of 1023 pairs of such resightings). Switching was observed for 9.6% of resightings of a single migrant individual in occasion o and occasion *o+2* (out of 519 pairs of such resightings), that is ca. twice the proportion of switching from one occasion to the next – which is expected given that, after 2 occasions, the individuals had the opportunity to switch twice. And switching was observed for 16.1% of resightings of a single migrant individual in occasion o and occasion *o+3* (out of 174 pairs of such resightings), that is ca. three times the proportion of switching from one occasion to the next – which is expected after 3 occasions. These figures suggest that the probability of switching (whatever the departure and arrival migratory area) was low in each winter occasion over the study period.

There was too little information to make accurate inferences on switching probability

depending on the departure and arrival site, and each winter occasion in each year, within the context of current analyses. For example, from one winter occasion to the next across years, for each migratory area of departure and area of arrival, in 89.8% of cases no individual was observed switching in the focal year between the focal sites, in 7% of cases only one individual, in 3.0% of cases only two individuals, and in 2‰ of cases only three individuals. The information was even scarcer considering a lag of 2 or 3 occasions between resightings of a single migrant. Nonetheless, the few observed switching events did not seem to differ greatly from randomness, with no specific directionality (i.e. no area concentrating most departures or arrivals, relative to the number of individuals resighted in the focal area). Accordingly, there was no indication of major spatio-temporal biases in the switches.

S1.9 Details of observed spatio-temporal variation in sex ratio

In each area and each occasion, inspection of the sex ratios in the samples of individuals that had been resighted indicated no major sex biases in the observed spatial locations of shags that breed on IoM (Table S3). Indeed, the proportion of males and females in each migratory site were relatively similar in most occasions, with no area being clearly occupied only by females or males in any occasion. The largest deviations from parity or near-parity involved small numbers of individuals and hence are likely to be largely explained by demographic stochasticity.

Table S3. Observed spatio-temporal repartition of the sexes across the study period. Entries indicate the proportion of females among the individuals resighted in each observed area ('R': the residency area, 'Mi': migratory area i – on Fig. 1: i=1 for the orange points, i=2 for the brown area, i=3 for the yellow area, and i=4 for the pink area) and each occasion ('occ.') across years. The total number of individuals (males and females) resighted in the area at the time considered is given in parentheses.

Occ.	Area	Year									
		(1) 2009-10	(2) 2010-11	(3) 2011-12	(4) 2012-13	(5) 2013-14	(6) 2014-15	(7) 2015-16	(8) 2016-17	(9) 2017-18	(10) 2018-19
1	R	0.47 (722)	0.48 (827)	0.49 (1024)	0.49 (1215)	0.45 (658)	0.45 (678)	0.46 (742)	0.48 (757)	0.49 (840)	0.48 (579)
2	R	0.45 (60)	0.42 (205)	0.49 (68)	0.46 (369)	0.42 (337)	0.42 (259)	0.42 (323)	0.43 (212)	0.47 (499)	
	M1	1 (1)	0.6 (5)	NaN (0)	0.57 (30)	0.5 (12)	0.55 (11)	0.33 (3)	0.6 (5)	0.59 (17)	
	M2	0.25 (4)	0.33 (6)	0.5 (4)	0.44 (9)	0 (5)	0.25 (8)	0.5 (2)	0.5 (6)	0.71 (7)	
	M3	0.67 (12)	0.29 (7)	0.52 (21)	0.67 (42)	0.64 (36)	0.46 (13)	0.5 (22)	0.58 (19)	0.57 (14)	
	M4	0.5 (8)	0.78 (9)	0.82 (17)	0.69 (51)	0.78 (18)	0.64 (14)	0.85 (26)	0.74 (23)	0.72 (25)	
3	R	0.38 (64)	0.47 (113)	0.46 (155)	0.47 (345)	0.42 (193)	0.39 (248)	0.42 (207)	0.48 (93)	0.5 (347)	
	M1	0 (6)	0.33 (9)	0.89 (9)	0.53 (15)	0.38 (21)	0.42 (12)	0.56 (16)	0.8 (5)	0.27 (15)	
	M2	0.4 (5)	0.3 (23)	0.33 (15)	0.33 (42)	0.33 (36)	0.33 (12)	0.45 (11)	0.47 (15)	0.5 (12)	
	M3	0.36 (11)	0.44 (27)	0.55 (33)	0.39 (41)	0.69 (32)	0.6 (30)	0.43 (30)	0.59 (34)	0.41 (17)	
	M4	0.62 (13)	0.71 (14)	0.77 (31)	0.78 (54)	0.67 (21)	0.75 (20)	0.81 (21)	0.79 (19)	0.73 (26)	
4	R	0.34 (65)	0.63 (108)	0.43 (112)	0.43 (191)	0.4 (167)	0.41 (184)	0.42 (207)	0.33 (92)	0.49 (217)	
	M1	0 (1)	NaN (0)	0.71 (7)	0.57 (7)	0.4 (10)	0.5 (2)	NaN (0)	0.33 (3)	0.17 (6)	
	M2	0.38 (24)	0.31 (16)	0.37 (35)	0.33 (43)	0.35 (31)	0.44 (16)	0.44 (16)	0.24 (21)	0.45 (20)	
	M3	0.08 (13)	0.07 (15)	0.25 (28)	0.36 (53)	0.55 (33)	0.36 (22)	0.5 (26)	0.39 (28)	0.37 (19)	
	M4	0.2 (5)	0.33 (3)	0.7 (10)	0.82 (33)	0.77 (13)	0.62 (8)	0.75 (16)	0.68 (19)	0.8 (25)	
5	R	0.67 (6)	0.53 (274)	0.52 (222)	0.43 (222)	0.47 (127)	0.41 (177)	0.53 (219)	0.43 (184)	0.49 (298)	
	M1	0 (3)	0 (2)	0.75 (8)	0.6 (5)	NaN (0)	0 (1)	0.5 (2)	0.4 (5)	0 (3)	
	M2	0.33 (33)	0.5 (16)	0.34 (29)	0.44 (63)	0.29 (38)	0.46 (13)	0.29 (28)	0.47 (19)	0.4 (25)	
	M3	0.14 (7)	0.11 (28)	0.24 (37)	0.36 (44)	0.27 (66)	0.33 (21)	0.26 (42)	0.3 (20)	0.3 (23)	
	M4	0 (1)	1 (3)	0.8 (5)	0.8 (5)	0.67 (3)	0.67 (3)	0.9 (10)	0.73 (11)	0.89 (18)	

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APPENDIX S2

Additional details on modelling and Stan code

Contents:

S2.1 Details of the prior distributions

We used uninformative uniform priors for all parameters. All parameters were probabilities, either single probabilities of binary outcomes (e.g. survival probability of residents at a given occasion) or sets of probabilities of categorical outcomes, i.e. probability simplexes summing up to 1 (e.g. set of probabilities of moving to each of the migratory areas conditional on departing from the residency area at a given winter occasion). Accordingly, we used uniform(0,1) distribution as the prior for any single probability of a binary outcome, and Dirichlet(1,…,1) as the prior for any set of probabilities of a categorical outcome. By using such priors, we remained objective regarding our general preconceptions on the values that the parameters could take.

Such priors are commonly employed, and are typically appropriate in Bayesian analyses of (multistate) capture-recapture models (see e.g. Kéry & Schaub 2012). It was also convenient to use uninformative uniform priors given the complexity of formulating priors that would properly capture the different levels of prior knowledge available on different parameters. Further, it would have been challenging to define joint distributions leading to sensible priors on compound, higher-level aspects of the biological system being modelled (e.g. the migratory

fraction). Accordingly, and by using uninformative uniform priors for all parameters, we relied essentially on the information contained in the data in providing evidence regarding inferences on the posterior probability of the model parameters.

S2.2 Rationale underlying the model code

We formulated a general code (see below) that can be directly applied to data from any partially migratory population with seasonal encounters, with flexibility regarding the data structure. The key attributes are that individual capture-resighting data are collected across one residency site (as named in the code bellow) or "area" (as named in main text) and n migratory sites ($n{\geq}1$; "areas" in main text), which gives $n+2$ possible observation events (i.e. $n+1$ events for positive resightings in each surveyed site and 1 event for absence of resighting). The study timeframe is regular, consisting of one breeding season in the beginning of each year (during which all individuals are located in the residency site) and x subsequent winter occasions, which gives $x+1$ capture-resighting occasions per year. However, resighting effort in the last year can stop before the last possible occasion of the year. All the necessary information regarding the spatio-temporal specificities of the observation design is provided as data input, together with the unique capture-recapture histories (capture-resighting and observability sequences; see Appendix S1) and corresponding individual frequencies in each possible sex assignment (i.e. female, male, or unknown).

The capture-recapture histories must agree with the observation design. From the time when the individuals enter the dataset up to the last time point, each point in the corresponding capture-recapture sequence is an observation event coded as 1, or 2, or ..., or $n+2$ (see e.g. in code below). Further, each point in the corresponding observability sequence is either 0 or 1 depending on whether the individual was observable or not (see Appendix S1, and code below). By convenience, these sequences are filled with 0s before the individual enters the dataset. Note that the model code is currently general enough to be fitted to datasets in which new

2

individuals enter at any occasion across years (although here, Isle of May shags entered the dataset only during breeding occasions). Moreover, we formulated a single code for the analyses with and without sex effects. A variable provided as data input specifies whether sex effects are included (and hence only the resighting histories of individuals of known sex are analysed) or not (and hence all resighting histories of individuals of known and unknown sex are analysed).

Whatever the dataset, the code follows the model structure presented in the main text. Nonetheless, this code can be easily tweaked to apply or remove specific constraints. For example, one could exclude the "ghost area" (i.e. unobservable migratory state) to comply with the assumption of no Markovian temporary emigration outside the observed sites. To do so, one would change the code below to specify (i) that the number of sites is equal to the number of observation events minus one (instead of the number of observation events, l. 83 in the code below), (ii) that the number of observable migratory sites is equal to the number of migratory sites (instead of the number of migratory sites plus one, l. 85 in the code below), and (iii) to remove l. 235–236 that are meant to set detection probability at zero in the penultimate state (i.e. the unobservable migratory area if there is one). One could also tweak the code to apply or remove specific dependences on parameter variation (e.g. location, time- or occasion-dependence, etc.), or even use hyper-parameters controlling distributions underlying hierarchical variations ("random effects", e.g. across individuals, sites, or time). More generally, this code has the potential to be extended for various further investigations related to partial migration dynamics.

Small "hacks" can be used so that specificities of the model structure could be added or removed by means of bespoke inclusion variables provided as data input. To do so, the modeller would use appropriate if/else statements (given the potential values of the inclusion variables) in the declaration of (transformed) parameters, following a similar logic as employed

in the code below to include or not sex-dependence in the parameters. Such "hacks" would allow the use of a single flexible code for any model structure, but at the expense of over-complexifying the code and potentially slowering its execution for posterior sampling.

S2.4 References

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APPENDIX S3

Preliminary analysis of model capabilities

Contents:

S3.1 Checking model capability for inference

Before analysing the real dataset but with knowledge of its structure and apparent properties, we assessed the performance of our model (without sex effects) in terms of providing useful, unbiased and accurate estimates of the survival probabilities of migrants and residents, as well as movement and detection parameters.

To do so, we simulated datasets for the same number of individuals entering the dataset in each breeding season as in the real dataset (i.e. same sample sizes and initial times of individual capture-recapture histories) and the same observability sequences (see Appendix S1, S2). We simulated individual histories based on the model structure (see Stan simulation code below) using reasonable parameter values chosen given knowledge derived from previous analyses of Isle of May shags (Frederiksen, Daunt, Harris, & Wanless, 2008; Grist et al., 2014, 2017) and crude expectations derived from our broad understanding acquired during data collection and inspection (see main text; Appendix S1; and next section). We then fitted the model to the simulated datasets to draw posterior samples from which to evaluate how the model was able to estimate the parameter values used to simulate the data.

To assess whether the parameters were identifiable, and assess bias and precision, we plotted graphical summaries of the posterior distributions alongside the priors and the parameter values used to simulate data. Here, we provide the example of one simulated dataset. Other simulated datasets (e.g. with different assumptions regarding the number of individuals moving to the "ghost" area, or the occurrence of decreases in survival probability, etc.) led to similar conclusions.

All these simulations and analyses suggested that all survival probabilities were effectively identifiable, as were most other parameters. All parameter values used for the simulation were contained in their posterior probability distribution (the simulated parameter values were often close to the mean of the corresponding posterior distributions, rarely away from the 95%CI limits, and always within the 99% limits), thus indicating no major biases. Most importantly given our present objectives, survival probabilities were all estimable with high precision. However, uncertainty in the posterior of some other parameters was high, due to small sample sizes for resightings in some combinations of time and state. In particular, inferences on the probability of moving to a given migratory area (conditional on departing) and the probability of returning from a given migratory area (back to the residency area) were prone to uncertainty and seemed often weakly identifiable (i.e. with a posterior distribution looking clearly similar to the prior distribution) in our simulations.

The derived migratory fraction was well estimated with good precision, but in mid-winter time occasions (occasion 3 and 4: October and November-December) the migratory fraction was often biased up or biased down – although the estimates were not radically different from the simulated values. The biases in this compound derived quantity in mid-winter occasions are likely to be due to a lack of information in the data regarding the location of individuals and an accumulation of uncertainty among migratory sites. Nonetheless, departure and resighting probabilities were usually estimable with relatively good precision. Overall, these

investigations suggest that our model is reliable and that our dataset should be sufficiently informative to tackle our main objective: the estimation of seasonal survival probabilities in migrants versus residents.

S3.2 Example of model performance in analysis of simulated data

For the present example, we drew survival probabilities of residents and migrants independently at each time step, at random from a normal distribution on the logit scale with a mean of $\log(0.98/(1-0.98))$ and a variance of 0.1. Accordingly, these survival probabilities were drawn with small temporal deviations around the expectation of 0.98 on the natural scale (see Fig. S6, S7). Given that there are 5 time steps per year, this leads to the expectation of $0.98^5=0.9$ for the annual survival probability, which is realistic for adult shags that breed on the Isle of May under relatively good year-round conditions (see Frederiksen et al., 2008). However, for two time steps, we arbitrarily set survival to low values in order to simulate the occurrence of high mortality induced by ECEs (see Frederiksen et al 2008; main text, Appendix S1). We did so for survival probability in late winter 2012-13 and 2017-18, hence matching two periods of extreme weather that were known to have occurred in the east coast of Scotland (see main text, Appendix S1). We set survival probability at 0.55 for residents and 0.85 for migrants in late-winter 2012-13, and 0.70 for residents and 0.40 for migrants in 2017-18, hence inducing large differences between residents and migrants to simulate strong selection during these ECEs but with no a priori on consistency in the direction of such selection.

Having different survival probabilities for migrants and residents in the last time step of the data was also intended to provide the opportunity to clearly assess whether these parameters were effectively identifiable separately from resighting probability in the last time point, and from each other. In general, the final survival and detection probabilities often cannot be identified separately (due to parameter redundancy; only their product is fully identifiable), as well understood in a capture-recapture model with two states (alive/dead) and two events

(resighted/not resighted) in which the two parameters (survival and resighting probability) are fully time-dependent (i.e. the Cormack-Jolly-Seber model; McCrea & Morgan 2014). However, it is also known that adding structures of dependencies or covariation can make initially redundant parameters become identifiable separately (McCrea & Morgan 2014).

In the current case, our simulations indicate that our model structure provides effective identifiability of the only three parameters involved in the last time step: survival probability of residents and migrants, and detection probability in the residency area. This is likely to be because transition from six different states is formulated probabilistically by only two elementary parameters: survival of residents for the first state, and migrants for the other five states. Because surviving individuals transition to the same state ('R') for the breeding season, only one resighting probability is to be estimated. This reduces the number of unknowns, and instead of having two identifiable products (of pairs of redundant parameters: 'survival probability * resighting probability') that are independent, we have two products that both involve the same resighting probability. As a consequence, there is apparent effective identifiability (and indeed, posterior distributions of the parameters clearly peak off the uniform[0,1] prior), although it might be a specific numerical case. Finally, exploratory analyses of a more complex model that included additional terminal occasions showed that estimated survival probabilities of residents and migrants for 2017-2018 are correct as reported and interpreted in the main text.

Other parameter values were chosen using the same kind of procedure as for survival probabilities (i.e. drawn at random from a distribution with reasonable expectation and temporal deviations around it; but see values in Fig. S9 to S19). Detection probability in the residency area was drawn to be always very high during the breeding season, and relatively high but quite variable during the winter occasions. Detection probabilities in the migratory areas were drawn so that it was always low in the first migratory site (mimicking the area grouping together all

opportunistic resighting locations that were not regularly surveyed), and usually moderate but quite variable in the other migratory areas (mimicking the areas that were regularly surveyed). The probability of departing from the residency area was drawn to be quite variable among years, but with a relatively high (0.5) expectation just after the breeding season, a moderate expectation just after September (0.35), and a low expectation in mid-winter and late-winter (0.15). The probability of moving to a given migratory area (conditional on departure) was drawn to be the highest for the "ghost" area (around 0.5), and hence from very low to relatively low for the other areas. The probability of returning (to the residency area) was drawn to be very low just after September, relatively low in mid-winter, and moderate to relatively high in late-winter. The probability of switching to another migratory site (conditional on not returning) was set to 0.03.

Once the data were simulated, sampling of the posterior was performed using 10 MCMC chains with 1000 warmup iterations and then 1000 monitored iteration for sampling, yielding 10,000 iterations in the end. There was no indication of issues regarding the reliability of the inference algorithm (in particular, no indication of divergent numerical trajectories). The Gelman-Rubin-Brooks $\hat{R}$ statistics indicated good convergence of the Markov chains, with all $\hat{R}$<1.01 (Brooks & Gelman 1998). Effective sample sizes were all >2000, and MCMC standard errors were all <5% of the standard deviation of the corresponding posterior sample, indicating that the uncertainty associated with the Monte Carlo approximation (due to the imperfection of the pseudorandom sampling procedure) was negligible.

Hereafter, we present graphics of most parameters: we plotted the parameter values used for data simulation alongside their prior distributions in the model, and their posterior distributions obtained from the analysis of the simulated data (Fig. S6 to S20).
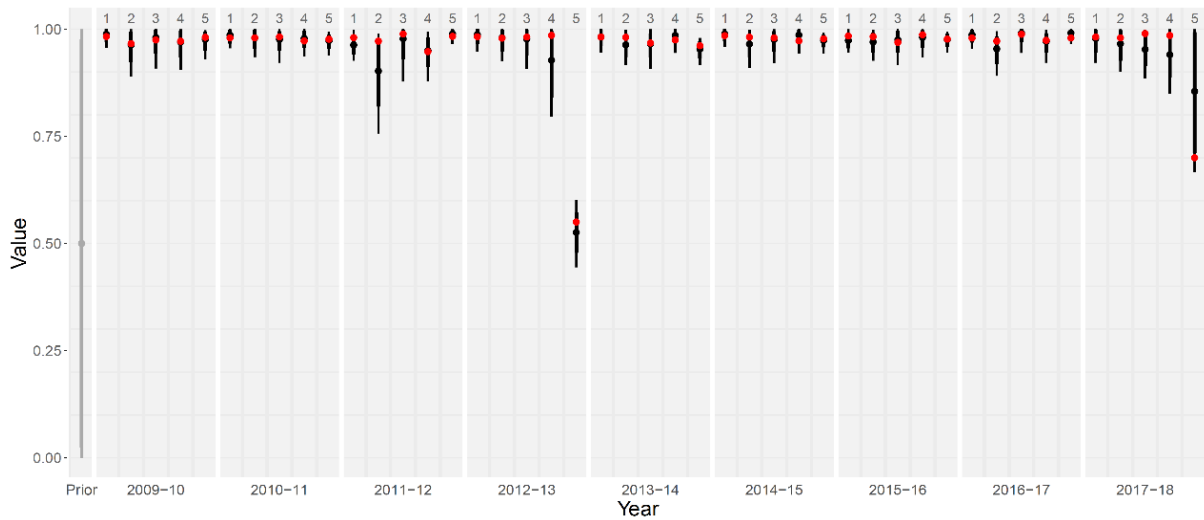
Figure S6. Estimation of seasonal survival probability of residents from simulated data. Survival time steps span consecutive time points (departure time point is indicated by the corresponding annual occasion, numbered 1-5 on the top row). The prior distribution is in grey (same prior for all parameters on this graph) and the posterior distribution is in black: the central dot indicates the mean, the inner segment is the 95% interval and the outer segment is the 99.9% interval. Red dots indicate the values used to simulate the dataset being analysed
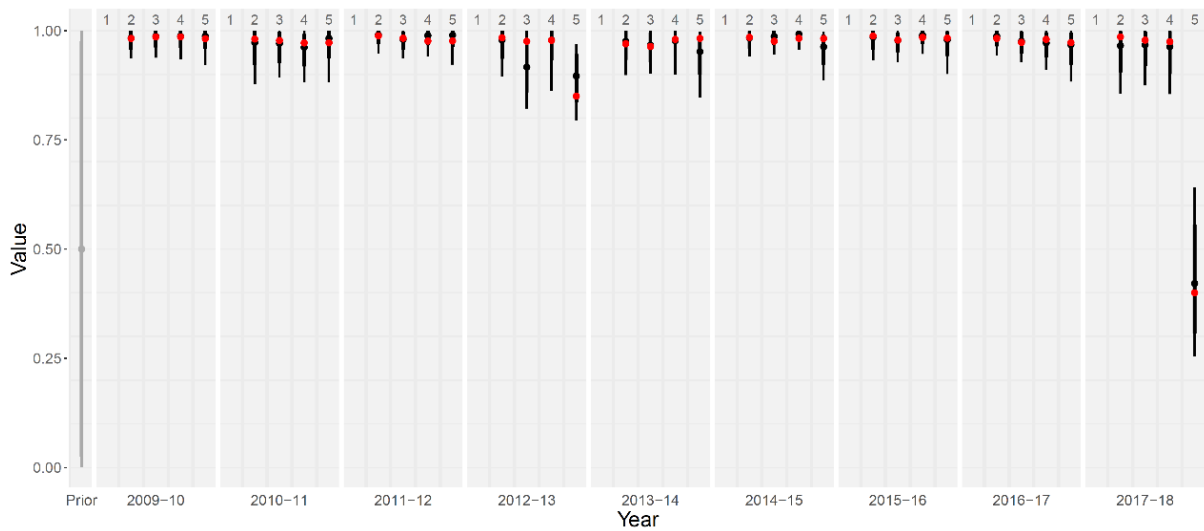
Figure S7. Estimation of seasonal survival probability of migrants from simulated data. See legend of Fig. S6 for further specifications. Note that all the individuals are located in the residency area during the breeding season (occasion 1 in each year), hence there is no survival probability of migrants for time steps starting at occasion 1.
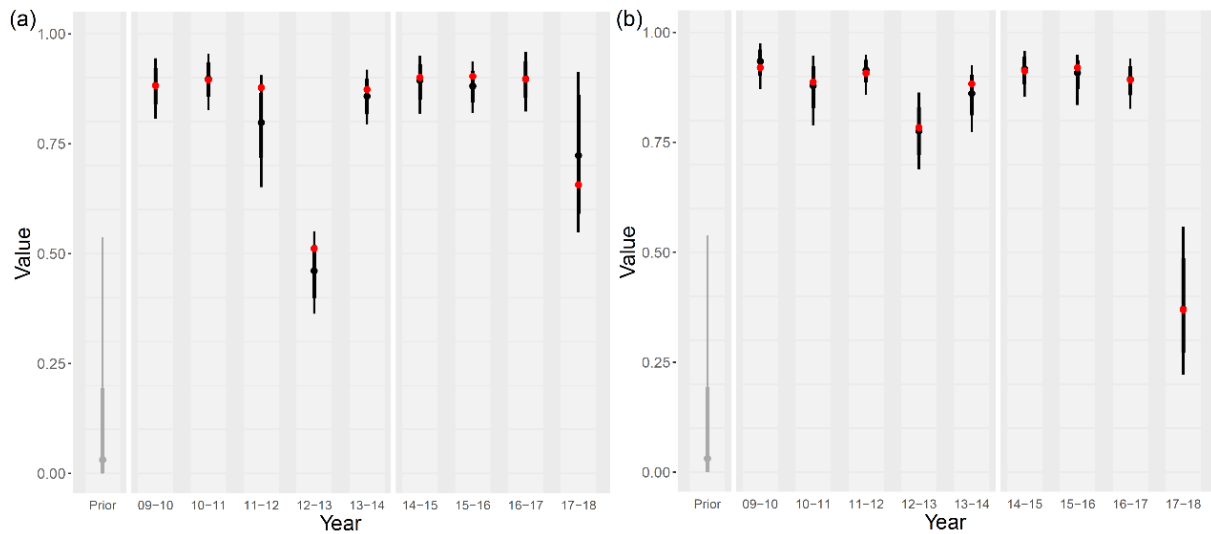
Figure S8. Estimation of annual survival probability of (a) full-winter residents and (b) full-winter migrants (derived from seasonal survival probabilities) from simulated data. See legend of Fig. S6 for further specifications on plotted values.
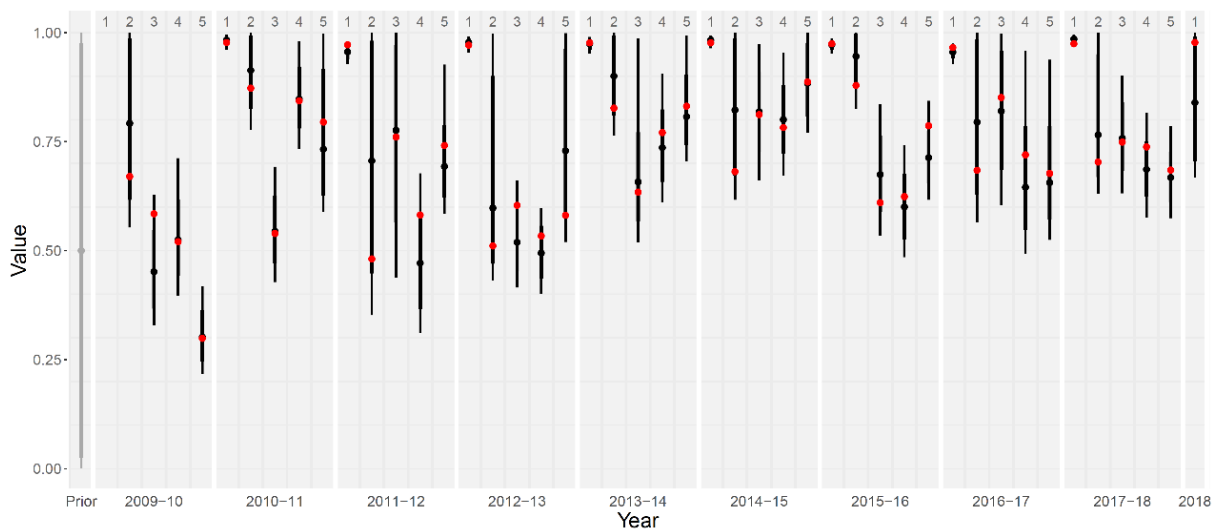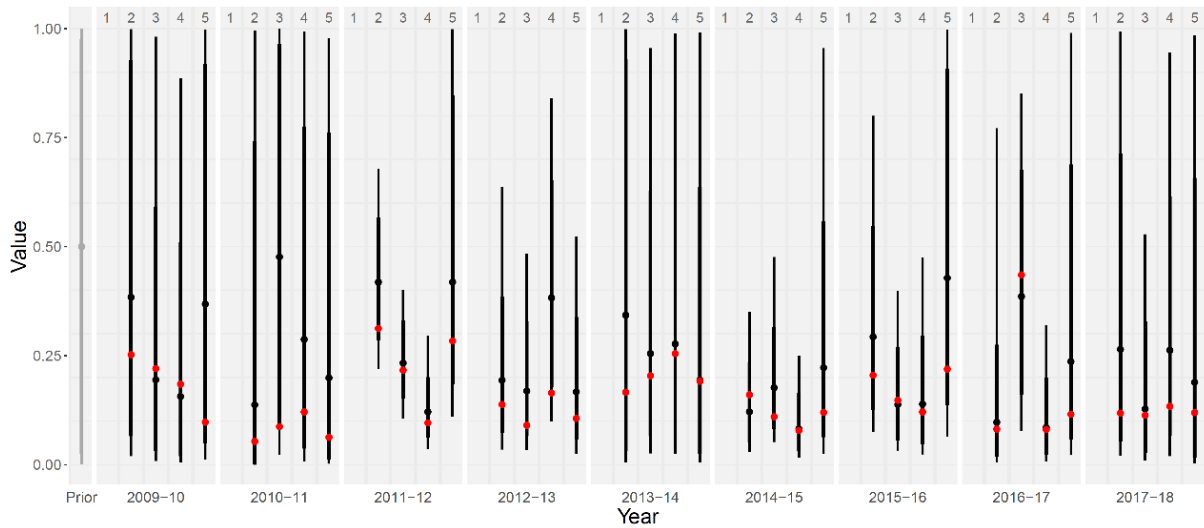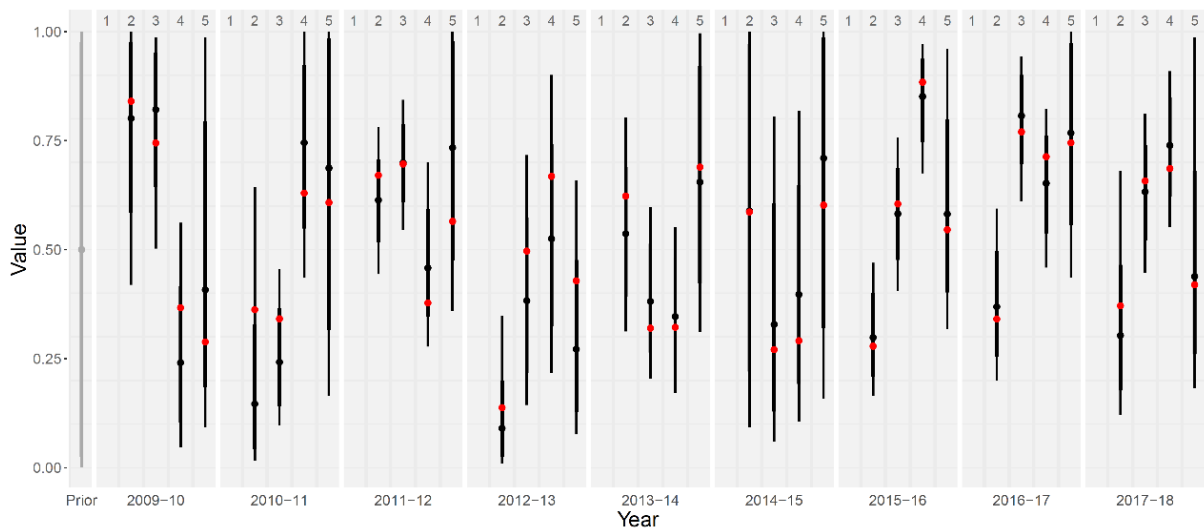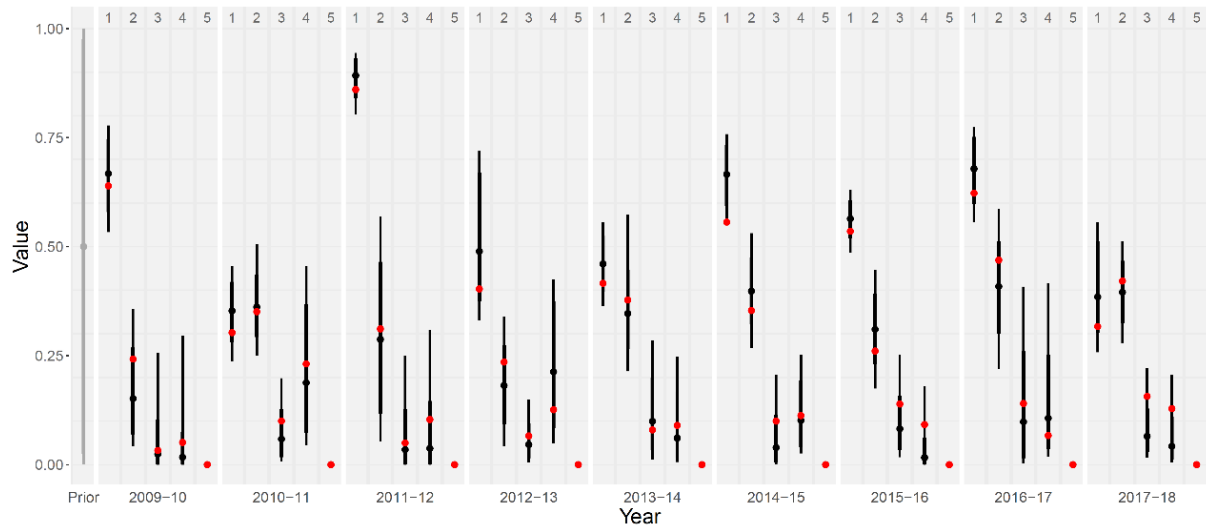

Figure S9. Estimation of the resighting probability in the residency area from simulated data. See legend of Fig. S6 for further specifications. Note that all the individuals present are sighted with certainty in the first time point of the study (they are all entering the dataset, in the residency site), accordingly there is no resighting probability at this occasion.

Figure S10. Estimation of the resighting probability in migratory area 1 from simulated data. See legend of Fig. S6 for further specifications. Note that all the individuals are in residency area during the breeding season (occasion 1), accordingly there is no resighting probability in any migratory area at this occasion.

Figure S11. Estimation of the resighting probability in migratory area 4 from simulated data. See legend of Fig. S6 for further specifications. Note that all the individuals are in residency area during the breeding season (occasion 1), accordingly there is no resighting probability in any migratory area at this occasion. Graphical summaries for the estimation for migratory area 2 and 3 are not shown, but the general pattern is the same (although with different simulated values).

Figure S12. Estimation of the probability of departing from the residency area from simulated data. See legend of Fig. S6 for further specifications. Note that all residents are constrained to stay in the residency area from late winter (occasion 5) to the breeding season (occasion 1), accordingly there is no estimated departing probability at this time step (i.e. it is constrained to be 0).
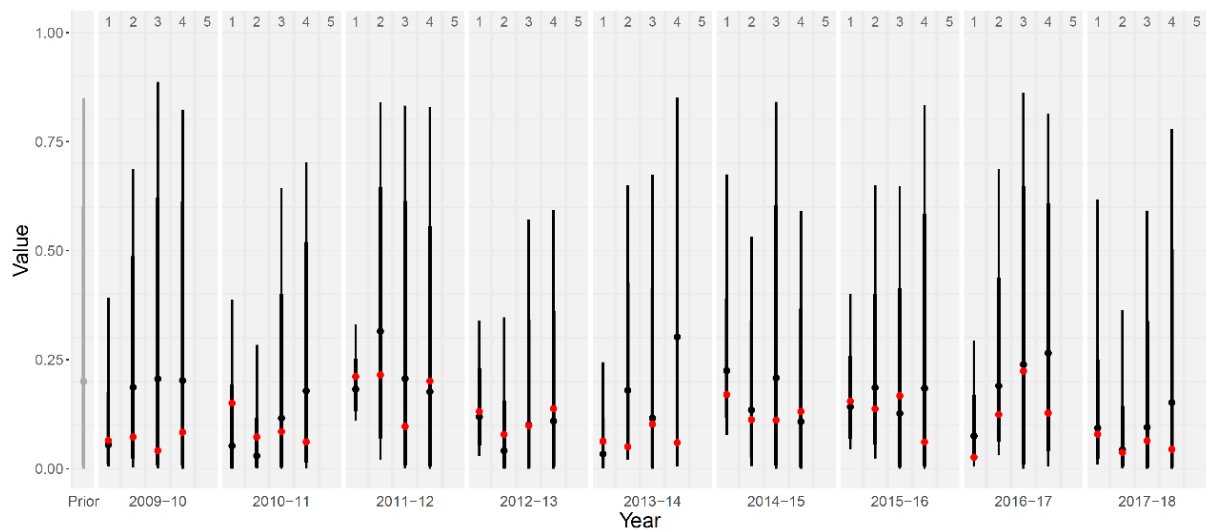

Figure S13. Estimation of the probability of moving to migratory area 1 (conditional on departure from the residency area) from simulated data. See legend of Fig. S6 for further specifications. Note that all residents are constrained to stay in the residency area from late winter (occasion 5) to the next breeding season (occasion 1), accordingly there is no probability of moving to any migratory area at this time step.
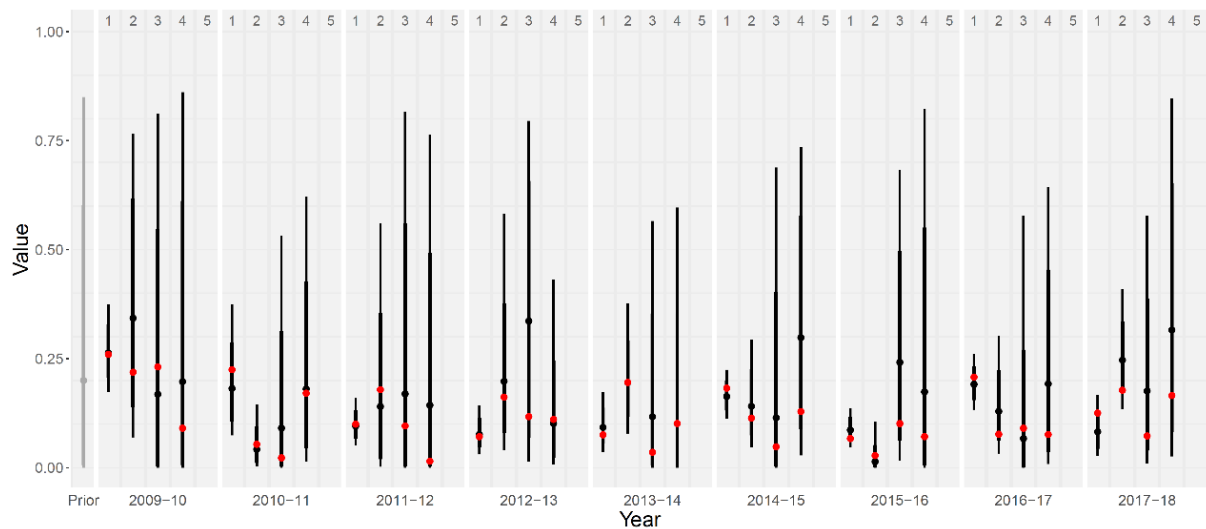
Figure S14. Estimation of the probability of moving to migratory area 2 (conditional on departure from the residency area) from simulated data. See legend of Fig. S6 for further specifications. Note that all residents are constrained to stay in the residency area from late winter (occasion 5) to the next breeding season (occasion 1), accordingly there is no probability of moving to any migratory area at this time step. Graphical summaries for the estimation for migratory area 3 and 4 are not shown, but the general pattern is the same (although with different simulated values).
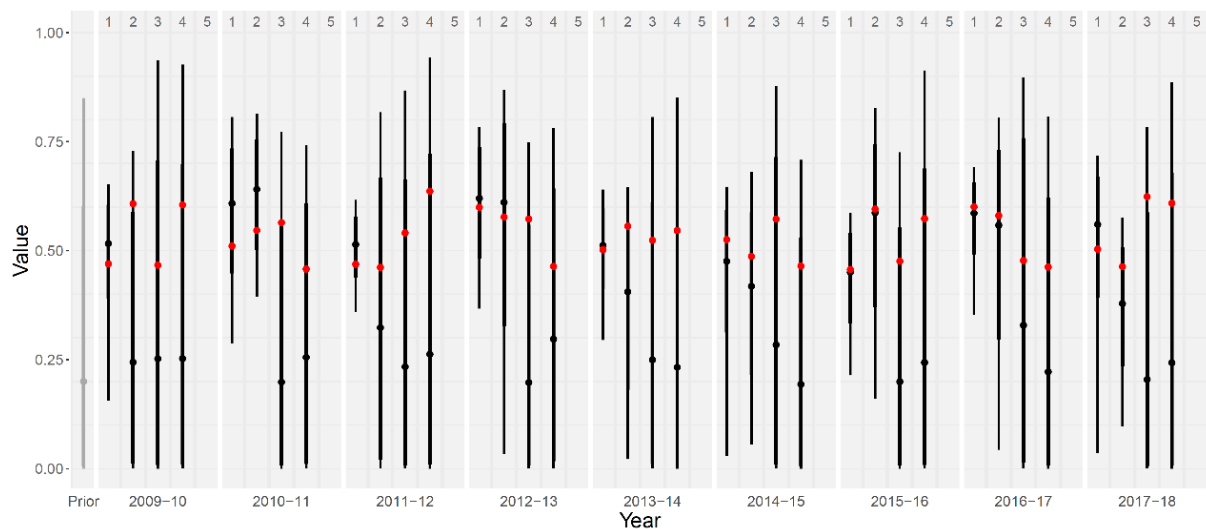

Figure S15. Estimation of the probability of moving to migratory area 5 – the "ghost" area, corresponding to an unobservable state – (conditional on departure from the residency area) from simulated data. See legend of Fig. S6 for further specifications. Note that all residents are constrained to stay in the residency area from late winter (occasion 5) to the next breeding season (occasion 1), accordingly there is no probability of moving to any migratory area at this time step.
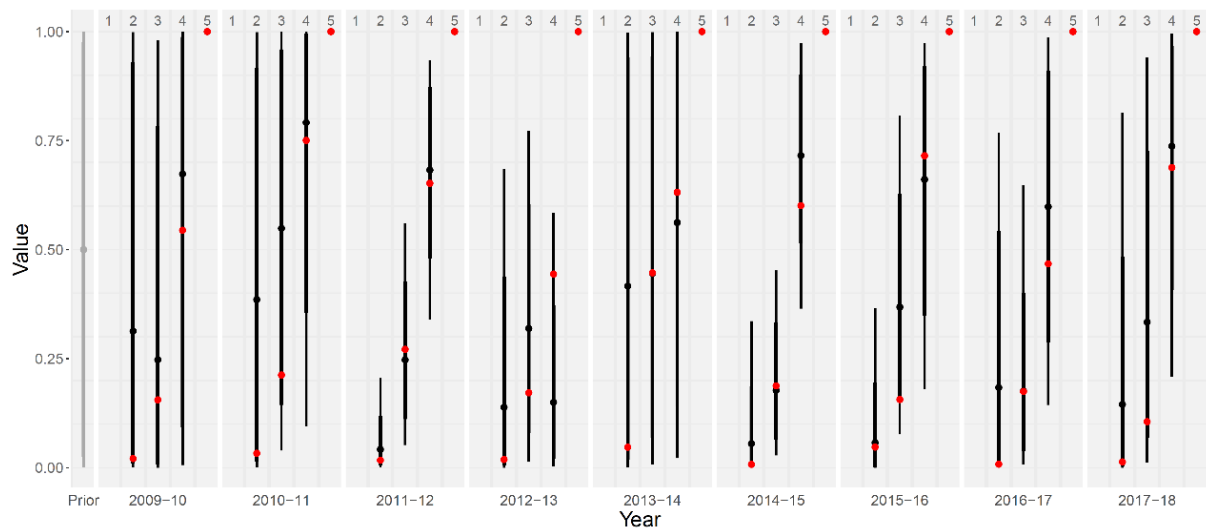
Figure S16. Estimation of the probability of returning to the residency area from migratory area 1 from simulated data. See legend of Fig. S6 for further specifications. Note that all individuals are in the residency area during the breeding season (occasion 1), accordingly there is no probability of returning from any migratory area at the time step starting from occasion 1. Further, all migrants are returning to the residency area between late-winter (occasion 5) and the next breeding season, accordingly the probability of returning from any migratory area is constrained to be 1 at this time step.
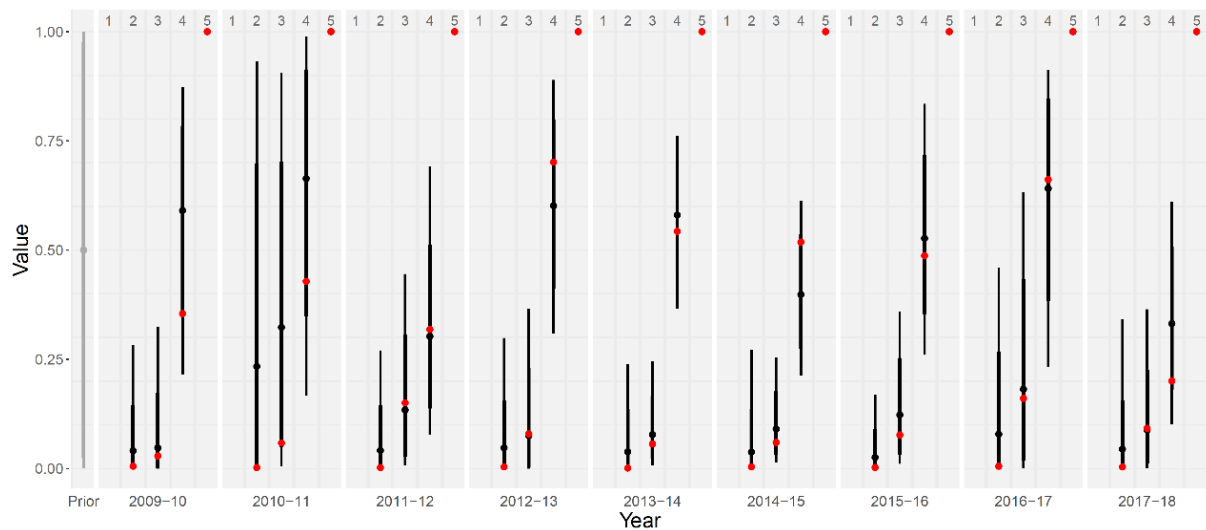

Figure S17. Estimation of the probability of returning to the residency area from migratory area 3 from simulated data. See legend of Fig. S6 for further specifications. Note that all individuals are in the residency area during the breeding season (occasion 1), accordingly there is no probability of returning from any migratory area at the time step starting from occasion 1. Further, all migrants are returning to the residency area between late-winter (occasion 5) and the next breeding season, accordingly the probability of returning from any migratory area is constrained to be 1 at this time step. Graphical summaries for the estimation for migratory area 2 and 4 are not shown, but the general pattern is the same (although with different simulated values).
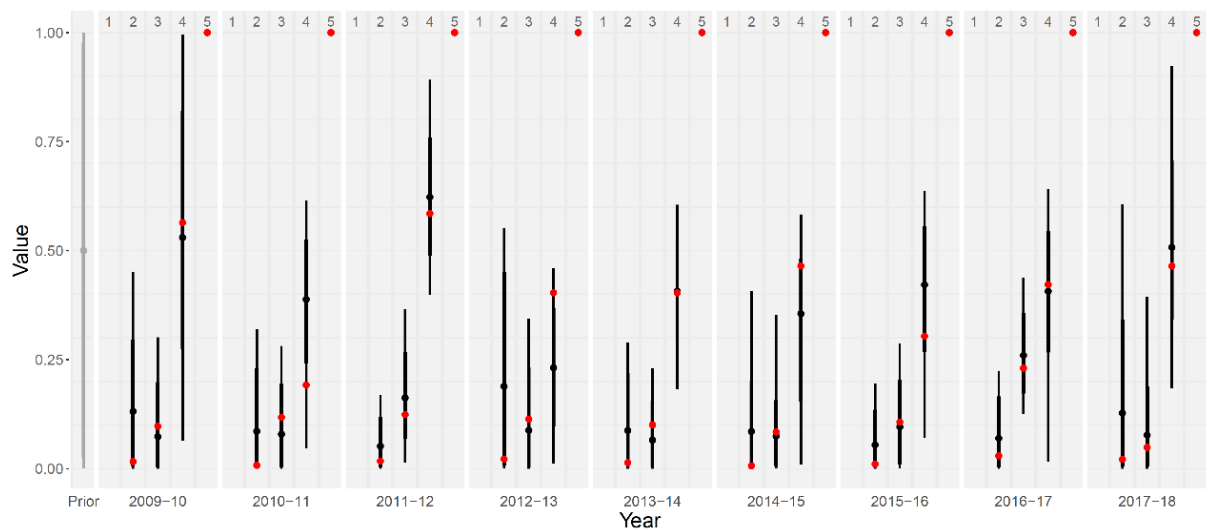
Figure S18. Estimation of the probability of returning to the residency area from migratory area 5 – the "ghost" area, corresponding to an unobservable state – from simulated data. See legend of Fig. S6 for further specifications. Note that all individuals are in the residency area during the breeding season (occasion 1), accordingly there is no probability of returning from any migratory area at the time step starting from occasion 1. Further, all migrants are returning to the residency area between late-winter (occasion 5) and the next breeding season, accordingly the probability of returning from any migratory area is constrained to be 1 at this time step.
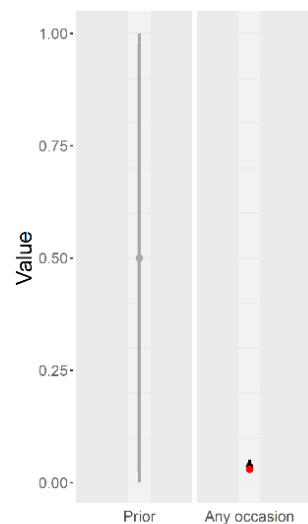

Figure S19. Estimation of the probability of switching to another migratory area (i.e. the probability of not remaining in the same migratory area, on Fig. 2b: $1-\sigma_{ii}=4*\sigma_{ik}$, with $k \neq i$). See legend of Fig. S6 for further specifications. Note that this probability is set constant across time (and apply to time steps between winter occasions) in our model.
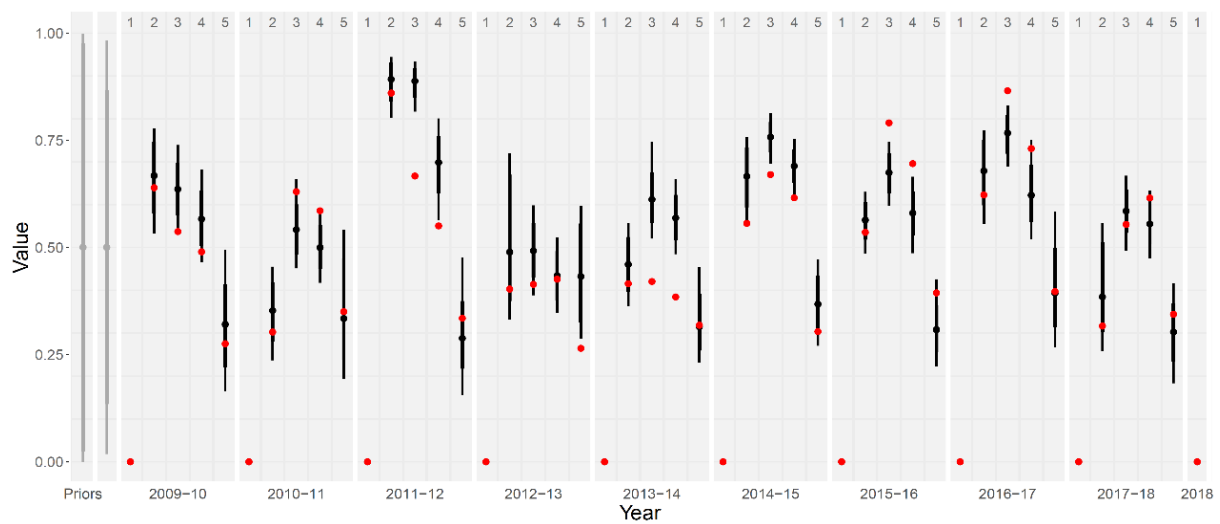
Figure S20. Estimation of the migratory fraction (derived from movement and survival parameters). See legend of Fig. S6 for further specifications. The first prior is for the migratory fraction in occasion 2, the second prior is for the migratory fraction in occasion 3 to 5. Note that all individuals are located in the residency area during the breeding season (occasion 1), accordingly the migratory fraction is constrained to be 0 in this occasion.

S3.4 References

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APPENDIX S4

Posterior predictive checks

Contents:

S4.1 Posterior predictive checks of goodness of fit

We evaluated the goodness of fit of our main models through posterior predictive checks (Gelman, Meng, & Stern, 1996; Gelman et al., 2014; and see e.g. Chambert, Rotella, & Higgs, 2014). Such checks assess the ability of the model to generate data that resemble the original data. To do so, we visually assessed the discrepancy between original observations and their posterior predictions (i.e. distributions of the replicated data generated under the model). If the model fits the data, the data should fall into the posterior predictive distribution, while a lack of fit would be indicated by a systematic discrepancy between real and replicated data (i.e. the real data point would be outside the distribution of the replicated data; Gelman et al., 2014).

We first focused on a general aspect of the data: the number of individuals in each possible observation event across time, once they entered the dataset (Fig. S21 to S26). Accordingly, in each sample of the posterior distribution (i.e. at each of the 15,000 monitored iteration of the MCMC chains), we used the parameter values to draw replicates of the capture-resighting sequence of every individual, from the time they entered the dataset. We then plotted summaries of the posterior predictive distributions of the counts for each observation event across time, alongside counts derived from the real data. For the model without sex effects, all

the real counts of the observation events were highly plausible under their posterior predictive distribution (Fig. S21 to S26), indicating a good fit. These posterior checks led to similar conclusion for the model with sex effects (graphics not shown). These checks point towards good performances of our inferences on the survival, movement and resighting probabilities. Indeed, these inferences can be used to predict individual trajectories that could lead to the cross-sectional censuses of the real observations events that happened at each occasion across the study period.
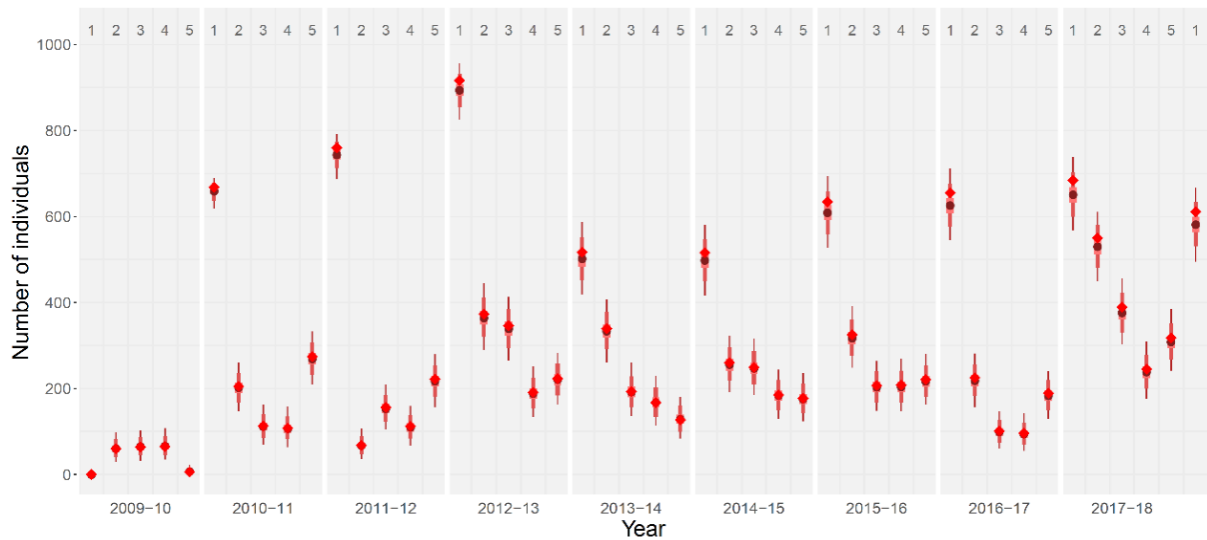

Figure S21. Real counts and posterior predictive distributions of the number of individuals observed in the residency area (read area on Fig. 1) across the study period. Diamonds (bright red) indicate the count in the real data. Circles (darkest colour) indicate the posterior predictive mean, inner (thick) line segments indicate the 50% interval of the distribution, middle line segments indicate the 95% interval, and outer (thin) line segments indicate the 99.9% interval.

Figure S22. Real counts and posterior predictive distributions of the number of individuals observed in migratory area 1 (orange points on Fig. 1) across the study period. See Fig. S21 for legend specifications.

Figure S23. Real counts and posterior predictive distributions of the number of individuals observed in migratory area 2 (brown area on Fig. 1) across the study period. See Fig. S21 for legend specifications.

Figure S24. Real counts and posterior predictive distributions of the number of individuals observed in migratory area 3 (yellow area on Fig. 1) across the study period. See Fig. S21 for legend specifications.
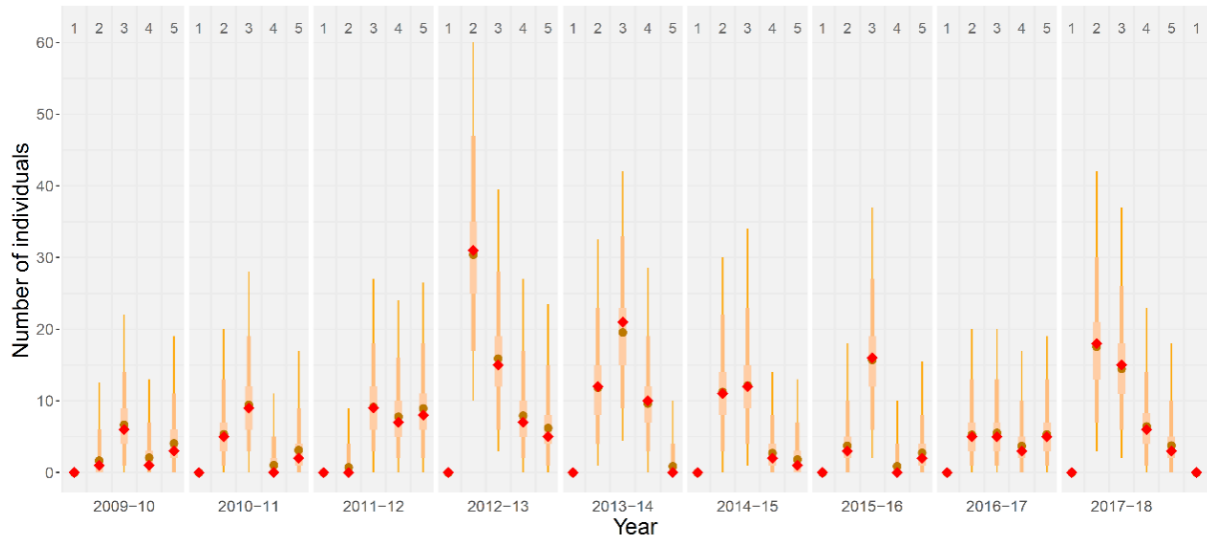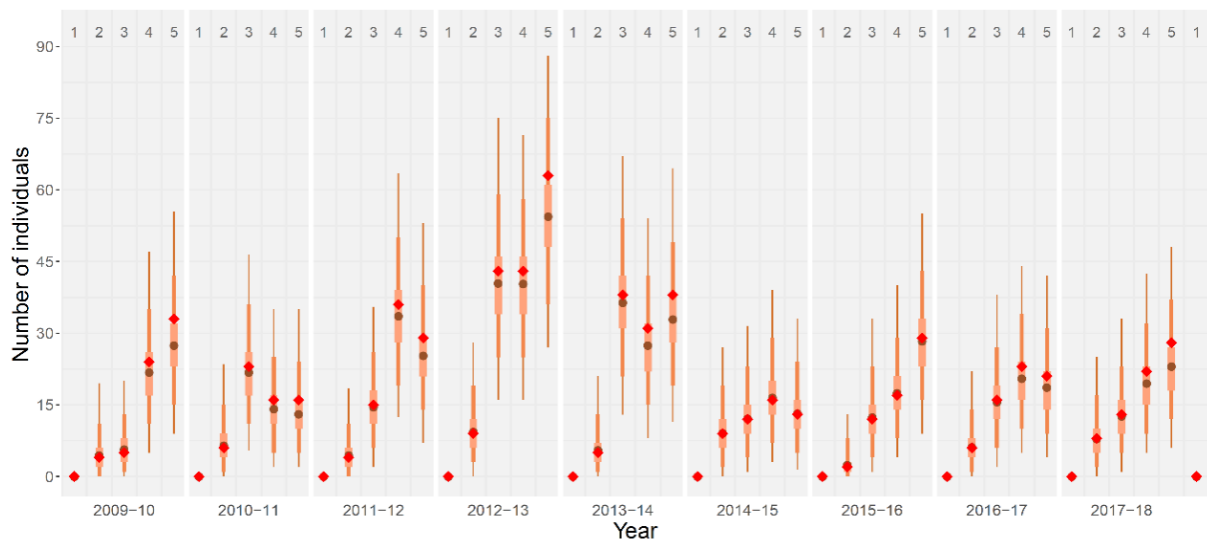

Figure S25. Real counts and posterior predictive distributions of the number of individuals observed in migratory area 4 (pink area on Fig. 1) across the study period. See Fig. S21 for legend specifications.
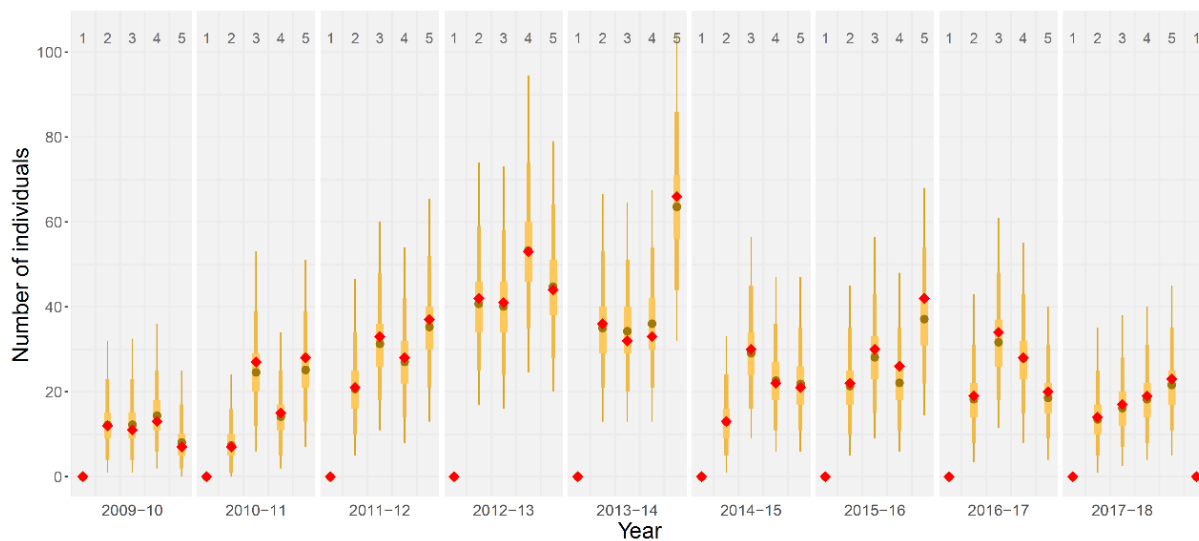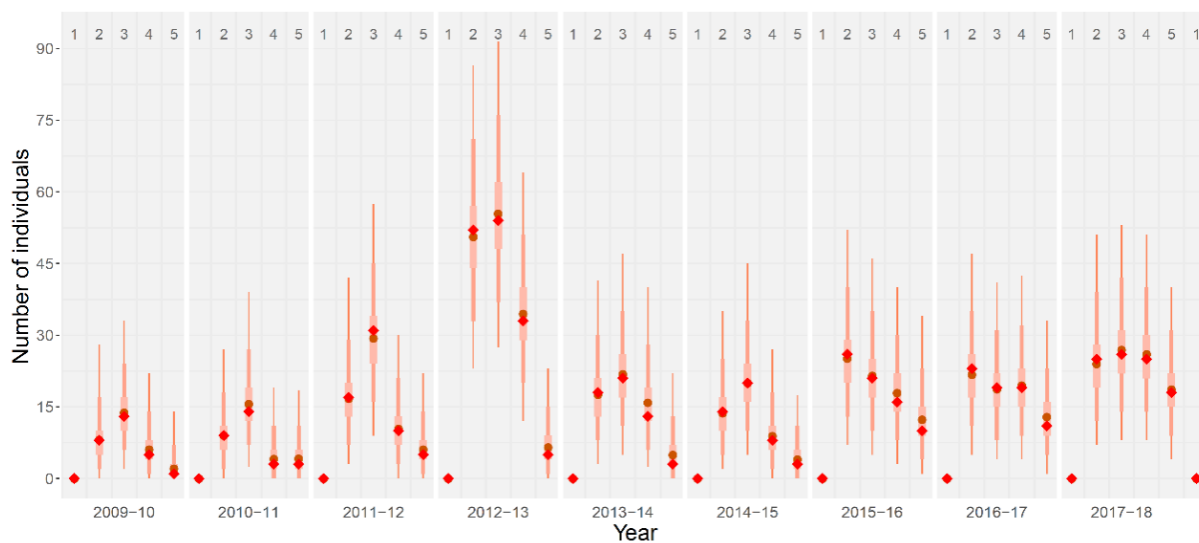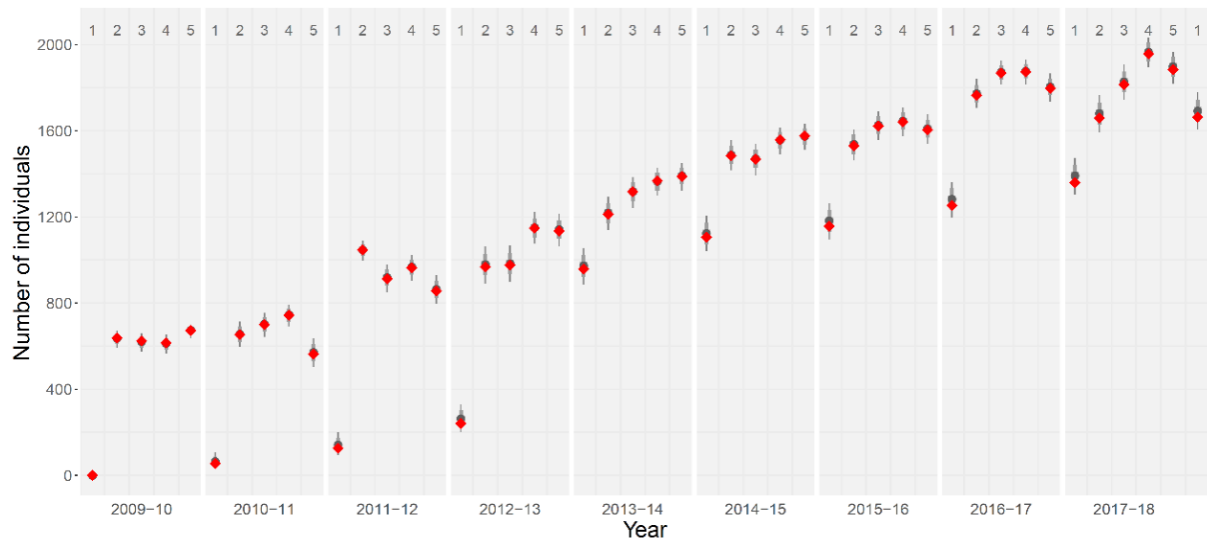
Figure S26. Real counts and posterior predictive distributions of the number of individuals that were not resighted across the study period. See Fig. S21 for legend specifications.

We then focused on finer details of the data: the number of individuals observed as residents, and migrants (whatever their migratory area), given previous (re-)sighting either as migrants or as residents in a given occasion, for every possible occasion across the study period (e.g. Fig. S27 to S35). For example, given that 723 individuals entered the data in 2009 (during occasion 1, the breeding season), we replicated 723 trajectories starting from the resident state in occasion 1 in 2009 (at each of 15,000 monitored iterations of the MCMC chains). We hence compared how many of these individuals were resighted either as residents or as migrants in every subsequent occasion in the real data with their corresponding posterior predictive distributions (Fig. S27). Then, we did the same for the 25 individuals that were resighted as migrants in occasion 2 in 2009 (Fig. S28; and replicating histories starting from the migratory state of the real observation for each of the 25 individuals). We did the same for the 60 individuals that were resighted as residents in occasion 2 in 2009 (Fig. S29), and so on given real data censuses of observed residents and migrants in all subsequent occasions (e.g. Fig. S30 to S35).

The fit was good considering resighting sequences subsequent to sighting in the residency area at each breeding season across the study period (e.g. Fig. S27, S30, S33; other possible departure occasions not shown). The fit was also good considering resighting sequences subsequent to sighting in the residency area or in a migratory area in winter occasions, up to the next breeding season in the following breeding seasons (e.g. Fig. S28–29, S31–32, S34–35; other possible departure occasions not shown). Indeed, most of the corresponnding data points were comprised within the bulk of their posterior predictive distribution; they were very rarely outside the 95%CRI, and always within the 99.9%CRI. These checks therefore show the good performances of our model in replicating individual trajectories that lead to censuses of observed migrants and residents that look similar to the real data. It indicates that the model is self-consistent in predicting the population proportions of individuals that will survive, be in the residency area or a migratory area, and be resighted there, across the study period, at least when starting from a breeding season (with all individuals being in the residency area), within any given annual cycle and over years. In conclusion, our model is reliable regarding cross-sectional, population-level inferences on survival, movement, and resighting processes made at any occasion. We found only a few occasional systematic discrepancies (notably, data points outside the 95%CRI of their posterior predictive distributions) of small amplitude (always within the 99.9% limits of their posterior predictive distribution), indicating some small lack of fit, likely to be due to subtle heterogeneities (e.g. related to punctual age, or cohort differences) that are not taken into account given the current resolution of our model. Such subtle differences may be of interest for finer demographic analyses of partial migration, but were not of concern given our present objectives.

However, again considering the sequences starting from winter occasions, migrants were clearly more likely to remain migrants over years, and residents to remain residents, in the real data than in their posterior predictive distributions (e.g. Fig. S28–29, S31–32, S34–35; other possible

departure occasions not shown here). Indeed, corresponding data points were very often outside the 95%CRI and often clearly outside the 99.9%CRI. This was not of concern regarding our present objectives of cross-sectional, population-level inferences on survival probability in residents vs. migrants. Nonetheless, this indicated that our model could be improved to include individual memory regarding the previous location and hence being able to fit individual trajectories in a longitudinal fashion more adequately. Such improvements would allow to make inferences on individual migratory strategies, their degree of canalization and plasticity, and potential carry-over effects on survival. These improvements might also allow getting more precision in the survival estimates of migrants vs. residents.

Figure S27. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting on the Isle of May during the breeding season (occasion 1) in 2009–10. Diamonds (brightest points) indicate the count in the real data, circles indicate the posterior predictive mean, inner (thick) line segments indicate the 50% interval of the distribution, middle segments indicate the 95% interval, and outer (thin) line segments indicate the 99.9% interval.

Figure S28. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting as residents during September (occasion 2) in 2009–10. See Fig. S27 for legend specifications.

Figure S29. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting as migrants during September (occasion 2) in 2009–10. See Fig. S27 for legend specifications.
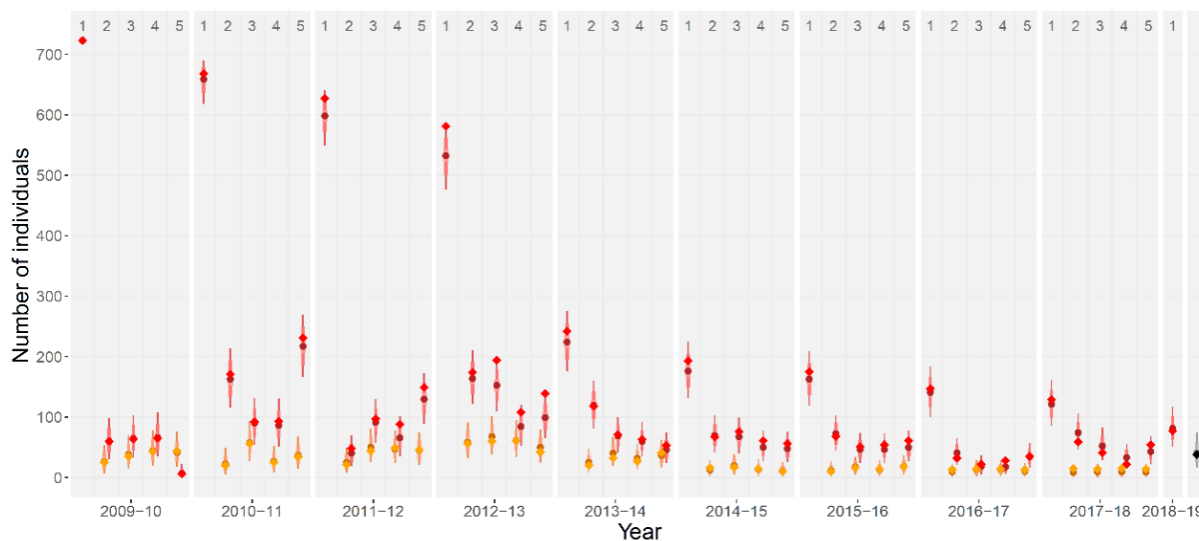
Figure S30. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting as on the Isle of May during the breeding season (occasion 1) in 2012–13. See Fig. S27 for legend specifications.

Figure S31. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting as residents during October (occasion 3) in 2012–13. See Fig. S27 for legend specifications.
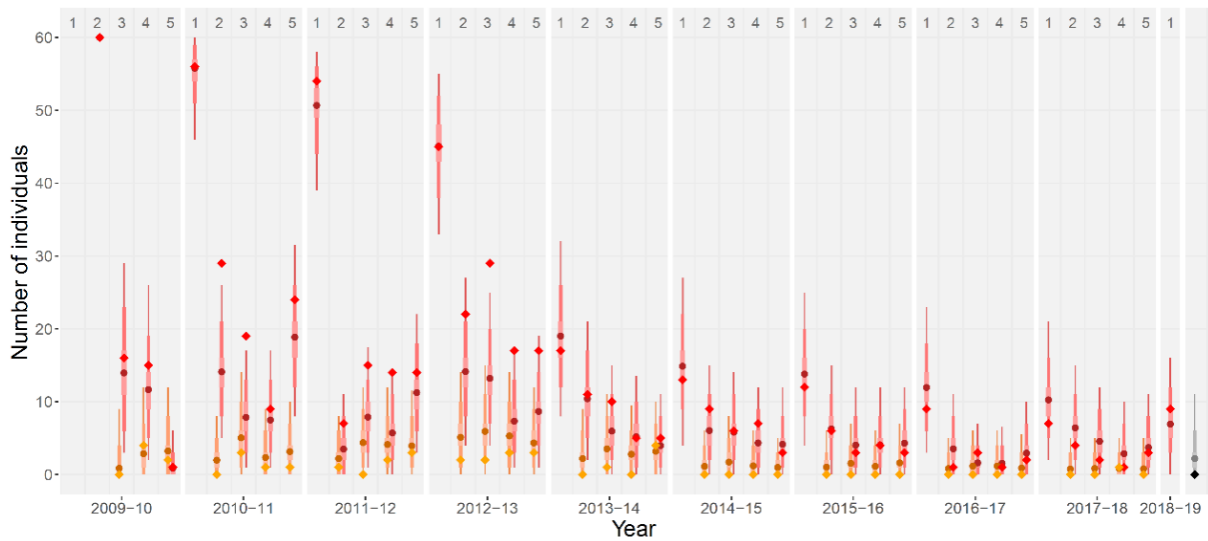
Figure S32. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting as migrants during October (occasion 3) in 2012–13. See Fig. S27 for legend specifications.

Figure S33. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting on the Isle of May during the breeding season (occasion 1) in 2016–17. See Fig. S27 for legend specifications.
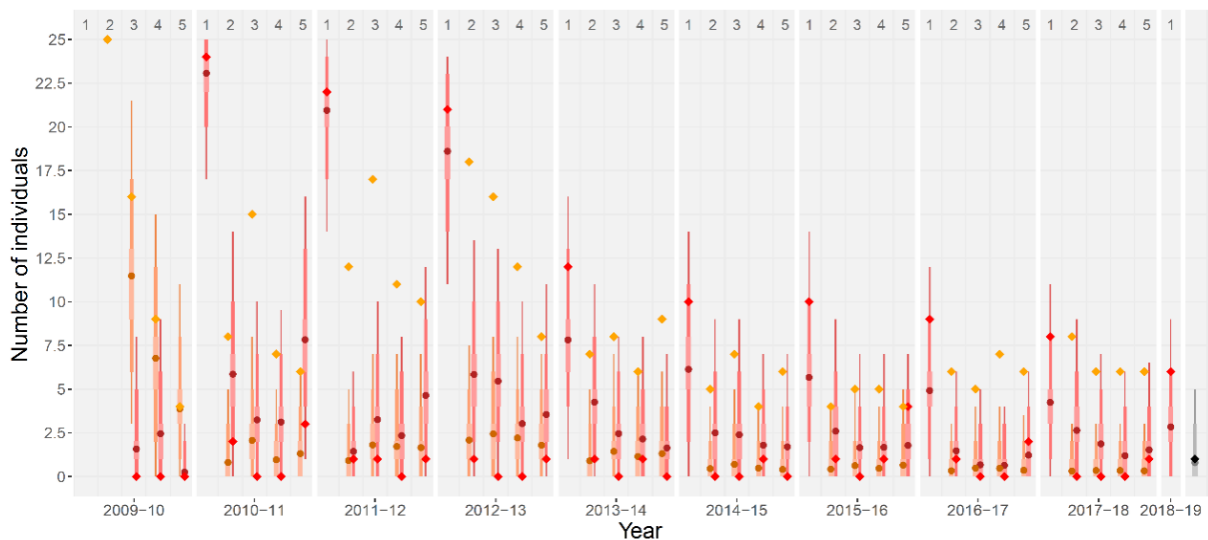
Figure S34. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting as residents during mid-winter (November-December, occasion 4) in 2016–17. See Fig. S27 for legend specifications.
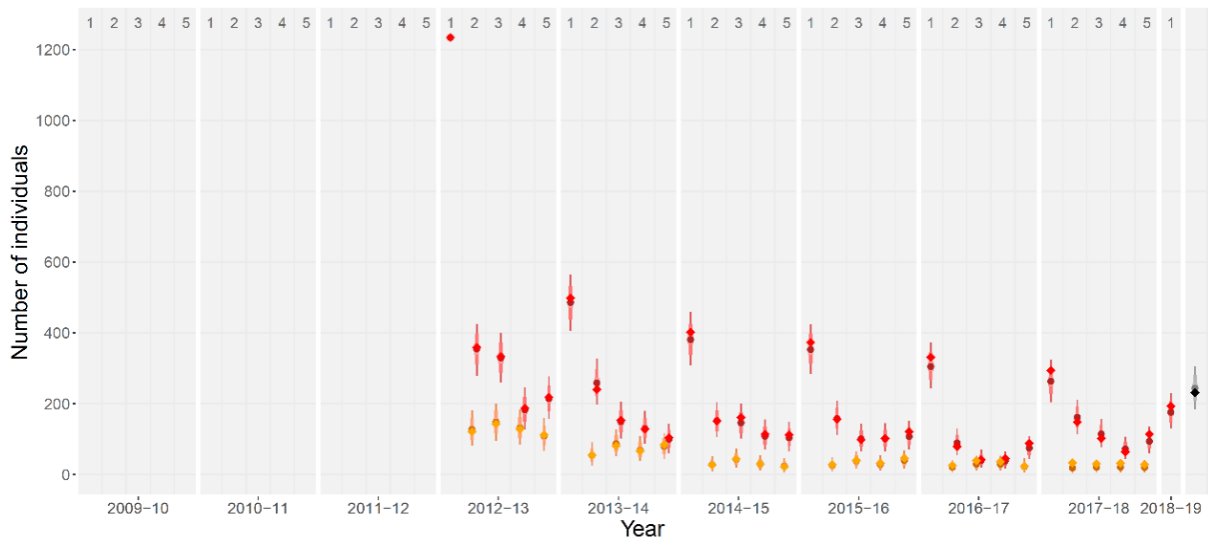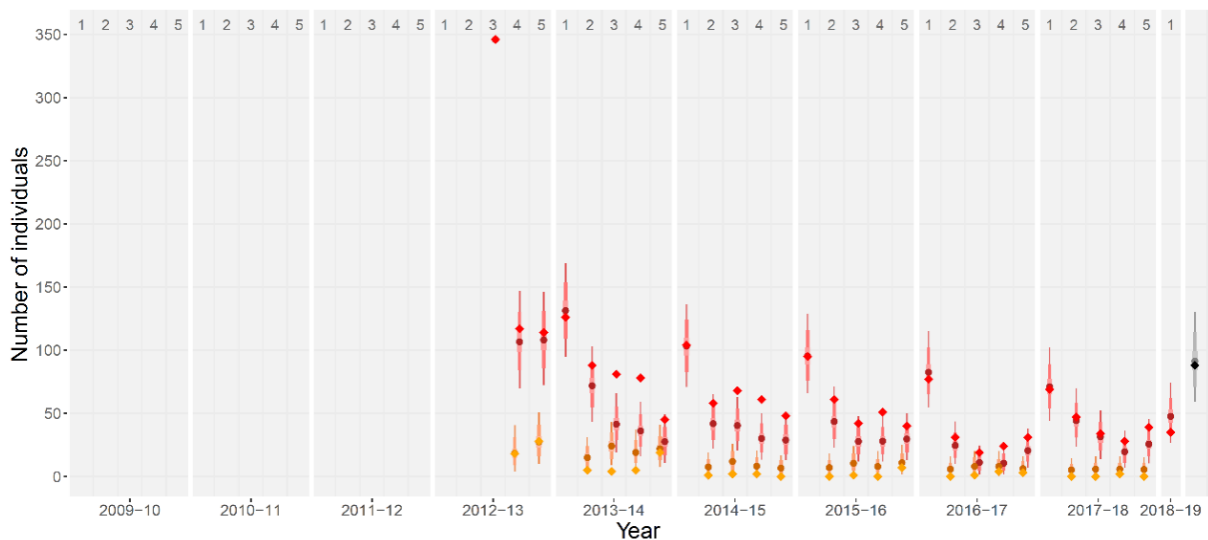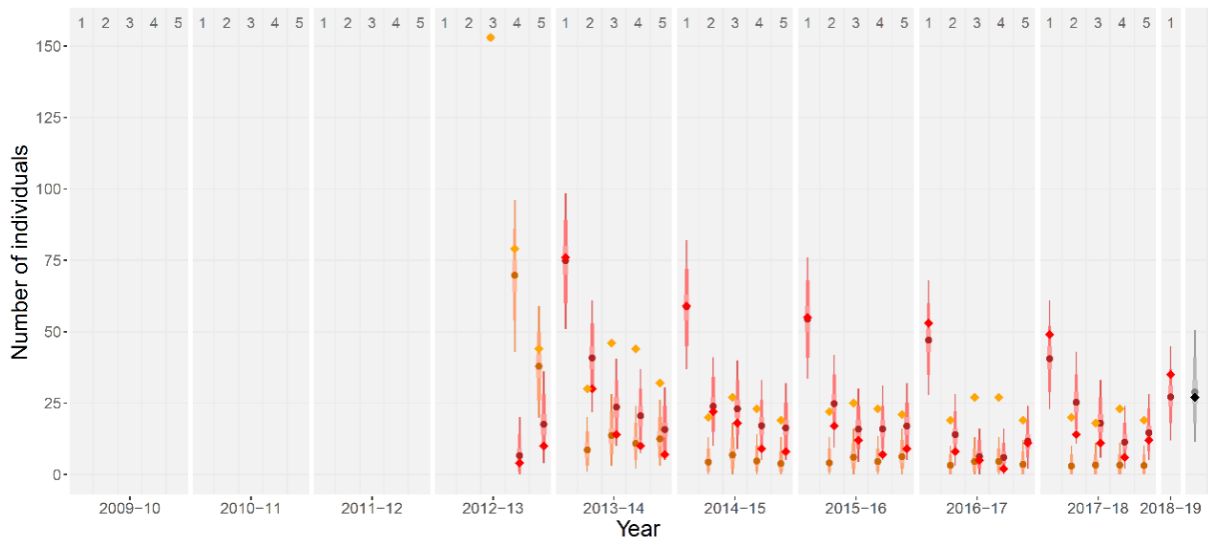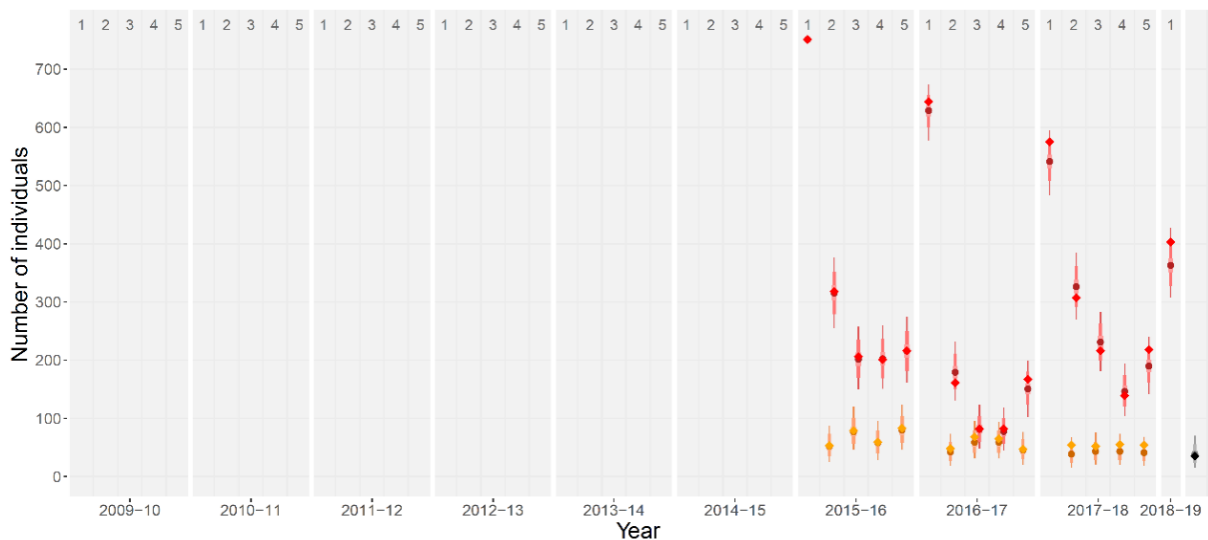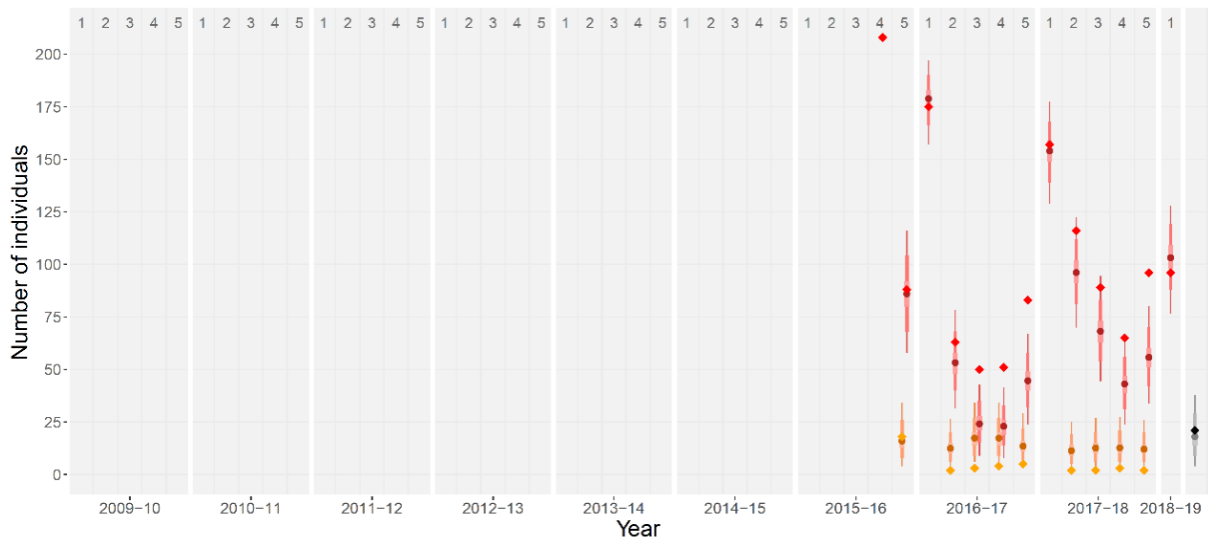

Figure S35. Real counts and posterior predictive distributions across the study period of the number of individuals resighted as residents (in red) or migrants (in orange) or never resighted again (in grey), given sighting as residents during mid-winter (November-December, occasion 4) in 2016–17. See Fig. S27 for legend specifications.
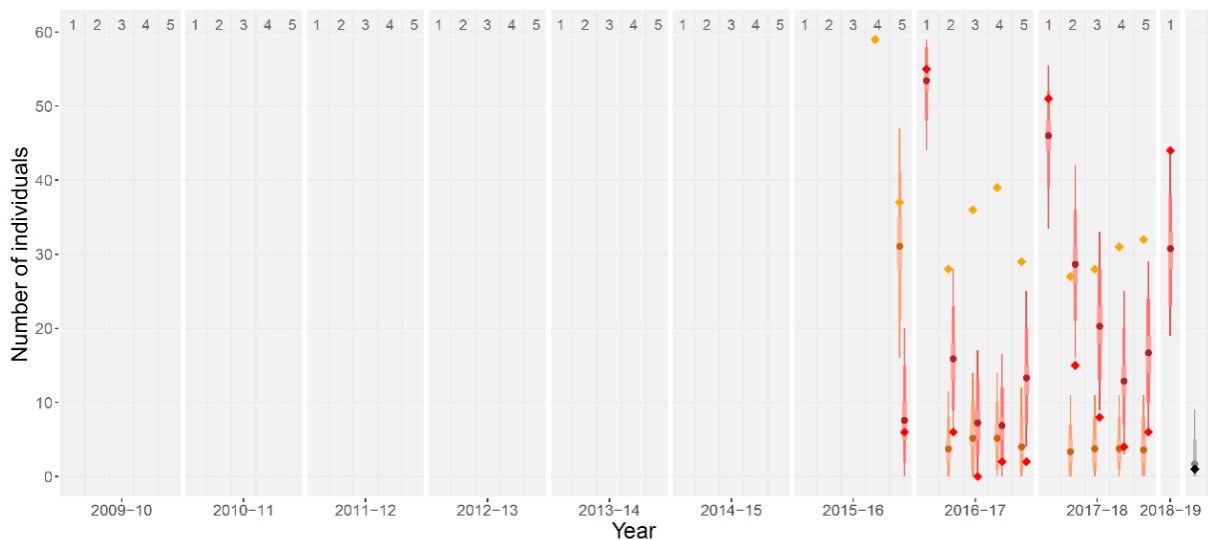
S4.2 Stan code for replicating data from posterior samples

The following bits of code are intended to be included within the main model code (provided in Appendix S2), so that data will be replicated at each iteration of the Markov chains for posterior sampling. The counts of the number of individuals in each possible observation event across time, once they entered the dataset, are named "counts" or "event counts" in the code below. The finer counts of the number of individuals observed as residents, and migrants (whatever their migratory area), given previous (re-)sighting either as migrants or as residents in a given occasion, for every possible occasion across the study period, are designated here as "fates" and stored in an object named "farray" for "fates array". In the "fates array", rows indicate the time and super-state (i.e. resident or migrant) being the starting point of the focal individual resighting sequences, and columns indicate all the possible resighting times and super-states (given sighting at the aforementioned starting point) plus a last column for the individuals that are never resighted again.

```
1    ... // keep previous blocks as in the original code (see Appendix S2)
2
3    generated quantities {
4
5      ... // keep declaration of the variables as in the original code (see Appendix S2)
6
7      int farray_rep[N_osite*(N_time-N_year)+N_year-1,N_osite*(N_time-N_year)+N_year]; // replicate of the "fates array", for posterior checking
8      int counts_rep[N_event,N_time]; // replicate of event counts at each time, for posterior checking
9      // above: monitored, below: unmonitored
10     int<lower=0,upper=N_state> state_rep[N_time]; // temporarily store replicated individual state
11     int<lower=0,upper=N_event> crs_rep[N_time]; // temporarily store replicated individual observation event
12     simplex[N_state] ps_bis; // temporarily store state-transition probabilities given replicated state, as a simplex for use in categorical_rng()
13     simplex[N_event] po_bis; // temporarily store observation probabilities given replicated state, as a simplex for use in categorical_rng()
14     int current_row; // temporarily store focal row of the "fates array" (see below)
15     int freqh; // temporarily store the number of individuals that have the same unique capture-resighting history in the original dataset
16
17     ... // keep the rest of the content of the generated quantity block as in the original code (see Appendix S2)
18
19        farray_rep = rep_array(0,N_osite*(N_time-N_year)+N_year-1,N_osite*(N_time-N_year)+N_year);
```

```
20          counts_rep = rep_array(0,N_event,N_time);
21          llk_rep = 0;
22
23      for (s in 1:N_sex) {
24          // replicate individual capture-recapture histories based on model parameter values in the posterior sample
25          // and fill the observation event counts and "fates array" to summarize the replicated histories
26          for (h in 1:N_crs)
27            for (r in F_time[h]:N_trans)
28              if (crs[h,r]>0 && crs[h,r]<N_event && sum(obs[h,r:N_time])>0) {
29                if (occ[r]==1)
30                  current_row = N_osite*(r-year[r])+year[r];
31                else
32                  current_row = N_osite*(r-year[r]-1)+year[r]+crs[h,r];
33                if (N_sex==1)
34                  freqh = sum(freq[h,]);
35                else
36                  freqh = freq[h,s];
37                for (i in 1:freqh) {
38                  state_rep[r] = crs[h,r];
39                  crs_rep[r] = crs[h,r];
40                  for (t in (r+1):N_time) {
41                    if(state_rep[t-1]<N_state) {
42                      ps_bis = ps[s,state_rep[t-1],t-1];
43                      state_rep[t] = categorical_rng(ps_bis);
44                    }
45                    else
46                      state_rep[t] = N_state;
47                    if (obs[h,t]==1) {
48                      po_bis = po[s,state_rep[t],t];
49                      crs_rep[t] = categorical_rng(po_bis);
50                      if (crs_rep[t]<N_event)
51                        if (occ[t]==1)
52                          farray_rep[current_row,N_osite*(t-year[t])+year[t]-1] += 1;
53                        else
54                          farray_rep[current_row,N_osite*(t-year[t]-1)+year[t]-1+crs_rep[t]] += 1;
55                    }
56                    else
57                      crs_rep[t] = N_site;
58                    if(r==F_time[h])
59                      counts_rep[crs_rep[t],t] += 1;
60                  }
61                  if (min(crs_rep[(r+1):N_time])==N_site)
62                    farray_rep[current_row,N_osite*(N_time-N_year)+N_year] += 1;
63                }
64              }
65        }
66
67      }
```

13

S4.3 Assessing confidence in the inferences

A crucial point of any statistical data analysis is to assess whether the inferences from the model make sense. The most straightforward way of doing so is to compare the inferences with knowledge that has not been included formally in the model (either in the priors or the likelihood). In our case, such information comes from previous analyses of annual survival in shags breeding on Isle of May that used dead recovery data from 1965–2005 and did not consider winter movements (Frederiksen, Daunt, Harris, & Wanless, 2008), from analyses of migratory movements and associated breeding success during 2010-2012 (Grist et al., 2014, 2017), and from broad understanding of our study system derived from field experience.

Regarding the survival probabilities that are of current primary interest, our estimated annual survival values under good or bad conditions are very similar to those estimated by Frederiksen et al. (2008). Further, the estimated timings of low survival matched known extreme climatic events that occurred during our study period. Furthermore, the fact that survival was lower in residents than migrants in two ECEs makes sense, given the northerly spatial distribution of migrants and the opportunity for sheltering against winter storms offered by such locations (see main text, Appendix S1). We also verified that the detection probability was very high during the breeding season, which was highly expected given the intensive effort carried on individual monitoring during the breeding season on the Isle of May (see main text, Appendix S1). Detection probability in winter in the different areas and time points also made sense given variability the resighting effort and efficiency carried out in the different areas (see main text, Appendix S1, Appendix S4). Moreover, inferences on movement parameters and resulting migratory fraction also made sense given previous analyses and field experience regarding the timings of migration (most departure in September-October, and most returns in February-March; Grist et al., 2014). This was also the

case regarding the proportion of individuals regularly resighted as residents or migrants, or never resighted during the winter and hence likely being migrants in an unobserved location modelled through the "ghost" site.

Another source of confidence in the results comes from sensitivity analyses that we performed during model development. We made a number of choices regarding model structure, that were motivated by the will to account for much of the potential spatio-temporal variation in individual histories, and by convenience for some parameters presumed to be less influential (see main text). We hence complied with our primary aim to make inferences on survival in residents vs. migrants at a fine temporal resolution while retaining as much as possible of the uncertainty associated with the movements and observation processes. Nonetheless, other plausible models could have been applied to our problem. We fitted some of these alternative models to our dataset in the course of model development, to check the answer they provided. We notably fitted an alternative model that considered only observable migratory states (i.e. no "ghost area"), we also fitted models that included location-dependent switching probabilities (conditional on not returning to the residency area), as well as models that did not included time-dependence in survival and/or movement probabilities. The most robust inferences are those that do not change radically between models. The key point that emerged is that all models that included temporal variation in survival provided very similar inferences on survival of migrants versus residents. The alternative models also provided analogous inferences regarding the migratory fraction, indicating that there was always a non-negligible part of the population located in migratory areas, typically roughly around a half. Models that did not included temporal variation in survival led to major sampling issues. The outputs (notably, bimodality in the posterior samples of survival and resighting probabilities) strongly suggested that the model could not properly fit the disappearance of many individuals

after the ECEs. All these observations were re-assuring regarding the robustness of the signal in our dataset for the main results presented and discussed in our paper.

We also applied our model and its above-mentioned alternative versions to a simplified version of the dataset in which all observed migratory areas were grouped as a single migratory area (i.e. there was only one possible observation event for migrant, with no distinction of the location). Accordingly, a single observable migratory state was considered, and no spatial heterogeneity in resighting probability was taken into account. The models fitted to this simplified dataset also provided very similar posterior probabilities for the survival probabilities of migrants and residents, and analogous inferences regarding the migratory fraction, which was again re-assuring regarding the robustness of our main results.

S4.4 References

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Frederiksen, M., Daunt, F., Harris, M. P., & Wanless, S. (2008). The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology, 77(5), 1020–1029. https://doi.org/10.1111/j.1365-2656.2008.01422.x

Gelman, A., Meng, X.-L., & Stern, H. (1996). Posterior predictive assessment of model fitness via realized discrepancies. Statistica Sinica, 6(4), 733–760.

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APPENDIX S5

Summary of the posterior samples

Contents:

S5.1 Foreword and sampling details

Here, we present graphical summaries of the posterior samples for every parameter in our main model (without sex effects) fitted to the complete dataset, except for seasonal survival probabilities (already presented in Fig. 3 of the paper). We also present graphical summaries of annual survival probabilities for different possible paths in the annual cycle, and the migratory fraction. Further, we present numerical summaries of the differences in survival probabilities between migrants and residents. For the model including sex effects fitted to the reduced dataset consisting of capture-resighting histories of sexed individuals, we present graphical summaries of the posterior samples for seasonal survival probabilities and the migratory fraction. We also present numerical summaries of the sex bias in survival of residents and migrants, and the resident-migrant survival difference, and the migratory fraction.

Detailed numerical summaries of the posterior samples for all parameters and derived quantities of the two models, and complete corresponding posterior samples, are archived as Rdata files with the dataset (Acker et al. 2020; https://doi.org/10.5061/dryad.c2fqz616r).

Sampling of the posterior distribution was performed using 10 Markov chains with 1000 warmup iterations followed by 1500 monitored iteration (with no thinning), yielding 15,000 samples in total. There was no indication of issues regarding the reliability of the inference algorithm (in particular, no divergent numerical trajectories). The Gelman-Rubin-Brooks *r-hat* statistics (Brooks & Gelman 1998) indicated good convergence of the chains, with all *r-hat* <1.01. Effective sample sizes were all >1500 (and much larger for most parameters, including survival probabilities), and Monte Carlo standard errors were all <5% of the standard deviation of the corresponding posterior sample (and much lower for most parameters, including survival probabilities). This indicates that uncertainty of estimates due to imperfect (pseudorandom) sampling is negligible. Precision of the sampling is sufficiently high so that all posterior means can be reported with 2 decimal place precision (and most of them could be reported with ≥3 decimal place precision). See Lunn, Jackson, Best, Thomas, and Spiegelhalter (2012) and Gelman et al. (2014) for further on MCMC methods for posterior sampling (and more generally on Bayesian data analysis).

S5.2 Survival probabilities

Seasonal survival in the model without sex effects

In the main text, we provided graphical summaries for seasonal survival probabilities in residents and migrants (Fig. 3). Hereafter, we provide numerical summaries of the difference in seasonal survival probability between residents and migrants (Table S4). This difference was calculated as "migrant survival probability minus resident survival probability" in each posterior sample (i.e. each iteration of the Markov chains).

Table S4. Posterior summary of the difference in seasonal survival probability between residents and migrants ("migrant minus resident survival probability").

Year	Occ.	Mean	SD	2.5%	97.5%	Pr(Δ>0)
2009–10	2	0.00	0.02	-0.04	0.04	0.38
	3	0.00	0.02	-0.04	0.04	0.49
	4	0.00	0.01	-0.03	0.03	0.55
	5	-0.01	0.02	-0.06	0.02	0.21
2010–11	2	-0.01	0.02	-0.05	0.03	0.35
	3	0.00	0.01	-0.03	0.03	0.59
	4	-0.01	0.02	-0.05	0.02	0.26
	5	0.01	0.02	-0.03	0.04	0.78
2011–12	2	0.00	0.03	-0.06	0.05	0.46
	3	-0.01	0.02	-0.06	0.03	0.27
	4	0.01	0.02	-0.03	0.04	0.66
	5	-0.01	0.02	-0.05	0.02	0.42
2012–13	2	-0.04	0.04	-0.13	0.04	0.16
	3	0.00	0.04	-0.07	0.08	0.52
	4	**0.02**	**0.07**	**-0.11**	**0.16**	**0.65**
	5	**0.31**	**0.05**	**0.20**	**0.41**	**1.00**
2013–14	2	0.00	0.03	-0.07	0.05	0.47
	3	-0.03	0.03	-0.09	0.03	0.18
	4	0.00	0.03	-0.06	0.06	0.51
	5	**-0.03**	**0.04**	**-0.11**	**0.04**	**0.20**
2014–15	2	-0.02	0.02	-0.07	0.01	0.14
	3	0.01	0.02	-0.03	0.04	0.69
	4	0.00	0.02	-0.05	0.04	0.49
	5	-0.01	0.02	-0.06	0.03	0.34
2015–16	2	-0.02	0.02	-0.06	0.01	0.17
	3	0.01	0.02	-0.02	0.04	0.69
	4	*0.05*	*0.02*	*0.01*	*0.09*	*0.99*
	5	-0.01	0.02	-0.06	0.03	0.36
2016–17	2	0.00	0.03	-0.07	0.04	0.46
	3	*0.05*	*0.03*	*-0.01*	*0.11*	*0.94*
	4	0.00	0.02	-0.04	0.04	0.46
	5	0.00	0.02	-0.06	0.04	0.52
2017–18	*2*	*-0.05*	*0.03*	*-0.12*	*0.00*	*0.04*
	3	0.02	0.03	-0.04	0.07	0.80
	4	0.00	0.03	-0.07	0.06	0.48
	5	**0.26**	**0.04**	**0.17**	**0.33**	**1.00**

Notes: 'Occ.' is the departure occasion of the time step considered, 'SD' is the standard deviation of the posterior distribution, '2.5%' and '97.5%' are the limits of the 95% credible interval (i.e. the 2.5% and 97.5% quantiles of the distribution), 'Pr(Δ>0)' is the posterior probability that the focal difference is positive. ECEs are in bold, and non-ECE episodes with strong support for a given sign difference are in italics. Note that comparison of the estimates between occasions should account for differences in the length of interval between occasions, and of occasions themselves.

We assessed the support of the difference through the posterior probability that it was positive, calculated as the proportion of posterior samples in which the difference was positive.

Note that we arbitrarily chose to focus on the probability that it was positive, but it is the complement of the probability that it was negative (and the probability that the reverse difference was negative). This choice thus does not matter in itself, but it is necessary to remain consistent across calculations in the way the difference is formulated and which sign (positive or negative) is used to assess its support.

Annual survival in the model without sex effects

In Fig. 4 of main text, we provided graphical summaries of annual survival probabilities for full-winter migration and residence. Here, we provide numerical summaries of the difference in annual survival probability between full-winter migration and residence (Table S5).

Table S5. Posterior summary of the difference in (derived) annual survival probability between full-winter residence and full-winter migration (calculated as "migrant survival probability minus resident survival probability").

Year	Mean	SD	2.5%	97.5%	Pr($\Delta>0$)
2009–10	-0.02	0.03	-0.08	0.05	0.28
2010–11	-0.01	0.03	-0.07	0.05	0.41
2011–12	-0.02	0.04	-0.09	0.06	0.35
2012–13	**0.21**	**0.04**	**0.12**	**0.29**	**1.00**
2013–14	**-0.06**	**0.05**	**-0.15**	**0.04**	**0.12**
2014–15	-0.02	0.03	-0.08	0.04	0.25
2015–16	0.03	0.03	-0.03	0.09	0.84
2016–17	0.04	0.04	-0.05	0.12	0.79
2017–18	**0.21**	**0.05**	**0.11**	**0.30**	**1.00**

Note: 'SD' is the standard deviation of the posterior distribution, '2.5%' and '97.5%' are the limits of the 95% credible interval (2.5% and 97.5% quantiles of the distribution), 'Pr($\Delta>0$)' is the posterior probability that the focal difference is positive. ECE years are in bold.

In addition, we provide graphical summaries for annual survival probabilities of two other possible paths through the annual cycle (Fig. 2a), to illustrate the importance of migration timings (Fig. S36): "late-winter departure" (i.e. remain resident up to occasion 4 and then be migrant in occasion 5, circannual phenotypic sequence 'R-R-R-R-M'), and "late-winter return"

(i.e. leaving the residency area by occasion 1 but returning by occasion 5, circannual phenotypic sequence 'R-M-M-M-R'). We also included full-winter migration and full-winter residence in this latter graph (Fig. S36). On this graph, it clearly appears that late-winter location which is driving the major differences in annual survival between the different paths, that resulted from the severe late-winter ECEs in 2012-13 and 2017-18.
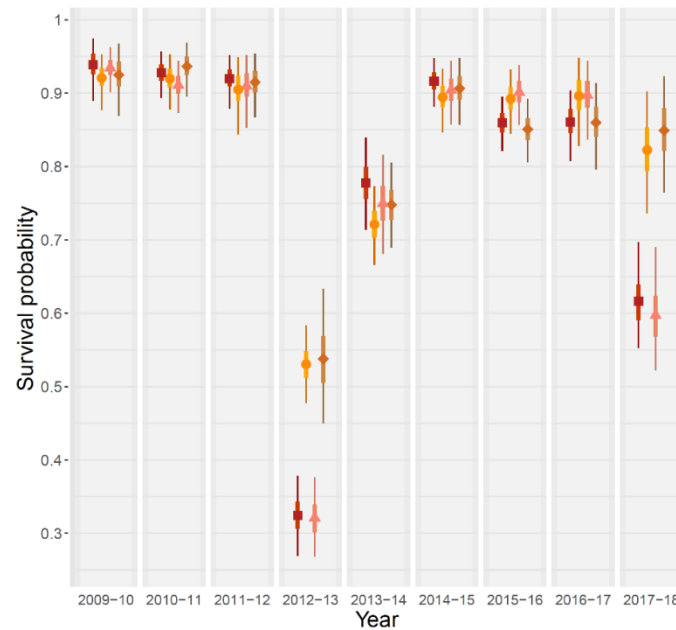

Figure S36. Annual survival probabilities of adult shags that bred on the Isle of May, derived for full-winter residence (i.e. annual path from occasion 1 to occasion 5 is RRRRR with 'R' for 'resident'; red squares), full-winter migration (i.e. annual path RMMMM with 'M' for 'migrant'; orange circles), late-winter return (i.e. annual path RMMMR; pink triangles) and late-winter migration (i.e. annual path RRRRM; brown diamonds). Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals.

Indeed, annual survival probability for late-winter departure was similar to that for full-winter migration (Δ: 0.03 [-0.05,0.11] in 2012-13 and 0.01 [-0.09,0.10] in 2017-18, Pr(Δ>0): 0.55 and 0.74 respectively) and clearly higher than for full-winter residence (Δ: 0.21 [0.14,0.30] in 2012-13 and 0.23 [0.15,0.30] in 2017-2018, Pr(Δ>0): 1.00 for both). In contrast, annual survival probability for late-winter return was clearly lower than for full-winter migration (Δ: -0.21 [-0.27,-0.14] in 2012-13 and -0.23 [-0.29,-0.15] in 2017-18, Pr(Δ>0): 0.00 for both) and similar to that for full-winter residence (Δ: 0.00 [-0.06,0.06] in 2012-13 and -0.02

[-0.08,0.04] in 2017-2018, Pr(Δ>0): 0.45 and 0.26 respectively). Accordingly, annual survival probability was clearly higher for late-winter departure than for late-winter return (Δ: 0.21 [0.09,0.35] in 2012-13 and 0.25 [0.14,0.36] in 2017-2018, Pr(Δ>0): 1.00 for both).

These results can be extended to a comparison of all 16 possible paths through the annual cycle of partial migration (Fig. 2a). This shows that the location in late winter (occasion 5) drives the annual survival differences between the different paths in 2012-13 and 2017-18 (Figure S37). In other years, there is no clear evidence for such differences, or the differences are relatively small (Figure S37; and see summaries provided in Electronic Supplementary Material and posterior samples archived with the data for further numerical details). Note that details of the probabilities of realizing each of the 16 possible paths, or dying before late winter, are in Appendix S5.6.
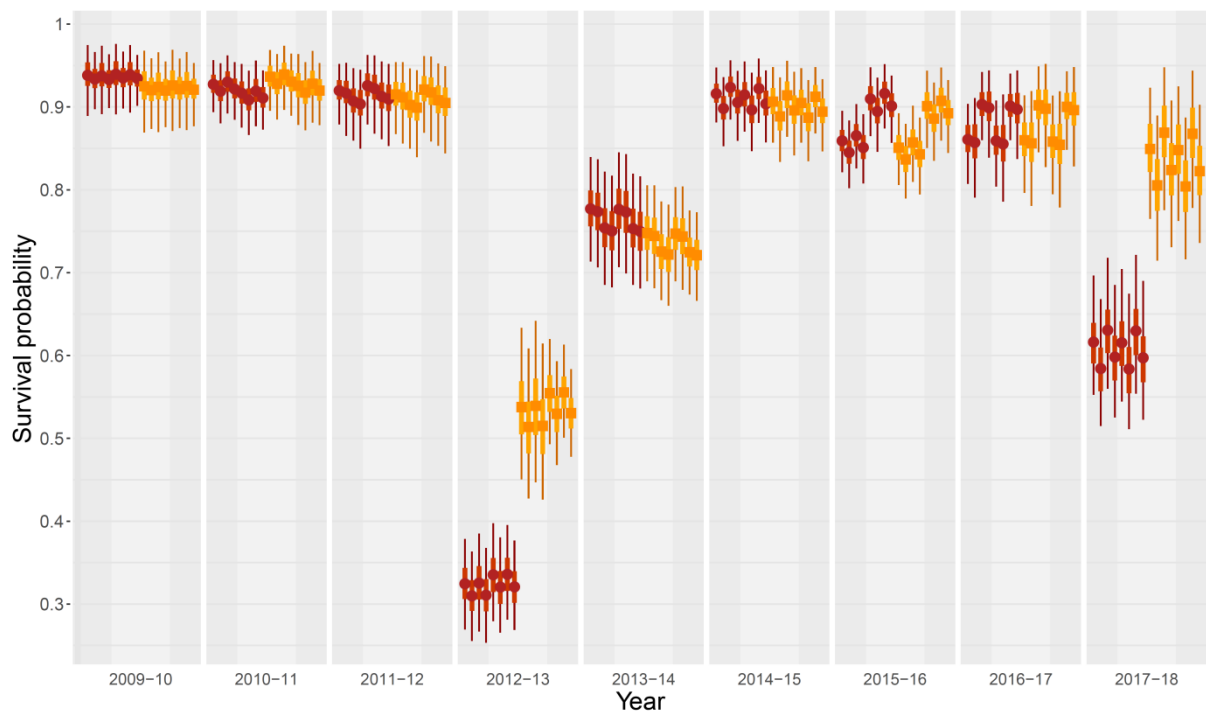
Figure S37. Annual survival probabilities of adult shags that bred on the Isle of May, derived for all 16 possible paths through the annual cycle (Fig. 2a). The 8 annual paths that end by the phenotype 'R' (i.e. resident in late winter, occasion 5) are in red, the 8 paths that end by the phenotype 'M' (i.e. migrant in late winter, occasion 5) are in orange. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals.

Seasonal survival in the model with sex effects

In the main text, we provided graphical summaries for sex-dependent seasonal survival probabilities in residents and migrants but only in ECE years (Fig. 5). Here, we provide the complete graphical summary for all years (Fig. S37). Further, we provide numerical summaries of the sex bias in seasonal survival probability in residents and migrants (i.e. 'female minus male survival difference'; Table S6, S7), and in the difference in survival between residents and migrants (i.e. 'migrant-resident male survival difference' minus 'migrant-resident female survival difference'). We also provide similar summaries of sex biases in annual survival probability for full-winter residence and migration (Table S8, S9; see Fig. 5 for graphics).
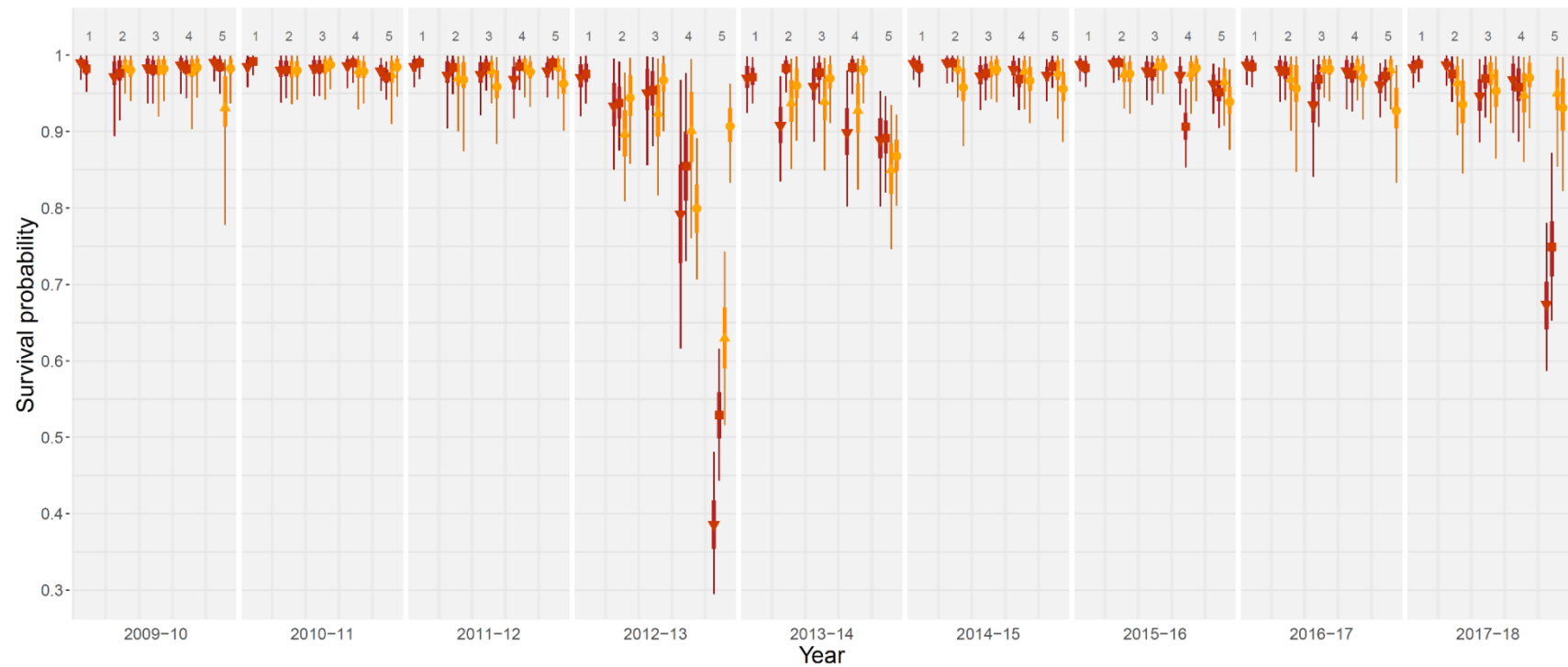
Figure S38. Migration- and sex-dependent seasonal survival probabilities of adult shags that bred on the Isle of May. Point estimates are posterior means (female residents: red down-triangles, male residents: red squares, female migrants: orange up-triangles, male migrants: orange circles), inner and outer line segments indicate 50% and 95% credible intervals. Survival time steps span consecutive time points (departure time point is indicated by the corresponding annual occasion, numbered 1-5 on the top row). In the breeding season, all surviving individuals are in the residency area, hence there is no migrant survival probability following annual occasion 1.

Table S6. Posterior summary of the sex bias in seasonal survival probability ("female minus male survival probability"), in resident and migrant adult shags that bred on the Isle of May.

Year	Occ.	Residents					Migrants				
		Mean	SD	2.5%	97.5%	Pr(Δ>0)	Mean	SD	2.5%	97.5%	Pr(Δ>0)
2009–10	1	0.01	0.02	-0.02	0.04	0.68					
	2	0.00	0.04	-0.09	0.07	0.46	0.00	0.02	-0.04	0.05	0.57
	3	0.00	0.02	-0.05	0.05	0.54	0.00	0.03	-0.07	0.05	0.50
	4	0.00	0.02	-0.04	0.05	0.61	-0.01	0.03	-0.08	0.04	0.45
	5	0.01	0.02	-0.02	0.04	0.64	-0.05	0.06	-0.21	0.03	0.14
2010–11	1	-0.01	0.01	-0.04	0.02	0.32					
	2	0.00	0.02	-0.05	0.04	0.50	0.00	0.02	-0.05	0.05	0.51
	3	0.00	0.02	-0.04	0.04	0.49	0.00	0.02	-0.05	0.03	0.42
	4	0.00	0.02	-0.04	0.03	0.41	0.00	0.03	-0.05	0.05	0.52
	5	0.01	0.02	-0.03	0.04	0.68	-0.01	0.03	-0.08	0.04	0.37
2011–12	1	0.00	0.01	-0.04	0.02	0.37					
	2	-0.01	0.03	-0.08	0.04	0.38	0.00	0.04	-0.07	0.09	0.48
	3	-0.01	0.02	-0.07	0.03	0.34	0.02	0.03	-0.04	0.10	0.74
	4	-0.02	0.02	-0.07	0.03	0.24	0.01	0.02	-0.04	0.06	0.61
	5	-0.01	0.02	-0.05	0.02	0.26	0.02	0.03	-0.03	0.09	0.80
2012–13	1	0.00	0.03	-0.06	0.05	0.45					
	2	0.00	0.05	-0.10	0.09	0.48	-0.05	0.06	-0.16	0.07	0.20
	3	0.00	0.05	-0.11	0.09	0.49	-0.04	0.06	-0.16	0.06	0.22
	4	**-0.06**	**0.11**	**-0.28**	**0.15**	**0.29**	**0.10**	**0.08**	**-0.06**	**0.24**	**0.90**
	5	**-0.14**	**0.06**	**-0.27**	**-0.01**	**0.01**	**-0.28**	**0.07**	**-0.41**	**-0.14**	**0.00**
2013–14	1	0.00	0.03	-0.05	0.05	0.49					
	2	-0.07	0.04	-0.15	0.00	0.02	-0.02	0.05	-0.12	0.07	0.32
	3	-0.02	0.03	-0.10	0.04	0.31	-0.03	0.05	-0.13	0.05	0.26
	4	-0.09	0.05	-0.19	0.00	0.03	-0.05	0.05	-0.16	0.03	0.12
	5	**0.00**	**0.05**	**-0.10**	**0.09**	**0.49**	**-0.02**	**0.06**	**-0.14**	**0.09**	**0.39**
2014–15	1	0.01	0.01	-0.02	0.04	0.66					
	2	0.00	0.01	-0.03	0.03	0.53	0.03	0.03	-0.03	0.11	0.77
	3	0.00	0.02	-0.05	0.04	0.45	0.00	0.02	-0.05	0.05	0.46
	4	0.01	0.02	-0.03	0.06	0.72	0.01	0.03	-0.05	0.07	0.67
	5	-0.01	0.02	-0.05	0.02	0.26	0.02	0.04	-0.05	0.10	0.74
2015–16	1	0.00	0.01	-0.02	0.03	0.62					
	2	0.00	0.01	-0.03	0.03	0.48	0.00	0.03	-0.05	0.06	0.47
	3	0.00	0.02	-0.04	0.05	0.54	0.00	0.02	-0.04	0.04	0.51
	4	0.07	0.03	0.01	0.13	0.98	-0.01	0.03	-0.06	0.04	0.38
	5	0.01	0.03	-0.04	0.07	0.66	0.03	0.04	-0.05	0.10	0.78
2016–17	1	0.00	0.02	-0.03	0.03	0.55					
	2	0.00	0.02	-0.05	0.05	0.55	0.01	0.05	-0.07	0.13	0.57
	3	-0.03	0.05	-0.14	0.05	0.22	0.00	0.02	-0.04	0.05	0.50
	4	0.00	0.03	-0.05	0.06	0.58	0.01	0.03	-0.04	0.07	0.68
	5	-0.01	0.02	-0.06	0.03	0.30	0.05	0.04	-0.02	0.15	0.91
2017–18	1	0.00	0.01	-0.04	0.02	0.38					
	2	0.01	0.02	-0.02	0.05	0.73	0.03	0.05	-0.06	0.13	0.72
	3	-0.02	0.04	-0.09	0.05	0.27	0.02	0.04	-0.06	0.12	0.67
	4	0.01	0.04	-0.07	0.09	0.60	-0.02	0.05	-0.12	0.06	0.31
	5	**-0.08**	**0.07**	**-0.22**	**0.07**	**0.15**	**0.02**	**0.06**	**-0.10**	**0.15**	**0.61**

Notes: 'Occ.' is the departure occasion of the time step considered, 'SD' is the standard deviation of the posterior distribution, '2.5%' and '97.5%' are the limits of the 95% credible interval (i.e. the 2.5% and 97.5% quantiles of the distribution), 'Pr(Δ>0)' is the posterior probability that the focal difference is positive. In the breeding season, all surviving individuals are in the residency area, hence there is no migrant survival probability following annual occasion 1 (and thus no sex difference in this occasion in migrants). ECEs are in bold.

Table S7. Posterior summary of the sex bias in the seasonal survival difference between resident and migrant shags that bred on the Isle of May (i.e. 'migrant-resident male survival difference' minus 'migrant-resident female survival difference'), providing estimates of sex-specific selection.

Year	Occ.	Mean	SD	2.5%	97.5%	Pr(Δ_Δ>0)
2009–10	2	-0.01	0.04	-0.10	0.08	0.43
	3	0.00	0.04	-0.07	0.09	0.53
	4	0.01	0.04	-0.06	0.10	0.61
	5	0.06	0.06	-0.03	0.22	0.86
2010–11	2	0.00	0.03	-0.07	0.07	0.50
	3	0.00	0.03	-0.05	0.06	0.56
	4	0.00	0.03	-0.06	0.06	0.43
	5	0.02	0.03	-0.04	0.09	0.71
2011–12	2	-0.01	0.05	-0.12	0.08	0.42
	3	-0.03	0.04	-0.12	0.04	0.22
	4	-0.02	0.03	-0.10	0.04	0.25
	5	-0.03	0.03	-0.11	0.03	0.16
2012–13	2	0.04	0.07	-0.10	0.18	0.73
	3	0.04	0.07	-0.10	0.19	0.71
	4	**-0.16**	**0.13**	**-0.41**	**0.09**	**0.10**
	5	**0.13**	**0.09**	**-0.05**	**0.32**	**0.92**
2013–14	2	-0.05	0.06	-0.17	0.07	0.19
	3	0.01	0.06	-0.10	0.13	0.58
	4	-0.03	0.07	-0.16	0.10	0.31
	5	**0.02**	**0.08**	**-0.14**	**0.17**	**0.58**
2014–15	2	-0.02	0.04	-0.11	0.04	0.26
	3	0.00	0.03	-0.07	0.06	0.48
	4	0.00	0.04	-0.08	0.08	0.50
	5	-0.03	0.04	-0.12	0.05	0.20
2015–16	2	0.00	0.03	-0.06	0.06	0.51
	3	0.00	0.03	-0.06	0.06	0.52
	4	0.07	0.04	0.00	0.16	0.97
	5	-0.02	0.05	-0.10	0.07	0.36
2016–17	2	-0.01	0.05	-0.13	0.09	0.46
	3	-0.03	0.05	-0.15	0.06	0.25
	4	-0.01	0.04	-0.09	0.07	0.42
	5	-0.07	0.05	-0.17	0.03	0.08
2017–18	2	-0.02	0.05	-0.13	0.09	0.39
	3	-0.04	0.06	-0.16	0.06	0.22
	4	0.03	0.06	-0.08	0.15	0.71
	5	**-0.09**	**0.08**	**-0.26**	**0.07**	**0.13**

Notes: 'Occ.' is the departure occasion of the time step considered, 'SD' is the standard deviation of the posterior distribution, '2.5%' and '97.5%' are the limits of the 95% credible interval (i.e. the 2.5% and 97.5% quantiles of the distribution), 'Pr(Δ_Δ>0)' is the posterior probability that the focal difference is positive. ECEs are in bold

Table S8. Posterior summary of the sex bias in (derived) annual survival probability of shags that bred on the Isle of May (expressed as "female minus male survival probability"), for full-winter residence and full-winter migration.

Year	Full-winter residence					Full-winter migration				
	Mean	SD	2.5%	97.5%	Pr($\Delta>0$)	Mean	SD	2.5%	97.5%	Pr($\Delta>0$)
2009–10	0.01	0.05	-0.09	0.10	0.64	-0.05	0.07	-0.22	0.06	0.27
2010–11	0.00	0.03	-0.07	0.06	0.46	-0.02	0.04	-0.10	0.05	0.29
2011–12	-0.05	0.04	-0.13	0.02	0.08	0.04	0.05	-0.06	0.16	0.79
2012–13	**-0.13**	**0.05**	**-0.23**	**-0.04**	**0.00**	**-0.19**	**0.05**	**-0.30**	**-0.08**	**0.00**
2013–14	**-0.14**	**0.06**	**-0.27**	**-0.02**	**0.01**	**-0.10**	**0.05**	**-0.20**	**0.01**	**0.03**
2014–15	0.00	0.03	-0.06	0.07	0.55	0.06	0.05	-0.03	0.15	0.90
2015–16	0.08	0.04	0.00	0.15	0.98	0.02	0.04	-0.06	0.11	0.70
2016–17	-0.03	0.05	-0.13	0.05	0.23	0.07	0.06	-0.04	0.20	0.89
2017–18	**-0.07**	**0.07**	**-0.21**	**0.06**	**0.15**	**0.03**	**0.08**	**-0.11**	**0.18**	**0.67**

Notes: 'SD' is the standard deviation of the posterior distribution, '2.5%' and '97.5%' are the limits of the 95% credible interval (i.e. the 2.5% and 97.5% quantiles of the distribution), 'Pr($\Delta>0$)' is the posterior probability that the focal difference is positive. ECE years are in bold.

Table S9. Posterior summary of the sex bias in the (derived) annual survival difference between full-winter residence and full-winter migration (i.e. 'migrant-resident male survival difference' minus 'migrant-resident female survival difference'), providing evidence of sex-specific selection.

Year	Mean	SD	2.5%	97.5%	Pr($\Delta_\Delta>0$)
2009–10	0.06	0.09	-0.10	0.26	0.74
2010–11	0.02	0.06	-0.09	0.13	0.62
2011–12	-0.09	0.07	-0.24	0.05	0.10
2012–13	**0.06**	**0.08**	**-0.10**	**0.22**	**0.76**
2013–14	**-0.05**	**0.09**	**-0.23**	**0.14**	**0.31**
2014–15	-0.05	0.06	-0.18	0.07	0.19
2015–16	0.05	0.06	-0.07	0.18	0.81
2016–17	-0.11	0.09	-0.28	0.06	0.10
2017–18	**-0.11**	**0.09**	**-0.29**	**0.08**	**0.13**

Notes: 'SD' is the standard deviation of the posterior distribution, '2.5%' and '97.5%' are the limits of the 95% credible interval (i.e. the 2.5% and 97.5% quantiles of the distribution), 'Pr($\Delta>0$)' is the posterior probability that the focal difference is positive. ECE years are in bold.

S5.3 Resighting probabilities

Here we provide graphical summaries of the posterior distribution of the resighting probability in the residency area (Fig. S38) and in the migratory areas (Fig. S39 to S42), from the model without sex effects.
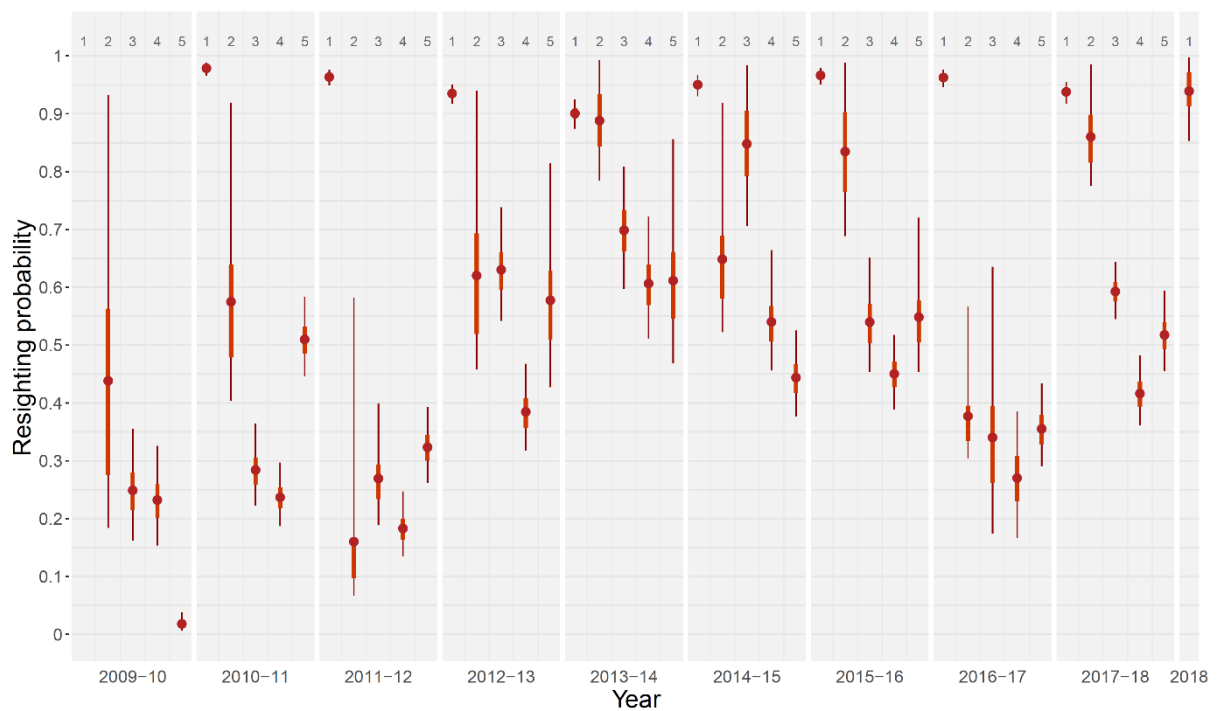

Figure S39. Resighting probability in the residency area of shags that bred on the Isle of May. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. The annual occasion, numbered 1-5, is indicated on the top row. In the first time point (occasion 1, year 1), all present individuals are entering the dataset and hence sighted with certainty. Therefore there is no resighting probability at occasion 1, year 1.
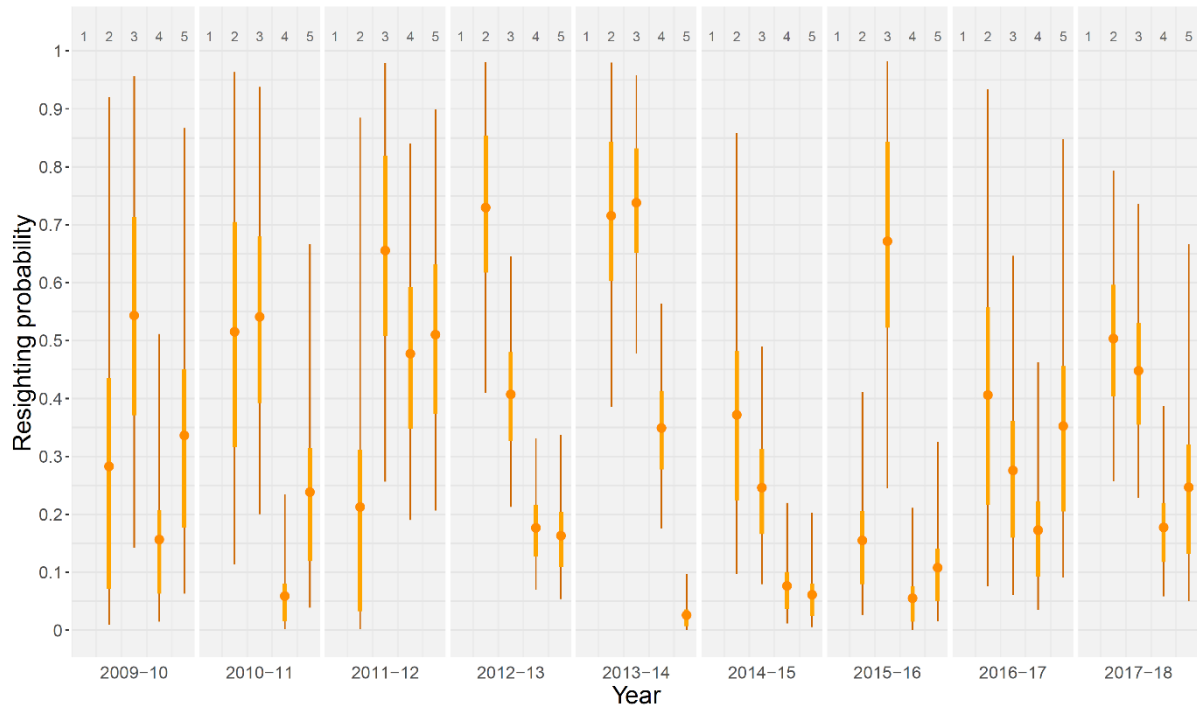
Figure S40. Resighting probability in migratory area 1 (orange points on Fig. 1), of shags that bred on the Isle of May. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. During the breeding season, all individuals are in the residency area, therefore there is no detection probability in any migratory area at occasion 1.
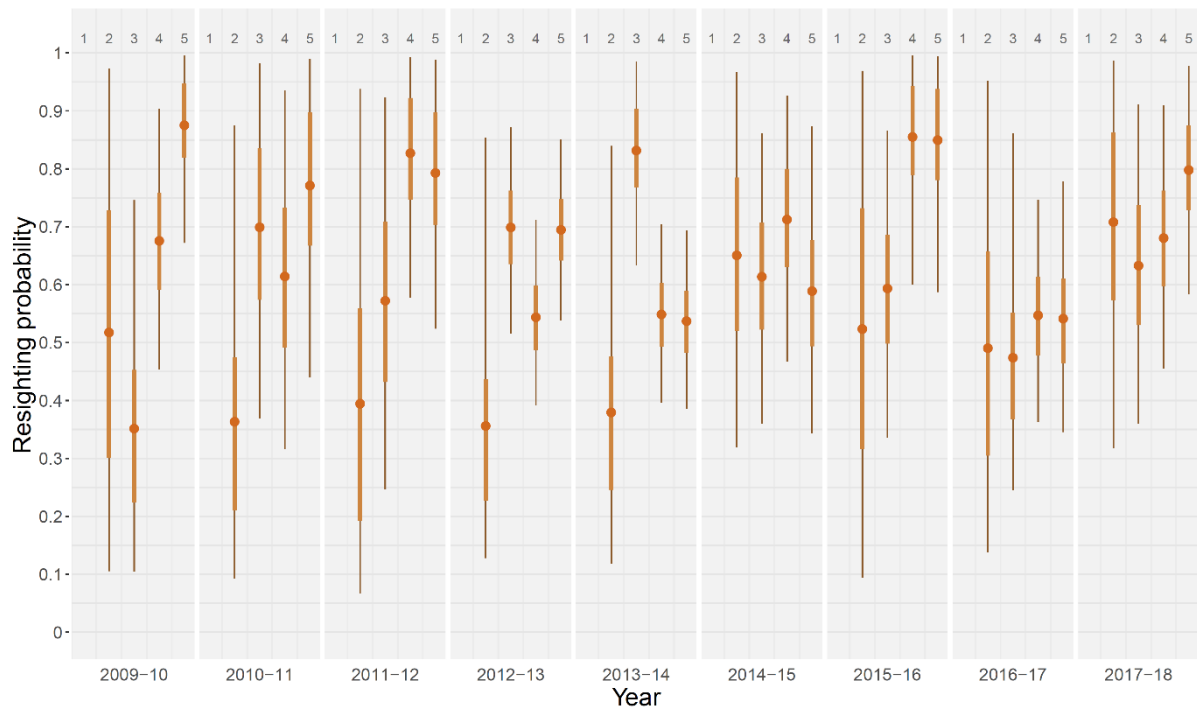
Figure S41. Resighting probability in migratory area 2 (brown area on Fig. 1), of shags that bred on the Isle of May. See Fig. S39 for legend specifications.
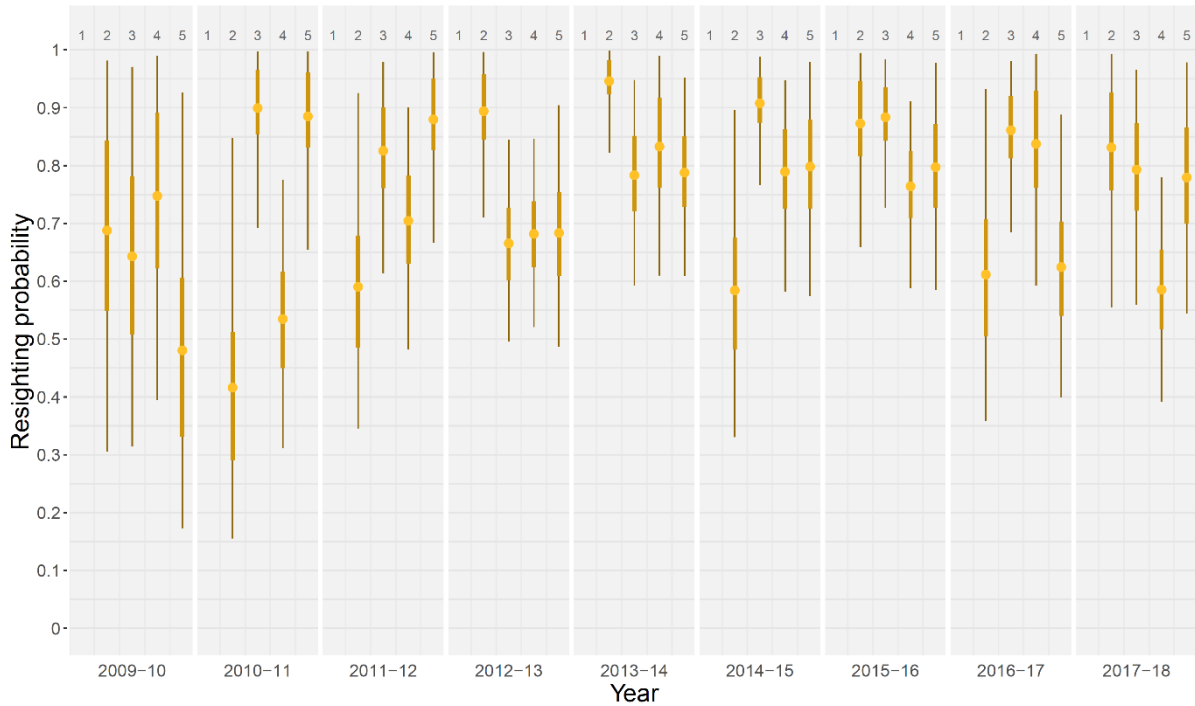
Figure S42. Resighting probability in migratory area 2 (yellow area on Fig. 1), of shags that bred on the Isle of May. See Fig. S39 for legend specifications.
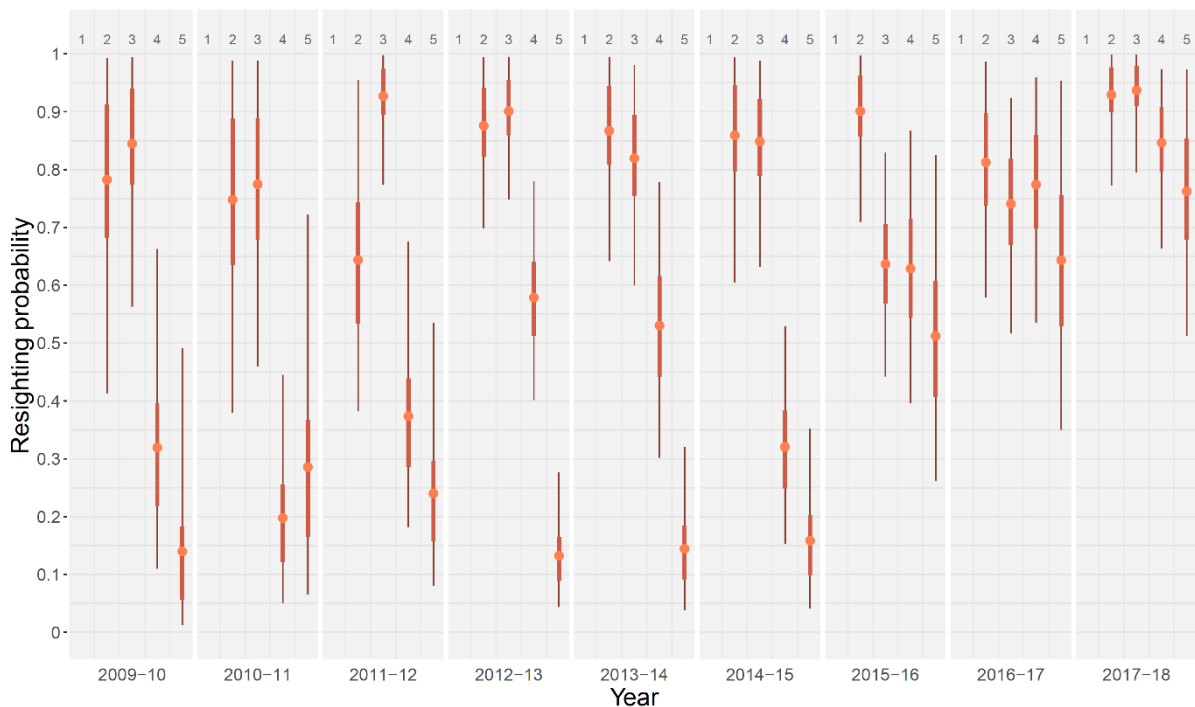
Figure S43. Resighting probability in migratory area 2 (pink area on Fig. 1), of shags that bred on the Isle of May. See Fig. S39 for legend specifications.

S5.4 Movement probabilities

Here we provide graphical summaries of the posterior distribution of the probability of departing from the residency area (Fig. S43), the probability of moving in each migratory area (conditional on departure; Fig. S44 to S48), the probability of returning from each migratory area (Fig. S49 to S53), and the probability to switch to another migratory area (conditional on not returning; Fig. S54), from the model without sex effects.
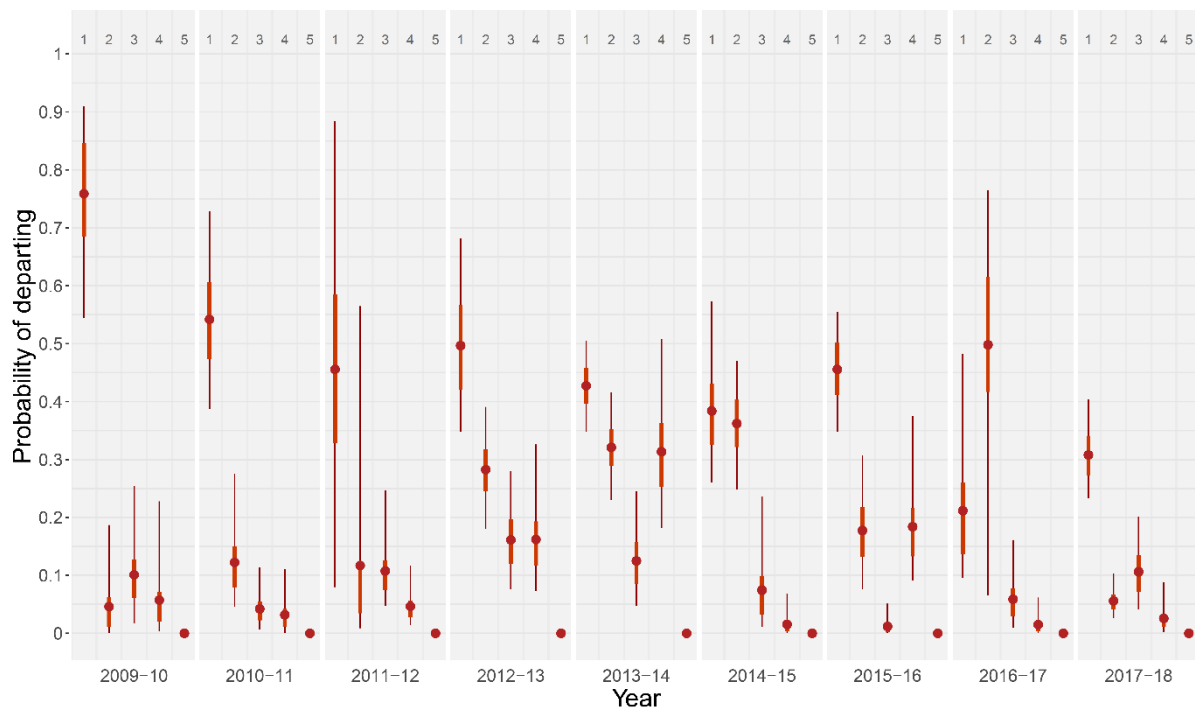
Figure S44. Probability of departing from the residency area, in shags that bred on the Isle of May. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. All residents stay in the residency area from late winter (occasion 5) to the breeding season (occasion 1), thus departing probability is constrained to 0 at this time step.
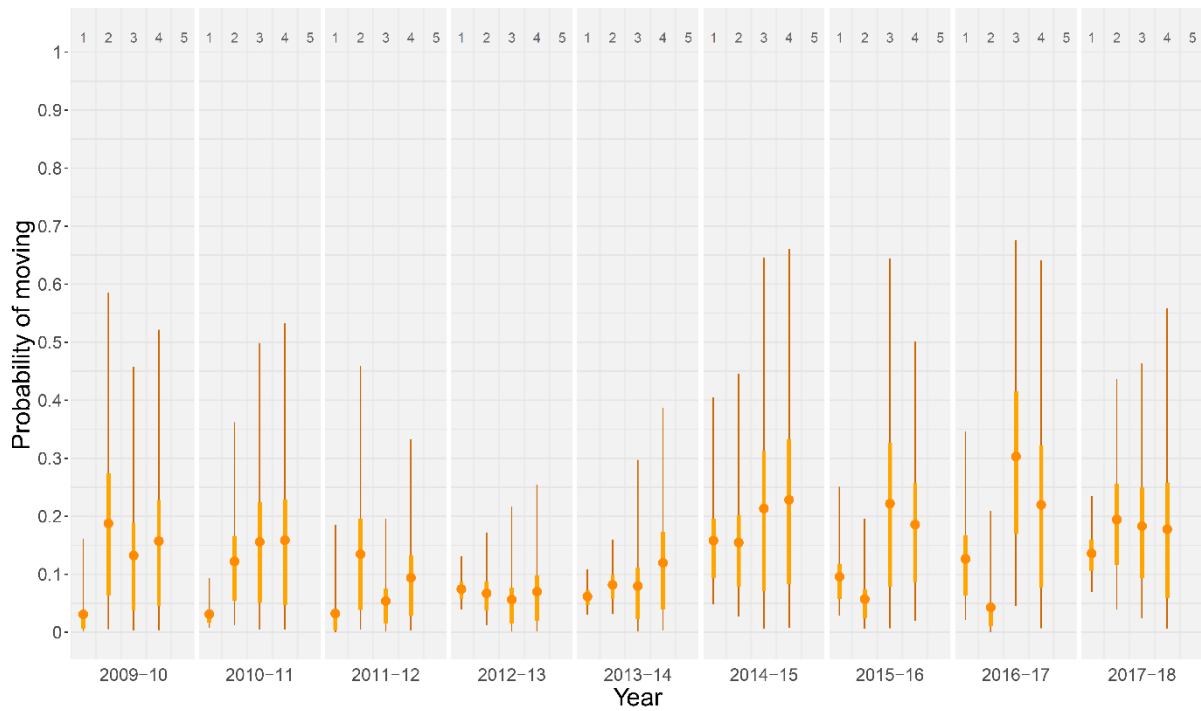
Figure S45. Probability of moving to migratory area 1 (oranges points on Fig. 1), conditional on departure, in shags that bred on the Isle of May. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. All residents stay in the residency area from late winter (occasion 5) to the breeding season (occasion 1), thus there is no probability of moving to any migratory area at this time step.
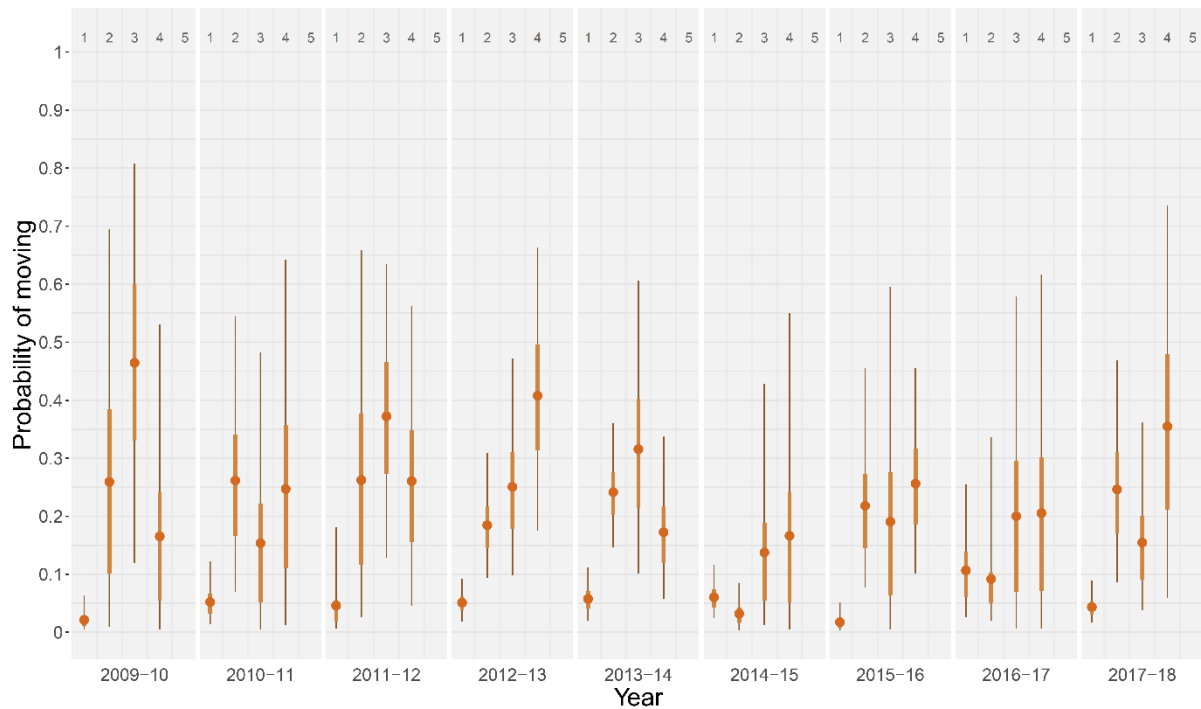

Figure S46. Probability of moving to migratory area 2 (brown on Fig. 1), conditional on departure, in shags that bred on the Isle of May. See further legend specifications in Fig. S44.
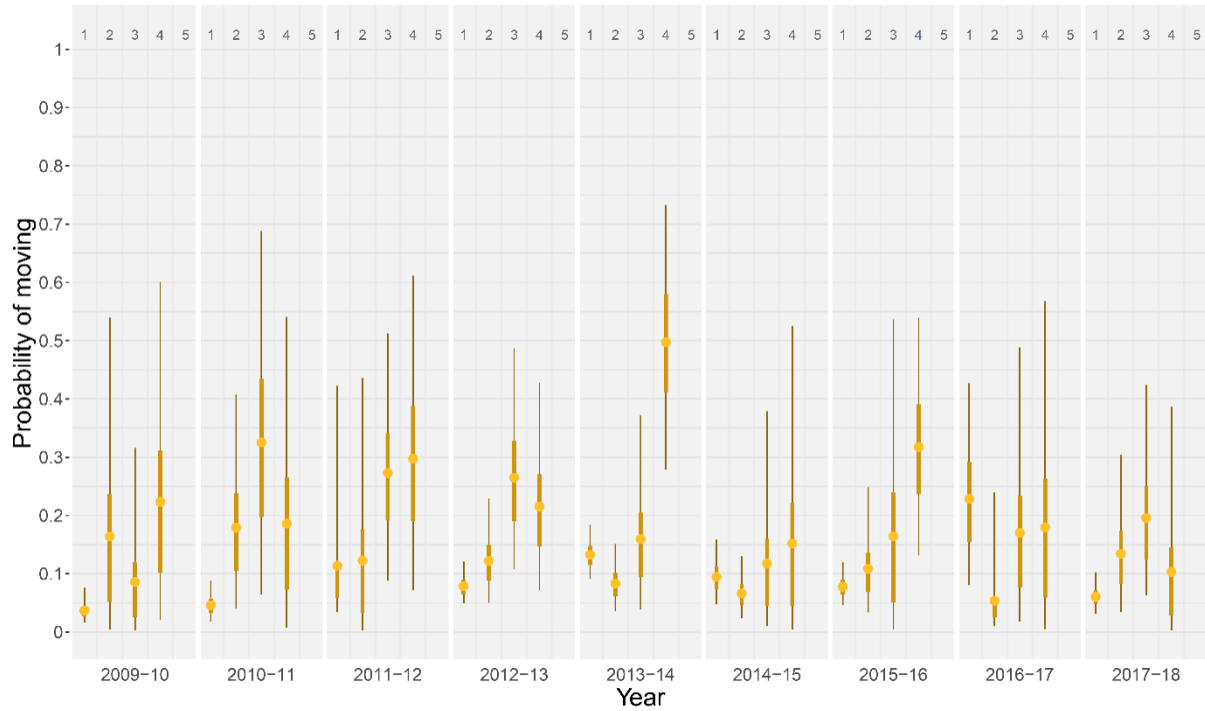
16

Figure S47. Probability of moving to migratory area 3 (yellow on Fig. 1), conditional on departure, in shags that bred on the Isle of May. See further legend specifications in Fig. S44.
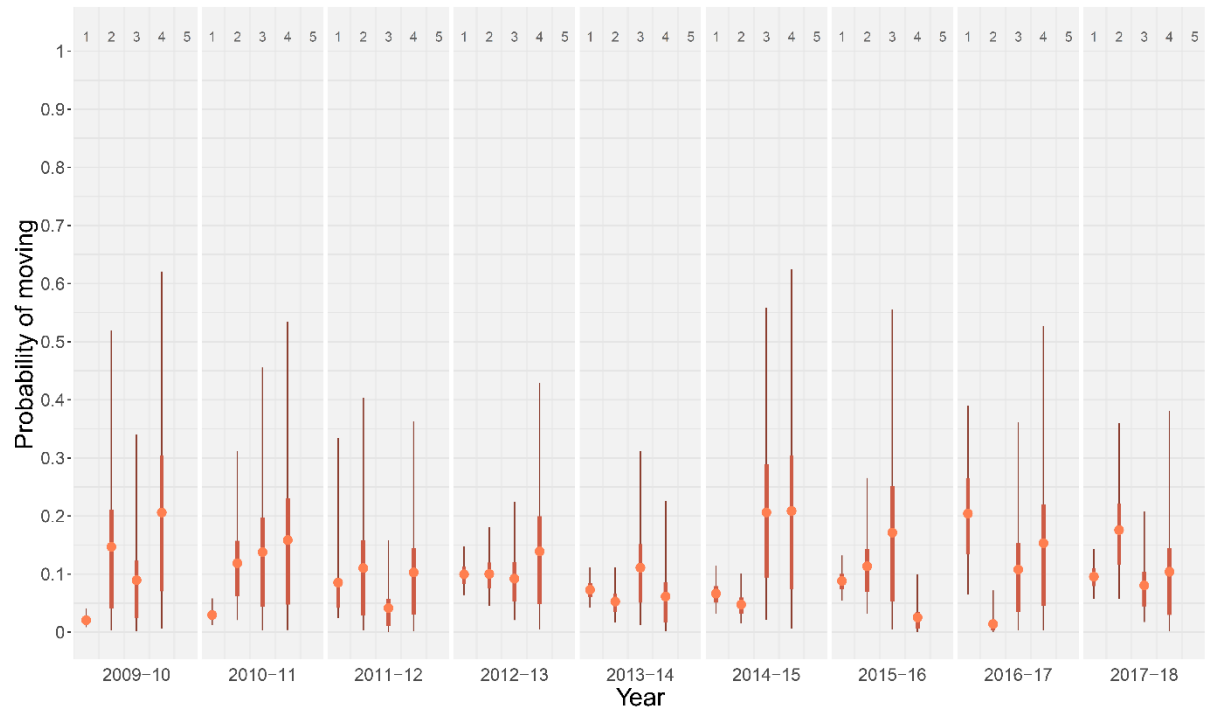

Figure S48. Probability of moving to migratory area 4 (pink on Fig. 1), conditional on departure, in shags that bred on the Isle of May. See further legend specifications in Fig. S44.
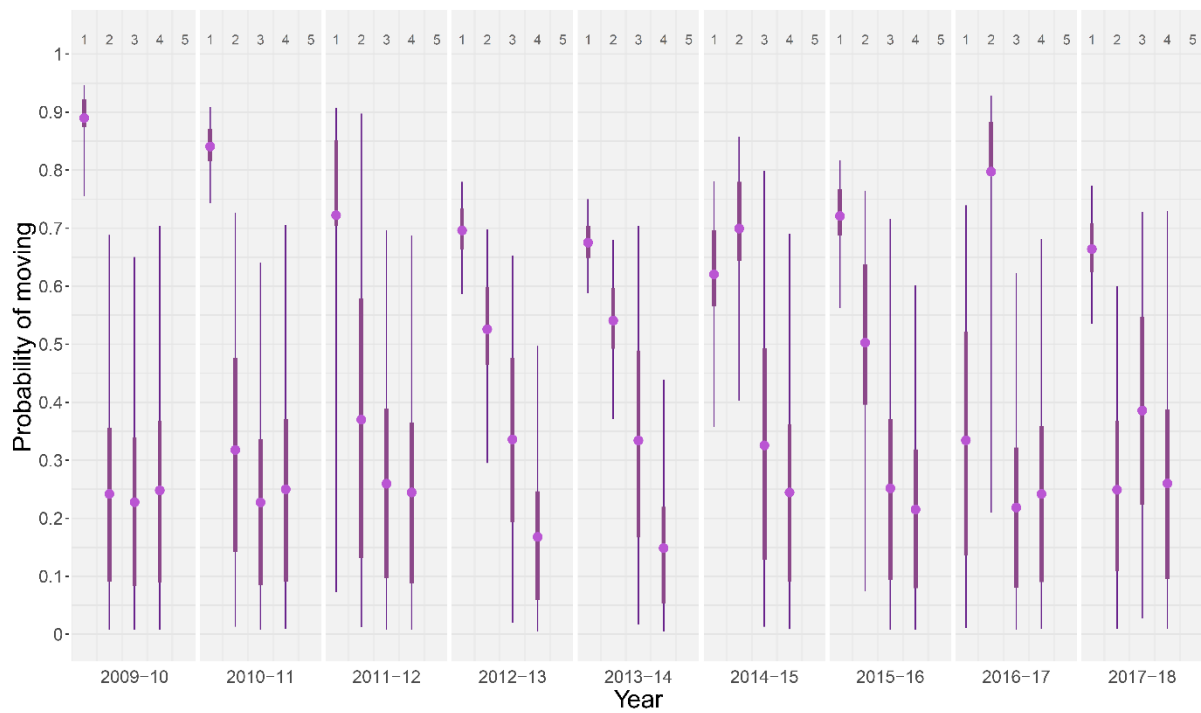
Figure S49. Probability of moving to migratory area 5 (i.e. the "ghost" area, corresponding to the unobservable migratory state), conditional on departure, in shags that bred on the Isle of May. See further legend specifications in Fig. S44.
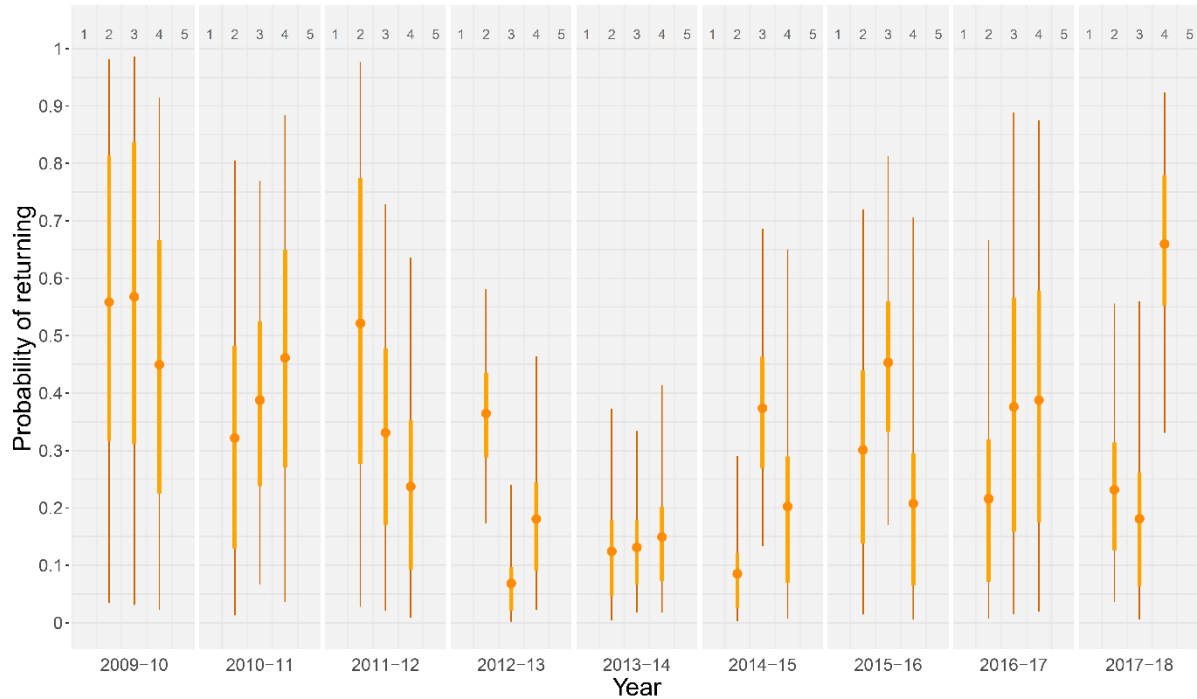
Figure S50. Probability of returning to the residency area from migratory area 1 (orange points on Fig. 1), in shags that bred on the Isle of May. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. All individuals are in the residency area during the breeding season (occasion 1), accordingly there is no probability of returning from any migratory area at the time step starting from occasion 1. Further, all migrants are returning to the residency area between late-winter (occasion 5) and the next breeding season, accordingly the probability of returning from any migratory area is constrained to be 1 at this time step.
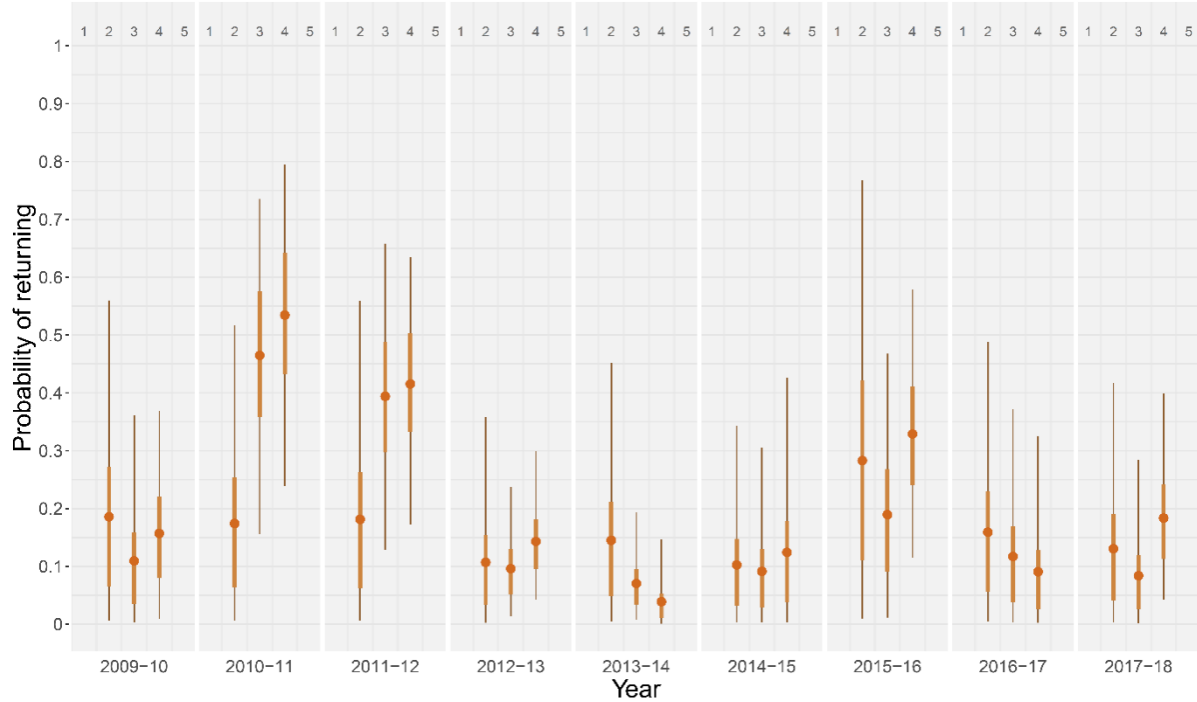
Figure S51. Probability of returning to the residency area from migratory area 2 (brown on Fig. 1), in shags that bred on the Isle of May. See Fig. S49 for further legend specifications.

Figure S52. Probability of returning to the residency area from migratory area 3 (yellow on Fig. 1), in shags that bred on the Isle of May. See Fig. S49 for further legend specifications.

Figure S53. Probability of returning to the residency area from migratory area 4 (pink on Fig. 1), in shags that bred on the Isle of May. See Fig. S49 for further legend specifications.

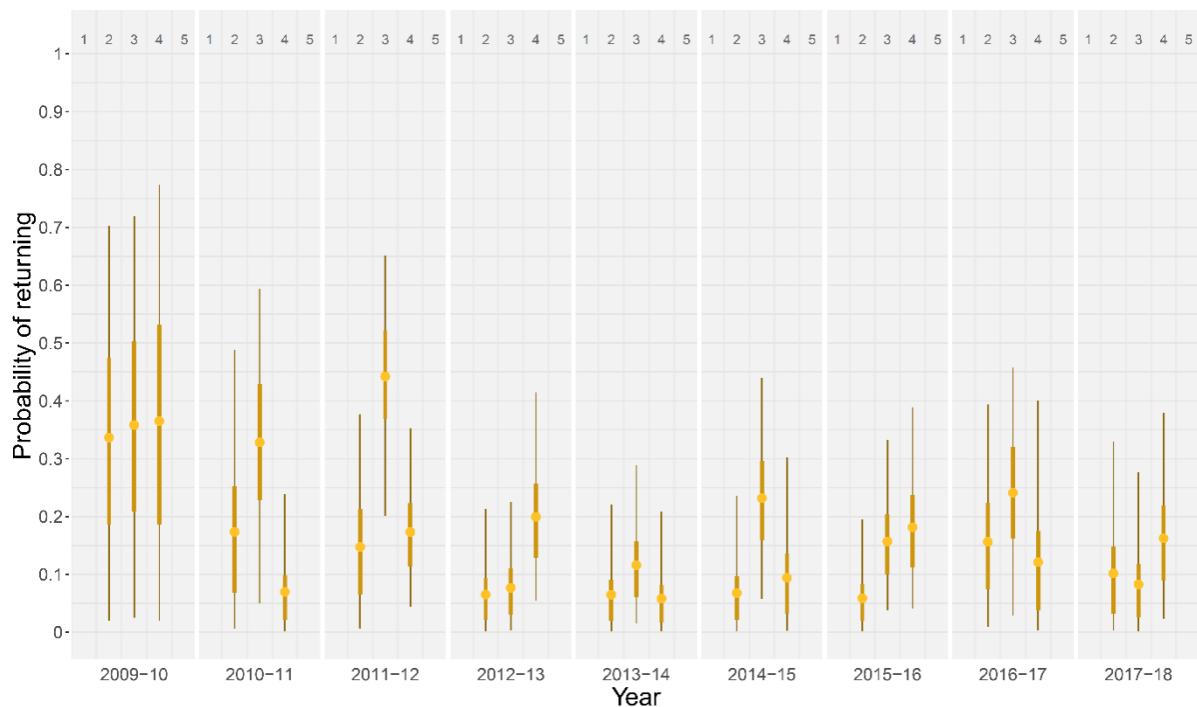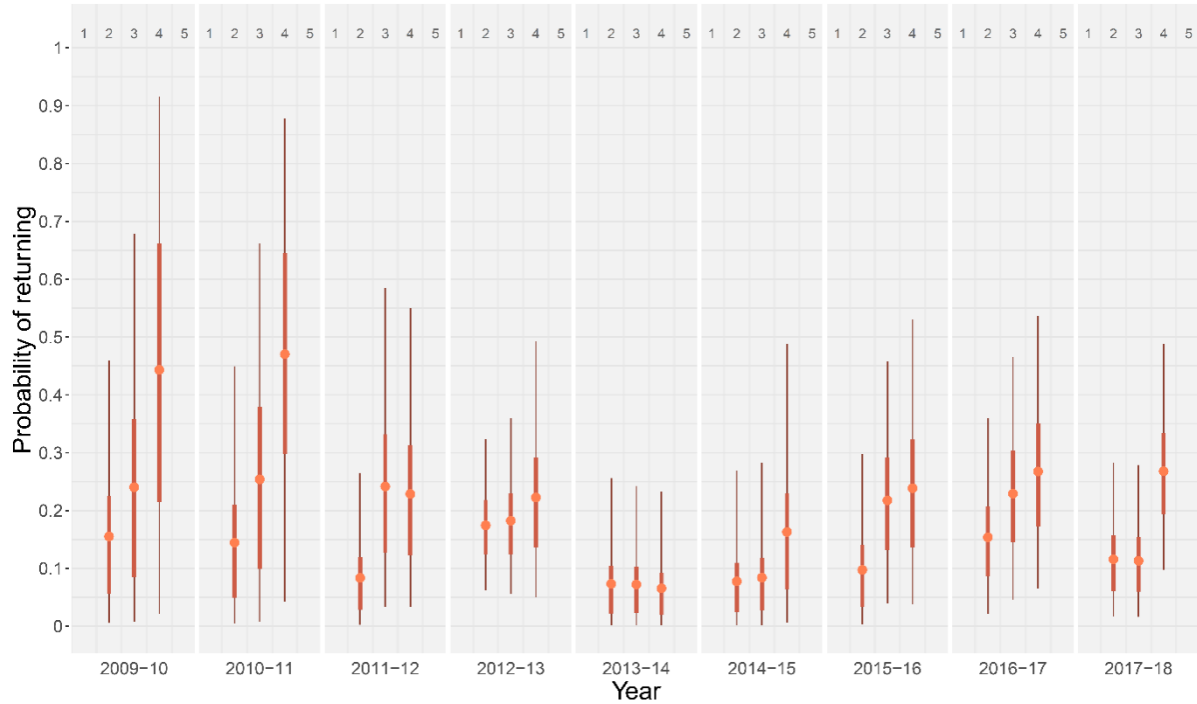

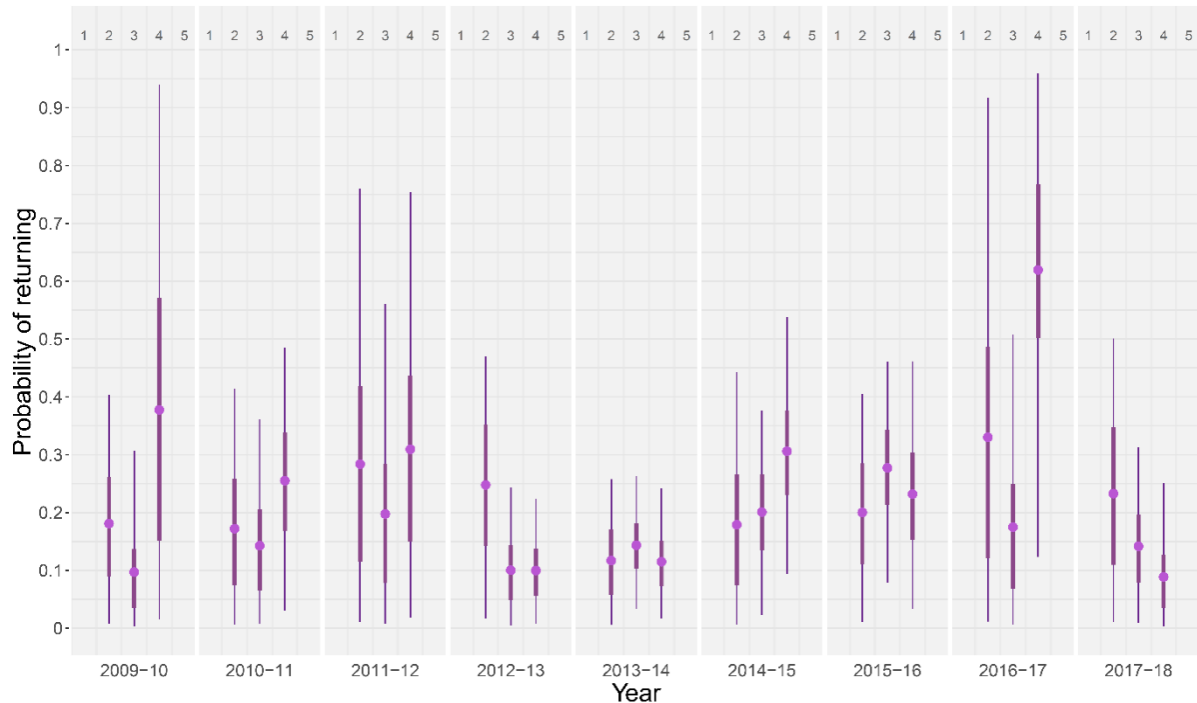**Figure S54**. Probability of returning to the residency area from migratory area 5 (i.e. the "ghost" area, corresponding to the unobservable migratory state), in shags that bred on the Isle of May. See Fig. S49 for further legend specifications.
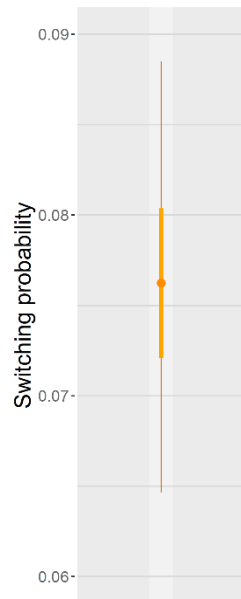
Figure S55. Probability of switching to another migratory area (i.e. the probability of not remaining in the same migratory area, on Fig. 2b: $1\text{-}\sigma_{ii}=4^{*}\sigma_{ik}$, with $k\neq i$), in shags that bred on the Isle of May. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. This probability was set constant across time (and apply to time steps between winter occasions) in our model.

S5.5 Migratory fraction

Here we provide graphical summaries of the migratory fraction, from the model without sex effects (Fig. S55). We also provide such graphical summaries from the model including sex effects (Fig. S56), as well as numerical summaries of sex differences in the migratory fraction (Table S10).
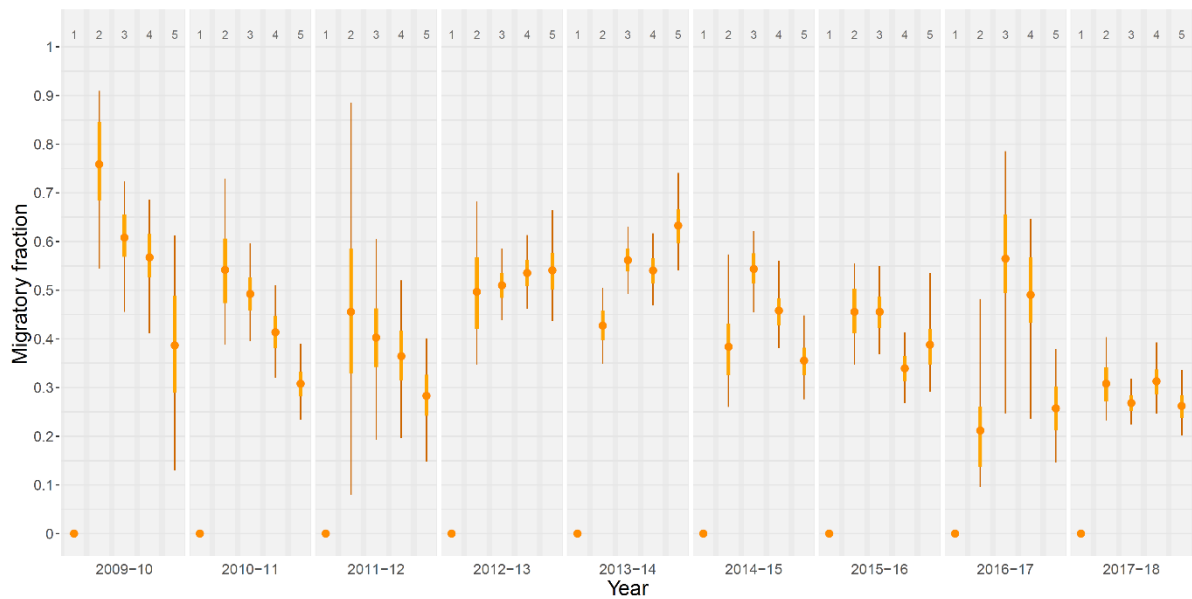
Figure S56. Migratory fraction of shags that bred on the Isle of May. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. The annual occasion, numbered 1-5, is indicated on the top row. In the breeding season, all individuals are in the residency area, thus the migratory fraction is constrained to be 0.

Figure S57. Sex-dependent migratory fraction of shags that bred on the Isle of May. Point estimates are posterior means (female: brown triangles, males :orange circles), inner and outer line segments indicate 50% and 95% credible intervals. The annual occasion, numbered 1-5, is indicated on the top row). In the breeding season, all individuals are in the residency area, hence the migratory fraction is constrained to be 0.
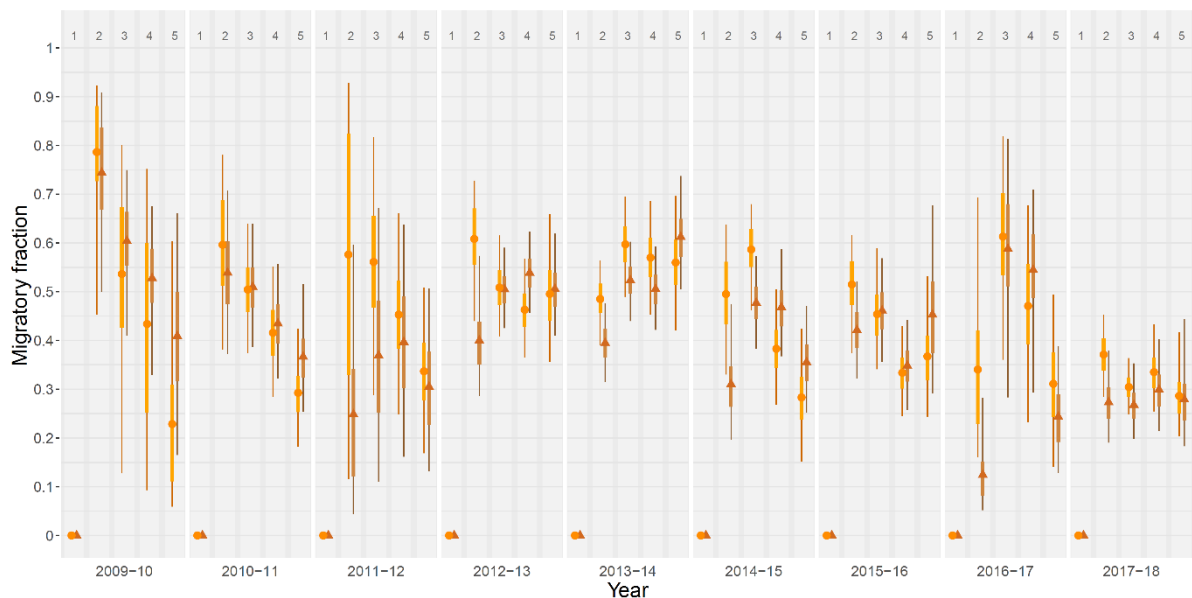
Table S10. Posterior summary of the sex bias in the migratory fraction of shags that bred on the Isle of May (i.e. 'female minus male migratory fraction').

Year	Occ.	Mean	SD	2.5%	97.5%	Pr(Δ>0)
2009–10	2	0.04	0.16	-0.29	0.33	0.63
	3	-0.07	0.19	-0.49	0.25	0.41
	4	-0.09	0.20	-0.47	0.27	0.37
	5	-0.18	0.19	-0.49	0.24	0.17
2010–11	2	0.06	0.14	-0.21	0.32	0.66
	3	-0.01	0.08	-0.17	0.15	0.47
	4	-0.02	0.08	-0.19	0.15	0.42
	5	-0.07	0.08	-0.24	0.09	0.17
2011–12	2	0.33	0.19	0.03	0.67	0.99
	3	0.19	0.15	-0.15	0.47	0.89
	4	0.06	0.14	-0.22	0.31	0.66
	5	0.03	0.12	-0.22	0.26	0.61
2012–13	2	0.21	0.09	0.03	0.37	0.99
	3	0.00	0.06	-0.12	0.13	0.52
	4	-0.08	0.06	-0.19	0.05	0.11
	5	-0.01	0.09	-0.17	0.16	0.44
2013–14	2	0.09	0.06	-0.03	0.20	0.93
	3	0.07	0.06	-0.05	0.19	0.88
	4	0.06	0.07	-0.07	0.20	0.83
	5	-0.05	0.08	-0.22	0.11	0.27
2014–15	2	0.19	0.10	-0.02	0.36	0.96
	3	0.11	0.07	-0.04	0.24	0.93
	4	-0.08	0.08	-0.24	0.06	0.12
	5	-0.07	0.08	-0.24	0.09	0.19
2015–16	2	0.09	0.08	-0.08	0.24	0.87
	3	-0.01	0.07	-0.14	0.14	0.45
	4	-0.01	0.06	-0.14	0.10	0.41
	5	-0.09	0.10	-0.30	0.09	0.19
2016–17	2	0.22	0.11	0.07	0.48	1.00
	3	0.03	0.16	-0.30	0.34	0.56
	4	-0.07	0.14	-0.35	0.21	0.30
	5	0.07	0.11	-0.15	0.29	0.72
2017–18	2	0.10	0.06	-0.02	0.21	0.94
	3	0.04	0.05	-0.06	0.12	0.79
	4	0.04	0.06	-0.07	0.14	0.75
	5	0.01	0.07	-0.14	0.13	0.57

Notes: 'Occ.' is the annual occasion, 'SD' is the standard deviation of the posterior distribution, '2.5%' and '97.5%' are the limits of the 95% credible interval (i.e. the 2.5% and 97.5% quantiles of the distribution), 'Pr(Δ>0)' is the posterior probability that the focal difference is positive.

S5.6 Annual-cycle path probabilities

Here we provide numerical summaries of the probabilities of realizing each of the different possible annual paths through the partial migration cycle (Fig. 2a) from occasion 1 (breeding season) to occasion 5 (i.e. the last occasion, late winter), or dying at some point before occasion

5, depending on being alive in occasion 1 of the focal year (Table S11). These derived probabilities were calculated in each posterior sample of the state-process probabilities.

Table S11. Posterior summaries of the annual-cycle path probabilities, i.e. the probabilities of winter fates in a given year depending on being alive in the occasion 1 of that year (derived from the main model without sex effects). Summaries across years are provided for each possible path through the partial-migration cycle, i.e. each possible annual sequence of phenotypes: migrant ('M') or resident ('R') ('R-X_2-X_3-X_4-X_5', where 'X_o' in occasion o is either 'R' or 'M'). Summary across years is also provided for all individual fates that led to death ('D') by occasion 5 ('R-X_2-X_3-X_4-D', where 'X_o' is either 'R', 'M', or 'D'), collapsed here together as one type of outcome.

Path	Range		Grand mean
	Min.	Max.	
R-R-R-R-R	**0.18 [0.10,0.27]**	**0.51 [0.42,0.60]**	**0.31 [0.26,0.36]**
R-R-R-R-M	0.01 [0.00,0.02]	0.09 [0.05,0.16]	0.03 [0.02,0.04]
R-R-R-M-R	0.00 [0.00,0.01]	0.01 [0.00,0.04]	0.01 [0.00,0.01]
R-R-R-M-M	0.00 [0.00,0.02]	0.05 [0.02,0.10]	0.03 [0.02,0.04]
R-R-M-R-R	0.00 [0.00,0.01]	0.07 [0.01,0.20]	0.02 [0.01,0.04]
R-R-M-R-M	0.00 [0.00,0.00]	0.01 [0.00,0.01]	0.00 [0.00,0.00]
R-R-M-M-R	0.00 [0.00,0.01]	0.17 [0.01,0.34]	0.03 [0.01,0.06]
R-R-M-M-M	0.01 [0.00,0.02]	0.14 [0.02,0.25]	0.07 [0.05,0.09]
R-M-R-R-R	0.03 [0.01,0.06]	0.13 [0.02,0.28]	0.07 [0.04,0.11]
R-M-R-R-M	0.00 [0.00,0.01]	0.01 [0.00,0.04]	0.01 [0.00,0.01]
R-M-R-M-R	0.00 [0.00,0.00]	0.01 [0.00,0.02]	0.00 [0.00,0.00]
R-M-R-M-M	0.00 [0.00,0.00]	0.01 [0.00,0.03]	0.01 [0.00,0.01]
R-M-M-R-R	0.02 [0.01,0.05]	0.08 [0.03,0.16]	0.05 [0.04,0.07]
R-M-M-R-M	0.00 [0.00,0.00]	0.02 [0.01,0.04]	0.01 [0.00,0.01]
R-M-M-M-R	0.03 [0.01,0.05]	0.18 [0.03,0.42]	0.07 [0.04,0.10]
R-M-M-M-M	**0.08 [0.04,0.15]**	**0.31 [0.08,0.51]**	**0.19 [0.16,0.22]**
R-X-X-X-D	0.06 [0.04,0.08]	0.31 [0.25,0.37]	0.11 [0.10,0.12]

Notes: All individuals are in the residency site during the breeding season, accordingly all paths start as resident ('R'). Each posterior summary is given as the posterior mean with 95% credible interval between brackets. For the focal path across the 9 years of study: 'Min' is the estimation for the year with the minimum posterior mean, 'Max' is the estimation for the year with the maximum posterior mean, and 'Grand mean' is the estimation for the average across years. Full-winter residence and full-winter migration, the two paths that are most likely to be realised, are in bold.

S5.7 References

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