Journal of Animal Ecology

DR PAUL ACKER (Orcid ID : 0000-0002-3815-772X)

DR HANNAH GRIST (Orcid ID : 0000-0001-7299-1868)

Handling Editor: Dr Lise Aubry

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

Paul Acker[1,2]*, Francis Daunt[3], Sarah Wanless[3], Sarah J. Burthe[3], Mark A. Newell[3], Michael P. Harris[3], Hannah Grist[1,4], Jenny Sturgeon[1], Robert L. Swann[5], Carrie Gunn[3], Ana Payo-Payo[1], and Jane M. Reid[1,2]

[1] School of Biological Sciences, University of Aberdeen, Aberdeen, UK

[2] Centre for Biodiversity Dynamics, Institutt for Biologi, NTNU, Trondheim, Norway

[3] UK Centre for Ecology & Hydrology, Bush Estate, Midlothian, UK

[4] Scottish Association for Marine Science, Scottish Marine Institute, Oban, UK

[5] Highland Ringing Group, Tain, UK

* Corresponding author. E-mail address: paul.acker@ntnu.no or paul.acker@noos.fr

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

Bayesian capture-recapture, eco-evolutionary dynamics, extreme climatic events, fluctuating selection, full annual cycle, partial migration, multi-state model, seasonal movement, sex-biased selection, Stan

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).

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

challenging, and has rarely been achieved for any trait in any system. One approach is to mark individuals with field-readable tags, and undertake year-round large-scale resightings. Such resightings are inevitably restricted and incomplete, to degrees that vary in time and space. Individual phenotypic expression of migration versus residence and associated survival, and hence survival selection, are therefore only partially observable. However, the required parameters can be estimated using advanced capture-recapture analyses that account for resighting failure and resulting uncertainty (Cam 2009).

Accordingly, we designed full-annual-cycle multi-state capture-recapture models that allow estimation of survival probabilities of seasonal migrants and residents within and across years, and hence allow estimation of survival selection on migration versus residence. We fitted these models to nine years of year-round resighting data from partially migratory European shags (*Phalacrocorax aristotelis*) experiencing non-extreme and historically extreme non-breeding season conditions. We *a priori* defined four ECEs that occurred during the study period, each comprising a different extreme winter storm event that caused major coastal and marine environment perturbations and widely observed mortality of birds and other marine wildlife (see *Methods*, Appendix S1). We first tested whether these four defined seasonal ECEs were associated with episodes of seasonal survival selection on migration versus residence, and whether these episodes intensified or opposed seasonal selection occurring under non-extreme conditions. We then tested whether the four ECEs were associated with sex-biased mortality and/or sex-biased seasonal selection, and quantified the degree to which episodes of seasonal survival selection scaled up to cause selection at the annual timescale. We thereby illustrate how ECEs can cause episodes of survival selection 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 (typically aged ≥3 years) alive prior to 1997, and subsequent unringed recruits, were similarly caught and ringed as far as feasible. During ten breeding seasons (April–June 2009–2018), ringed breeding adults were systematically identified at their nests (~95% of all breeders; Appendix S1). Further observations at adjacent roost areas allowed identification of ringed non-breeders and early-failed breeders, thereby ensuring very high breeding season adult resighting probability (Barlow, Daunt, Wanless, & Reid, 2013; Grist et al., 2017). Individuals were sexed based on vocalisations and/or genotype (Appendix S1).

During the intervening nine non-breeding seasons ("winters", September–February 2009-2018) we conducted resighting surveys around IoM and more widely to locate individuals and thereby distinguish residents and migrants. Key roost sites across eastern Scotland, identified during pilot fieldwork in 2008–2009, were surveyed every ~2 weeks (Fig. 1; Appendix S1). Additional known roost sites were surveyed less frequently, and opportunistic resightings from birdwatchers were actively solicited (Fig. 1).

The 2009–2018 study period encompassed diverse climatic conditions, from benign to historically extreme. In particular, the eastern Scotland coastline experienced severe storms in December 2012, February 2013, January 2014, and February-March 2018 (Appendix S1). These four events involved different forms of unusually strong and/or protracted onshore winds resulting in extremely rough sea states, coupled with intense precipitation or low temperature

(Appendix S1). We therefore expected these events to be biologically-relevant (following Bailey & van de Pol 2016) to our study system by causing low over-winter shag survival, as observed for similar storms in previous decades (Frederiksen et al., 2008) and confirmed by our analyses (see *Results*). We thus defined these four events as ECEs (further details in Appendix S1). Given the complex multidimensional nature and spatial structure of underlying weather conditions (Appendix S1), we had no strong *a priori* prediction on the strength, direction, consistency or sex-specificity of any resulting selection on migration versus residence, including in relation to any selection arising under more typical conditions.

Model design

Quantifying seasonal survival selection on migration versus residence from ring-resighting data requires unbiased estimation of survival probability conditional on winter location, given that location is unknown for unobserved individuals. This can be achieved by jointly modelling the processes of hidden individual state-transition (i.e. movement between residency and migratory area(s), and survival conditional on location) and partial observation of individual states (i.e. resighting efficiency, reflecting observer effort and conditions during resighting surveys). Accordingly, we formulated a discrete-time multi-state capture-recapture model (Lebreton & Pradel 2002) that represents full-annual-cycle dynamics of partial migration and the overlaid observational design. We modelled multiple migrant areas to account for spatial heterogeneity in resighting efficiency, therefore controlling for potential biases in observed movements and hence in estimates of survival for residents and migrants.

We defined three types of observation event: 'resighted at the residency area' (i.e. IoM area), 'resighted at a migratory area' (i.e. away from IoM, divided into multiple areas; Fig. 1) and 'not resighted'. We defined three types of underlying individual state: 'resident', 'migrant in a given area' and 'dead'. For current analyses we considered five possible migratory areas (Fig. 1): three regularly-monitored areas where winter resighting effort was typically high, one geographically-broad area representing all locations where resighting effort was low but non-zero, and one "ghost area" where resighting probability was zero (Schaub, Gimenez, Schmidt, & Pradel, 2004) representing unmonitored migrant locations that presumably exist on remote coasts. Accordingly, we modelled five migrant states (i.e. four observed migratory areas, plus the "ghost area" unobservable state) and four migrant observation events (referring to each observable migrant state).
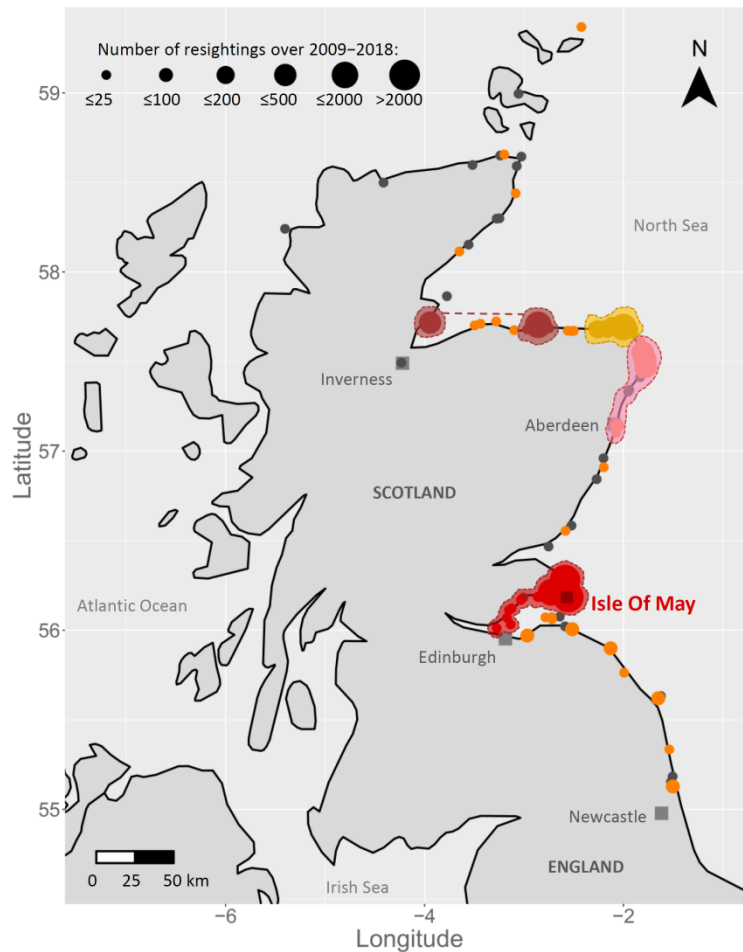
Figure 1. Locations of resightings of ringed adult shags that bred on IoM during 2009−2018. Shaded zones outline four systematically surveyed areas, comprising the residency area (red, IoM and nearby regularly visited day-roosts), and three main defined migratory areas (brown, yellow, pink). In one case, 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 fine-scale temporal variations in survival and movement probabilities (Appendix S1), and thereby isolate episodes of ECE-induced selection. The overall model structure therefore generates three

timeframes: years (y, one breeding season to the next), occasions within years (o), and the full temporal sequence of occasions across years (t; Fig 2).

In each breeding season (occasion 1 within each year), new individuals enter the dataset and all alive individuals are located in the residency area (i.e. the resident state; Fig. 2a). In each winter occasion (occasions 2–5 within each year), alive individuals can be located in the residency area or in a migratory area (i.e. the corresponding migrant state; Fig. 2a). Individuals can move between residency and migratory areas between winter occasions within a year (Fig. 2a). However, between each occasion 5 and subsequent occasion 1 individuals can only move to or remain in the residency area, and between each occasion 1 and subsequent occasion 2 individuals can only move from or remain in the residency area (Fig. 2a). The movement process is parameterised as dependent on the state and occasion at the start of each time step. Movements of current residents are described by the probabilities of departing (ε), and of moving to a specific migrant area conditional on departure (δ; Fig. 2b). Movements of current migrants are described by the probabilities of returning to the residency area (ω), and of switching between migratory areas conditional on not returning (σ; Fig. 2b). Mortality occurs between occasions according to occasion-dependent and migration-dependent (i.e. migrants vs. residents) survival probability (ϕ), and dead individuals cannot be resighted (Fig. 2b). At each occasion, alive individuals can be resighted where they are located or not resighted, according to occasion- and state-dependent resighting probability (p, which is zero in the "ghost area"; Fig. 2b).
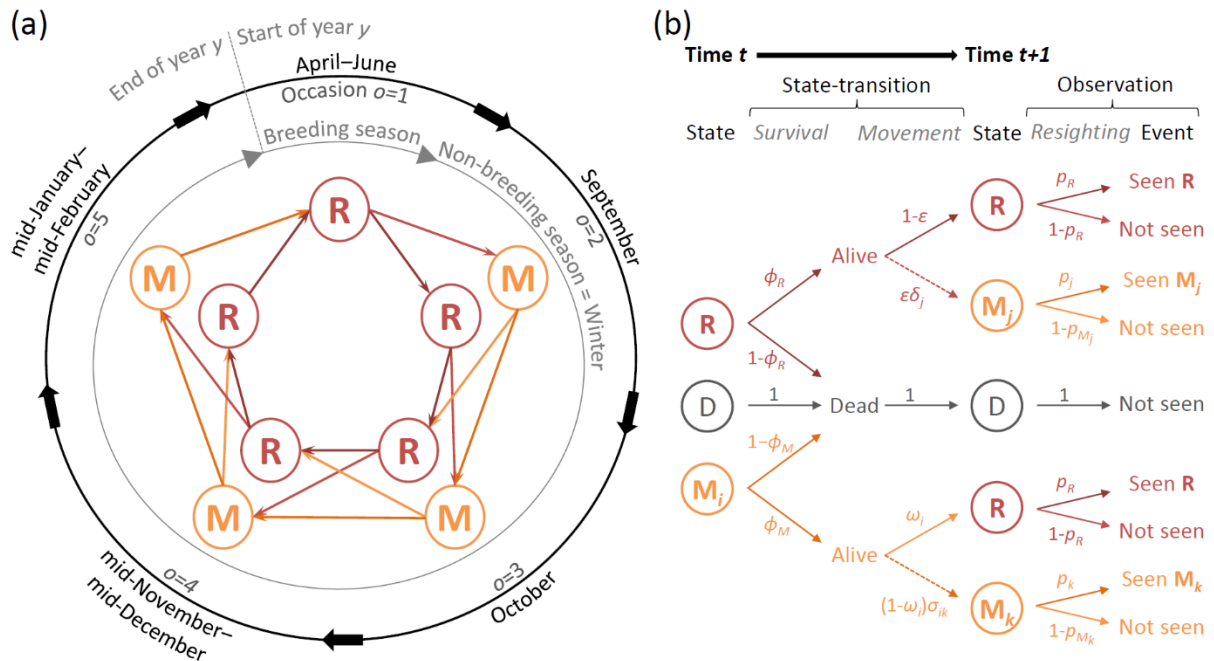
Figure 2. Structure of the multi-state capture-recapture model. Panel (a) illustrates the full-annual-cycle of partial migration, indicating possible transitions of surviving individuals between the 'resident' state (R) and 'migrant' states (M) between five consecutive defined occasions within a year. 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 residency and migrants return there to breed (i.e. $\varepsilon=0$, $\omega_i=1$, and δ_j, σ_{ik} are undefined), and then ($o=1$) all alive individuals are residents (i.e. p_j and subsequent ϕ_M, ω_i, σ_{ik} are undefined).

To fit this model, we compiled individual capture-resighting histories (i.e. sequences of observation events) for all adult shags known to have bred on IoM during 2009–2017, starting from their first observed breeding attempt during that period. We utilised 43214 sightings of 2274 eligible individual adults (including 2147 individuals of known sex) and collapsed multiple resightings of focal individuals in each occasion into a unique event (Appendix S1). Since previous studies and recent resightings show virtually no breeding dispersal from IoM (Aebischer 1995; Barlow et al., 2013; Appendix S1), estimated survival probabilities primarily represent true survival with little or no confounding permanent emigration.

Model analyses

We fitted and analysed our model with the current primary objective of estimating occasion-specific survival probabilities of residents and migrants in each year, and hence quantifying ECE-induced survival selection on migration versus residence across time. We built and analysed the model using Stan, a probabilistic programming language for Bayesian inference using Hamiltonian Monte Carlo, via package *rstan* (Carpenter et al., 2017) in R (R core team 2019). We formulated a general code, thereby providing tools for capture-recapture analysis of other partially-migratory populations (Appendix S2). We used objective ("uninformative") uniform priors for all parameters (Appendix S2). Details of posterior sampling procedures and diagnostics are in Appendix S5.

We first analysed a main model that included interacting migration-, occasion- and year-dependence (i.e. migration×time-dependence) in survival probability ϕ (Table 1). This model 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	Structure of model parameters					
	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 while retaining associated uncertainties. Key quantities are the probabilities of annual survival, and of being a migrant (yielding the "migratory fraction"). Annual survival probability given different possible paths through the partial-migration cycle (Fig. 2a) was computed as the product of corresponding survival probabilities across successive occasions (Appendix S2). For purposes of concise illustration, we mainly focus on two stereotypical paths that were most likely to be realised (Appendix S5): full-winter migration (i.e. leaving residency area by September and returning next breeding season: phenotypic sequence 'R-M-M-M-M' through the annual cycle, Fig. 2a) and full-winter residence (i.e. phenotypic sequence 'R-R-R-R-R', Fig. 2a). Details of estimates for other paths are in Appendix S5. These derived annual survival probabilities utilise cross-sectional estimates of seasonal survival conditional on migration. Consequently, they do not directly quantify fates of individuals undertaking particular full-winter strategies or consider any potential carry-over effects among occasions. The migratory fraction in each occasion was computed as the product of appropriate seasonal survival and movement probabilities (Appendix S2).

To explicitly test for differences in survival probability between residents and migrants, or between males and females, we computed posterior distributions of such differences ("Δ"). We assessed support for the sign of each difference through the posterior probability that it was positive ("$\Pr(\Delta>0)$"). $\Pr(\Delta>0)$ values close to 1 or 0 provide substantial support for positive or negative differences respectively, while values close to 0.5 indicate similar support for both (i.e. no clear evidence for either). We summarised parameter estimates and derived quantities as posterior means with 95% credible intervals ('95%CRI'; further details 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 associated with two ECEs (Fig. 3).
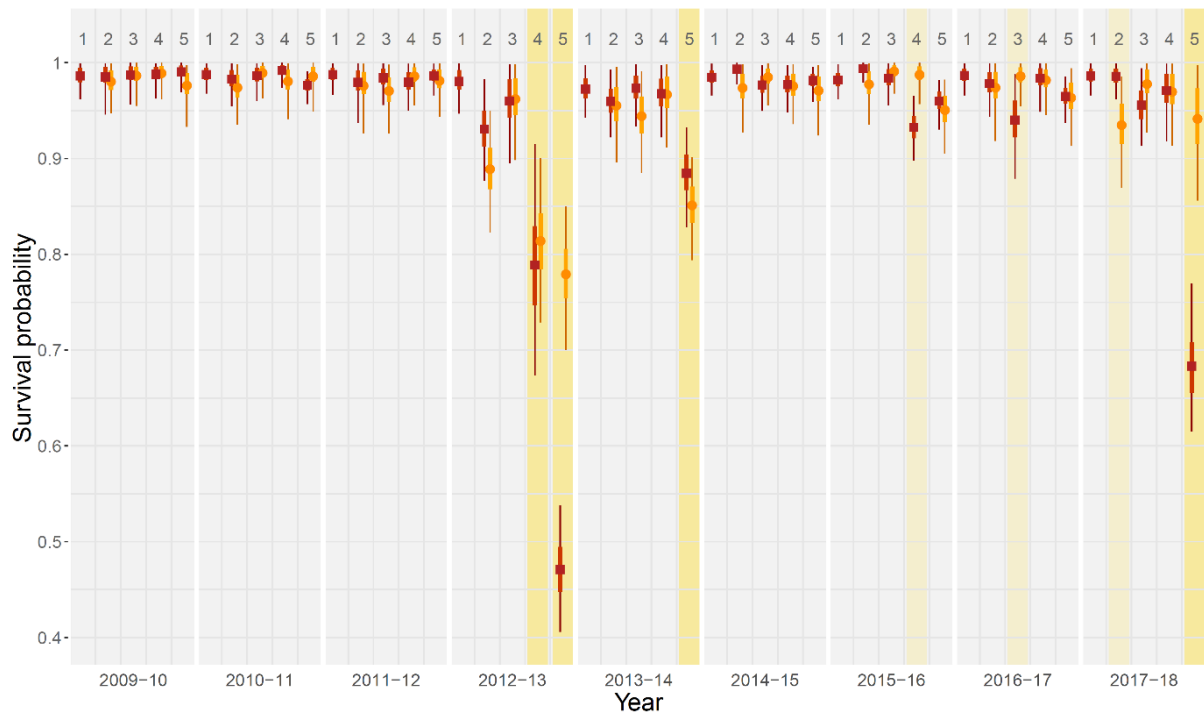
Figure 3. Seasonal survival probabilities of adult shags that bred on IoM, conditional on presence in the residency area (red squares) or a migratory area (orange circles) on each occasion. Point estimates are posterior means, inner and outer line segments indicate 50% and 95% credible intervals. Survival 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

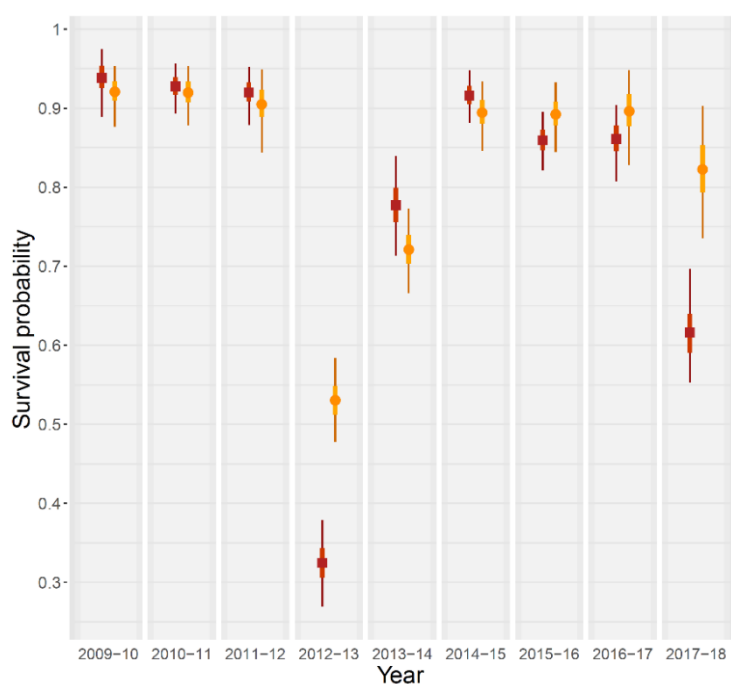across the six non-ECE winters (Fig. 4; Appendix S5).

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 ($\Delta \approx 0.2$; 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($\Delta>0$): 0.00) and residents (Δ: -0.14 [-0.27,-0.01], Pr($\Delta>0$): 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($\Delta>0$): 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).
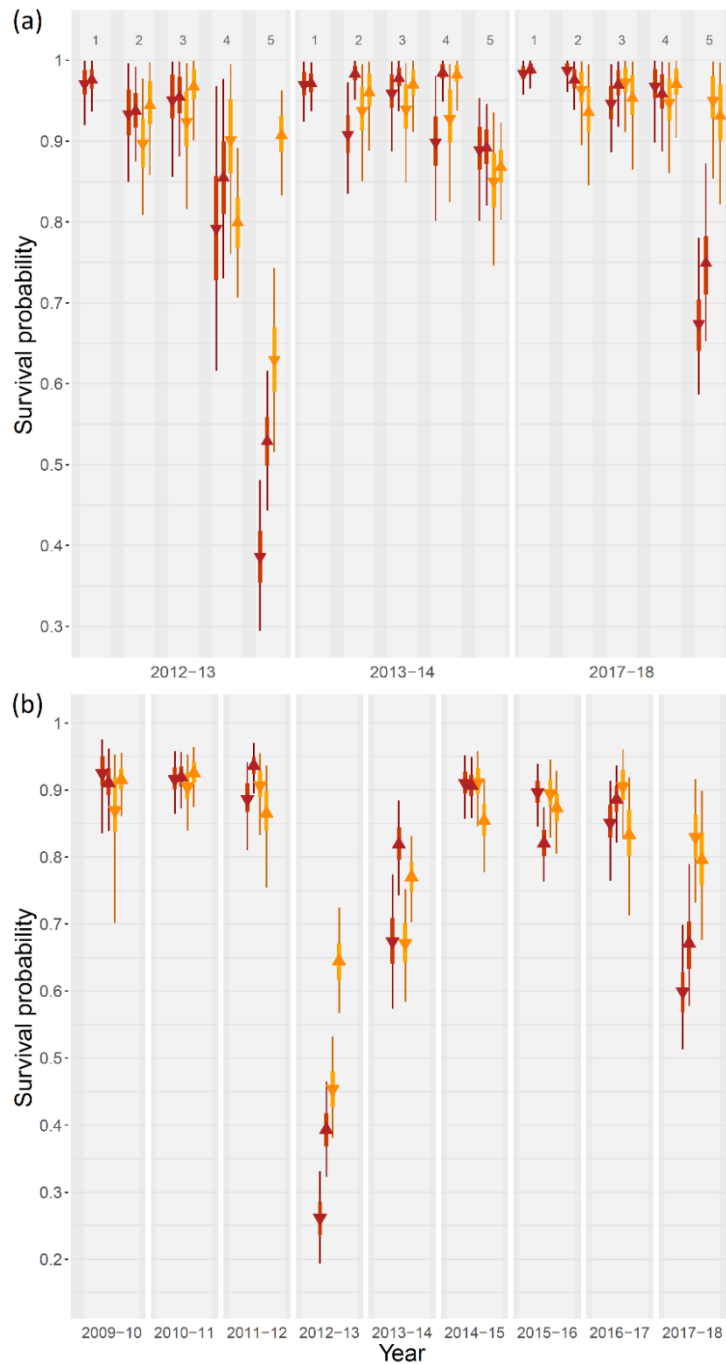
Figure 5. Migration- and sex-dependent survival probabilities of adult shags that bred on IoM. Panel (a) shows seasonal survival probabilities in the three years containing *a priori* defined ECEs (see Appendix S5 for other years). Panel (b) shows derived annual survival probabilities in all years for full-winter migration and full-winter residence. Point estimates are posterior means (residents: red, migrants: orange; females: down-triangles, males: up-triangles), inner and outer line segments indicate 50% and 95% credible intervals. On panel (a), the top row indicates initial occasion of the time step.

DISCUSSION

Understanding and predicting eco-evolutionary dynamics, including responses to increasing frequencies and/or magnitudes of ECEs caused by climate change, requires quantifying selective landscapes for key traits that mediate population responses to changing environments. Individual expression of migration versus residence is one such trait, that directly shapes spatio-seasonal population dynamics. However, the forms and magnitudes of phenotypic selection on migration versus residence occurring during extreme versus non-extreme climatic conditions have not previously been rigorously quantified. Our full-annual-cycle capture-recapture models applied to extensive resighting data from shags exposed to severe winter storms show that *a priori* defined ECEs that caused high mortality can also induce episodes of very strong selection against residence, dwarfing the weaker selection or neutrality otherwise observed.

Estimates of phenotypic selection on binary phenotypes are difficult to standardise and quantitatively compare with selection gradients for continuous traits (Kingsolver et al., 2001; Hereford, Hansen, & Houle, 2004). However, the observed differences between migrants and residents of ~0.3 in adult seasonal survival probability, and ~0.2 in annual survival probability, undoubtedly represent very strong selection. Further, fitness of relatively long-lived iteroparous species with low annual fecundity and delayed recruitment, such as shags, is highly sensitive to variation in adult survival (Sæther & Bakke 2000), which is often 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 scales (Appendix S1). However, this is likely to be highly challenging in the IoM shag system, due to the complex and divergent climatic attributes of ECEs (Appendix S1), and because winter locations of some focal shags are unknown (represented by the "ghost area" in our models).

In general, eco-evolutionary consequences of ECEs will further depend on magnitudes of sex-biased mortality and selection, but such effects have seldom been quantified for any trait in any system (Frederiksen et al., 2008; Moreno & Møller 2011; Bailey & van de Pol 2016; van de Pol et al., 2017). Our analyses show that adult female shags had substantially lower survival probabilities than males during the most severe ECE in 2012-13. This may reflect their smaller size and lower foraging efficiency in stormy conditions (e.g. Lewis, Phillips, Burthe, Wanless, & Daunt, 2015). However, the strong selection on migration versus residence induced by two ECEs affected both sexes. There was some evidence that selection against residence during the 2012-13 ECE was stronger in males, despite higher overall mortality in females. However, mortality occurring earlier during the 2012-13 winter meant that selection was not sex-biased at the annual level. This concurs with the absence of evidence for consistent sex biases in movement probabilities, and hence for sexual dimorphism in migration, in our system. Nevertheless, substantial sex-biased mortality such as we observed during one ECE would directly alter the adult sex-ratio. This could have multiple consequences in general, potentially including altering mating systems and forms of sexual selection (Widemo & Sæther 1999; Székely, Weissing, & Komdeur, 2014), and further decreasing effective population sizes (Boyce 1992). Such effects could further shape short-term and longer-term eco-evolutionary responses to ECEs (Székely et al., 2014; Haridas, Eager, Rebarber, & Tenhumberg, 2014).

Implications and prospects
Episodes of strong ECE-induced survival selection on migration versus residence, such as we observed, have potential to affect eco-evolutionary dynamics and resulting spatio-seasonal population dynamics over multiple timescales. By definition, such selection will immediately change the phenotypic distribution (i.e. population proportion of residents versus migrants), and hence change the magnitude of within-year population movement. Based on estimated survival probabilities of migrants and residents through the two selective ECEs (Fig. 1) and the

immediately preceding migratory fractions, posterior estimates for the immediate decreases in the proportion of residents are -0.12 [-0.04,-0.19] in 2013 and -0.07 [-0.04,-0.11] in 2018. This shows that strong selection combined with intermediate initial frequencies of migrants and residents generated appreciable short-term phenotypic shifts.

The longer-term consequences of such ECEs will depend on the degrees to which direct selection on migration versus residence (i.e. non-breeding season location) arising through adult survival concurs with selection arising through other fitness components (specifically, sub-adult survival, and indirectly through subsequent recruitment and breeding success), and to which net phenotypic shifts propagate across years and generations. Propagation will be determined by combinations of within-individual plasticity and additive genetic variance, and resulting heritability, in migration versus residence (e.g. Charlesworth 1994; Coulson, Tuljapurkar, & Childs, 2010). Our system provides valuable future opportunities to quantify these components, especially with further years of data following the 2018 ECE, although this will require further major technically-challenging analyses.

We previously showed that resident shags had higher breeding success than focal sets of migrants following the 2009−2012 winters (Grist et al., 2017). However, these winters were benign with uniformly high survival (Fig. 3), and potential carry-over effects of ECEs on subsequent differential breeding success of residents and migrants remain to be quantified. We also previously showed that locations of adult shags were highly repeatable within and among winters during 2009−2012 (Grist et al., 2014). Across the full winter, repeatabilities of individual resighting distances were 0.72 within winters and 0.59 among winters, increasing to 0.95 and 0.79 respectively across restricted mid-winter periods (Grist et al. 2014). These estimates suggest strong canalisation of individual migratory phenotype (see also Appendix S4), allowing for substantial heritability. However, some adult shags do switch between residence and migration within and among winters (Grist et al., 2014), as observed in other partially migratory systems (e.g. brown trout, *Salmo trutta*: Wysujack, Greenberg, Bergman, & Olsson, 2009; skylark, *Alauda arvensis*: Hegemann, Marra, & Tieleman, 2015; elk: Eggeman et al., 2016). Future analyses can test whether individuals surviving ECEs were more likely to subsequently switch between migration and residence.

Depending on the degree and form of density- and frequency-dependence in phenotypic expression of migration versus residence (Grayson & Wilburn 2009; Mysterud et al., 2011), such plastic responses could either 'trap' or 'rescue' populations facing increased risk of ECEs that

induce substantial mortality and strong phenotypic selection. Alternatively or additionally, depending on the magnitude of additive genetic variance, such selection could potentially drive rapid micro-evolutionary change and resulting 'evolutionary rescue' (Grant et al. 2017). Fully understanding and predicting such eco-evolutionary responses to ECEs will now require studies that can explicitly quantify and integrate all components of selection, genetic variation and plasticity that underlie the occurrence of major phenotypic responses to changing seasonality in key traits such as migration versus residence.

ACKNOWLEDGEMENTS

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).

REFERENCES

Acker, P., Daunt, F., Wanless, S., Burthe, S., Newell, M. A., Harris, M. P., ..., Reid, J. M. (2020) Data from: Strong survival selection on seasonal migration versus residence induced by

extreme climatic events. Dryad Digital Repository, https://doi.org/10.5061/dryad.c2fqz616r

Aebischer, N. J. (1995). Philopatry and colony fidelity of Shags *Phalacrocorax aristotelis* on the east coast of Britain. Ibis, 137(1), 11–18. https://doi.org/10.1111/j.1474-919X.1995.tb03214.x

Altwegg, R., Visser, V., Bailey, L. D., & Erni, B. (2017). Learning from single extreme events. Philosophical Transactions of the Royal Society, B 372(1723), 20160141. https://doi.org/10.1098/rstb.2016.0141

Avgar, T., Street, G., & Fryxell, J. M. (2014). On the adaptive benefits of mammal migration. Canadian Journal of Zoology, 92(6), 481–490. https://doi.org/10.1139/cjz-2013-0076

Bailey, L. D., & van de Pol, M. (2016). Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. Journal of Animal Ecology, 85(1), 85–96. https://doi.org/10.1111/1365-2656.12451

Barlow, E. J., Daunt, F., Wanless, S., & Reid, J. M. (2013). Estimating dispersal distributions at multiple scales: within-colony and among-colony dispersal rates, distances and directions in European Shags *Phalacrocorax aristotelis*. Ibis, 155(4), 762–778. https://doi.org/10.1111/ibi.12060

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. Ecology Letters, 15(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Boyce, M. S. (1992). Population viability analysis. Annual Review of Ecology, Evolution, and Systematics, 23(1), 481–506. https://doi.org/10.1146/annurev.ecolsys.23.1.481

Brown, C. R., & Bomberger Brown, M. (1998). Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. Evolution, 52(1), 1461–1475. https://doi.org/10.1111/j.1558-5646.1998.tb02027.x

Brown, C. R., and Bomberger Brown, M. (2000). Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). Behavioral Ecology and Sociobiology, 47(5), 339–345. https://doi.org/10.1007/s002650050674

Buchan C., Gilroy J. J., Catry I., and Franco A. M. A. (2019). Fitness consequences of different migratory strategies in partially migratory populations: A multi-taxa meta-analysis. Journal of Animal Ecology, 89(3), 678–690. https://doi.org/10.1111/1365-2656.13155

Cam, E. (2009). Contribution of capture-mark-recapture modeling to studies of evolution by natural selection. In: D. L. Thomson, E. G. Cooch, & M. J. Conroy, (Eds.), *Modeling Demographic Processes in Marked Populations. Environmental and Ecological Statistics, vol*

3. (pp. 83–129). New York, NY: Springer. Https://doi.org/10.1007/978-0-387-78151-8_5

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., ... Riddell, A. (2017). Stan: A probabilistic programming language. Journal of Statistical Software, 76(1). https://doi.org/10.18637/jss.v076.i01

Chapman, B. B., Brönmark, C., Nilsson, J.-Å., & Hansson, L.-A. (2011). The ecology and evolution of partial migration. Oikos, 120(12), 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Charlesworth, B. (1994). Evolution in age-structured populations. Cambridge, UK: Cambridge University Press. https://doi.org/https://doi.org/10.1017/CBO9780511525711

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLOS Biology, 8(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Coulson, T., Tuljapurkar, S., & Childs, D. Z. (2010). Using evolutionary demography to link life history theory, quantitative genetics and population ecology. Journal of Animal Ecology, 79(6), 1226–1240. https://doi.org/10.1111/j.1365-2656.2010.01734.x

Coumou, D., & Rahmstorf, S. (2012). A decade of weather extremes. Nature Climate Change, 2(7), 491–496. https://doi.org/10.1038/nclimate1452

Daunt, F., Afanasyev, V. J., Silk, R. D., & Wanless, S. (2006). Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. Behavioral Ecology and Sociobiology, 59(3), 381–388. https://doi.org/10.1007/s00265-005-0061-4

Daunt, F., Reed, T. E., Newell, M., Burthe, S., Phillips, R. A., Lewis, S., & Wanless, S. (2014). Longitudinal bio-logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate. Ecology, 95(8), 2077–2083. https://doi.org/10.1890/13-1797.1

Dingle, H. (2014). Migration: the biology of life on the move. Second edition. Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199640386.001.0001

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling, and impacts. Science, 289(5487), 2068–2074. https://doi.org/10.1126/science.289.5487.2068

Eggeman, S. L., Hebblewhite, M., Bohm, H., Whittington, J., & Merrill, E. H. (2016). Behavioural flexibility in migratory behaviour in a long-lived large herbivore. Journal of Animal Ecology, 85(3), 785–797. https://doi.org/10.1111/1365-2656.12495

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

Gaillard, J.-M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: a case of environmental canalization? Ecology, 84(12), 3294–3306. https://doi.org/10.1890/02-0409

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

Gonzalez, A., Ronce, O., Ferriere, R., & Hochberg, M. E. (2013). Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. Philosophical Transactions of the Royal Society B, 368, 20120404. https://doi.org/10.1098/rstb.2012.0404

Grant, P. R., & Grant, B. R. (1995). Predicting microevolutionary responses to directional selection on heritable variation. Evolution, 49(2), 241–251. https://doi.org/10.1111/j.1558-5646.1995.tb02236.x

Grant, P. R., Grant, B. R., Huey, R. B., Johnson, M. T. J., Knoll, A. H., & Schmitt, J. (2017). Evolution caused by extreme events. Philosophical Transactions of the Royal Society B, 372(1723), 20160146. https://doi.org/10.1098/rstb.2016.0146

Grayson, K. L., Bailey, L. L., & Wilbur H. M. (2011). Life history benefits of residency in a partially migrating pond-breeding amphibian. Ecology 92(6), 1236–1246. https://doi.org/10.1890/11-0133.1

Grayson, K. L., & Wilbur, H. M. (2009). Sex- and context-dependent migration in a pond-breeding amphibian. Ecology, 90(2), 306–312. https://doi.org/10.1890/08-0935.1

Green, D. J., Whitehorne, I. B. J., Middleton, H. A., & Morrissey, C. A. (2015). Do american dippers obtain a survival benefit from altitudinal migration? PLOS ONE, 10(4), e0125734. https://doi.org/10.1371/journal.pone.0125734

Grémillet, D., Tuschy, I., & Kierspel, M. (1998). Body temperature and insulation in diving great cormorants and European shags. Functional Ecology, 12(3), 386–394. https://doi.org/10.1046/j.1365-2435.1998.00199.x

Grist, H., Daunt, F., Wanless, S., Nelson, E. J., Harris, M. P., Newell, M., ... Reid, J. M. (2014). Site fidelity and individual variation in winter location in partially migratory European shags. PLOS ONE, 9(6), e98562. https://doi.org/10.1371/journal.pone.0098562

Grist, H., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., & Reid, J. M. (2017). Reproductive performance of resident and migrant males, females and pairs in a

partially migratory bird. Journal of Animal Ecology, 86(5), 1010–1021.

https://doi.org/doi.org/10.1111/1365-2656.12691

Hansen, B.B., Gamelon, M., Albon, S.D., Lee, A.M., Stien, A., Irvine, R.J., ... Grøtan, V. (2019).
More frequent extreme climate events stabilize reindeer population dynamics. Nature
Communications, 10(1), 1616. https://doi.org/10.1038/s41467-019-09332-5

Hairston, N.G., & Walton, W.E. (1986). Rapid evolution of a life history trait. Proceedings of the
National Academy of Sciences of the United States of America, 83(13), 4831–4833.
https://doi.org/10.1073/pnas.83.13.4831

Haridas, C.V., Eager, E.A., Rebarber, R., & Tenhumberg, B. (2014). Frequency-dependent
population dynamics: Effect of sex ratio and mating system on the elasticity of population
growth rate. Theoretical Population Biology, 97, 49–56.
https://doi.org/10.1016/j.tpb.2014.08.003

Harris, M.P., Buckland, S.T., Russell, S.M., & Wanless, S. (1994). Year-and age-related variation
in the survival of adult European shags over a 24-year period. The Condor, 96(3), 600–605.
https://doi.org/10.2307/1369462

Hebblewhite, M., & Merrill, E.H. (2011). Demographic balancing of migrant and resident elk in a
partially migratory population through forage–predation tradeoffs. Oikos, 120(2), 1860–1870.
https://doi.org/10.1111/j.1600-0706.2011.19436.x

Hegemann, A., Marra, P.P., & Tieleman, B.I. (2015). Causes and consequences of partial
migration in a passerine bird. The American Naturalist, 186(4), 531–546.
https://doi.org/10.1086/682667

Hereford, J., Hansen, T.F., & Houle, D. (2004). Comparing strengths of directional selection: how
strong is strong? Evolution, 58(10), 2133–2143. https://doi.org/10.1111/j.0014-
3820.2004.tb01592.x

Hoffmann, A.A., & Sgrò, C.M. (2011). Climate change and evolutionary adaptation. Nature,
470(7335), 479–485. https://doi.org/10.1038/nature09670

Hsiung, A.C., Boyle, W.A., Cooper, R.J., & Chandler, R.B. (2018). Altitudinal migration:
ecological drivers, knowledge gaps, and conservation implications. Biological Reviews, 93(4),
2049–2070. https://doi.org/10.1111/brv.12435

Jones, G. (1987). Selection against large size in the Sand Martin *Riparia riparia* during a
dramatic population crash. Ibis, 129, 274–280. https://doi.org/10.1111/j.1474-
919X.1987.tb03208.x

Keller, L.F., Arcese, P., Smith, J.N.M., Hochachka, W.M., & Stearns, S.C. (1994). Selection against inbred song sparrows during a natural population bottleneck. Nature, 372(6504), 356–357. https://doi.org/10.1038/372356a0

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., ... Beerli, P. (2001). The strength of phenotypic selection in natural populations. The American Naturalist, 157(3), 245–261. https://doi.org/10.1086/319193

Kruuk, L.E.B., Slate, J., & Wilson, A.J. (2008). New answers for old questions: the evolutionary quantitative genetics of wild animal populations. Annual Review of Ecology, Evolution, and Systematics, 39, 525–548. https://doi.org/10.1146/annurev.ecolsys.39.110707.173542

Lebreton, J.D., & Pradel, R. (2002). Multistate recapture models: Modelling incomplete individual histories. Journal of Applied Statistics, 29(1-4), 353–369. https://doi.org/10.1080/02664760120108638

Lewis, S., Phillips, R.A., Burthe, S.J., Wanless, S., & Daunt, F. (2015). Contrasting responses of male and female foraging effort to year-round wind conditions. Journal of Animal Ecology, 84(6), 1490–1496. https://doi.org/10.1111/1365-2656.12419

Lundberg, P. (1988). The evolution of partial migration in birds. Trends in Ecology and Evolution, 3(7), 172–175. https://doi.org/10.1016/0169-5347(88)90035-3

Marrot, P., Garant, D., & Charmantier, A. (2017). Multiple extreme climatic events strengthen selection for earlier breeding in a wild passerine. Philosophical Transactions of the Royal Society B, 372(1723), 20160372. https://doi.org/10.1098/rstb.2016.0372

Maxwell, S.L., Butt, N., Maron, M., McAlpine, C.A., Chapman, S., Ullmann, A., ... Watson, J. E. M. (2019). Conservation implications of ecological responses to extreme weather and climate events. Diversity and Distributions, 25(4), 613–625. https://doi.org/10.1111/ddi.12878

Moreno, J., & Møller, A.P. (2011). Extreme climatic events in relation to global change and their impact on life histories. Current Zoology, 57(3), 375–389. https://doi.org/10.1093/czoolo/57.3.375

Moritz, C., & Agudo, R. (2013). The Future of Species Under Climate Change: Resilience or Decline? Science, 341(6145), 504–508. https://doi.org/10.1126/science.1237190

Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V., & Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos, 120(2), 1817–1825. https://doi.org/10.1111/j.1600-0706.2011.19439.x

Newton, I. (2008). The migration ecology of birds. Oxford, UK: Elsevier.

https://doi.org/10.1016/B978-0-12-517367-4.X5000-1

Niu, S., Luo, Y., Li, D., Cao, S., Xia, J., Li, J., & M. D. Smith. (2014). Plant growth and mortality under climatic extremes: An overview. Environmental and Experimental Botany 98:13–19. https://doi.org/10.1016/j.envexpbot.2013.10.004

O'Donald, P. (1973). A further analysis of Bumpus' data: The intensity of natural selection. Evolution, 27(3), 398–404. https://doi.org/10.2307/2407303

Papastamatiou, Y.P., Meyer, C.G., Carvalho, F., Dale, J.J., Hutchinson, M.R., & Holland, K.N. (2013). Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. Ecology, 94(11), 2595–2606. https://doi.org/10.1890/12-2014.1

Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D.M., Kingsolver, J., Townsend Peterson, A., & Sagarin, R. (2005). Empirical perspectives on species borders: from traditional biogeography to global change. Oikos, 108(1), 58–75. https://doi.org/10.1111/j.0030-1299.2005.13150.x

Péron, G., Gaillard, J.-M., Barbraud, C., Bonenfant, C., Charmantier, A., Choquet, R., ... Marzolin, G. (2016). Evidence of reduced individual heterogeneity in adult survival of long-lived species. Evolution, 70(12), 2909–2914. https://doi.org/10.1111/evo.13098

van de Pol, M., Jenouvrier, S., Cornelissen, J.H.C., & Visser, M.E. (2017). Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. Philosophical Transactions of the Royal Society B, 372, 20160134. https://doi.org/10.1098/rstb.2016.0134

van de Pol, M., Vindenes, Y., Sæther, B.-E., Engen, S., Ens, B.J., Oosterbeek, K., & Tinbergen, J.M. (2010). Effects of climate change and variability on population dynamics in a long-lived shorebird. Ecology, 91(4), 1192–1204. https://doi.org/10.1890/09-0410.1

Pulido, F. (2007). The genetics and evolution of avian migration. Bioscience, 57(2), 165–174. https://doi.org/10.1641/B570211

Pulido, F. (2011). Evolutionary genetics of partial migration–the threshold model of migration revis(it)ed. Oikos, 120(12), 1776–1783. https://doi.org/10.1111/j.1600-0706.2011.19844.x

R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, J.M., Travis, J.M.J., Daunt, F., Burthe, S.J., Wanless, S., & Dytham, C. (2018). Population and evolutionary dynamics in spatially structured seasonally varying environments: Partially migratory meta-populations. Biological Reviews, 93(3), 1578–1603.

https://doi.org/10.1111/brv.12409

Sæther, B.-E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. Ecology, 81(3), 642–653. https://doi.org/10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2

Sanz-Aguilar, A., Béchet, A., Germain, C., Johnson, A. R., & Pradel, R. (2012). To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo. Journal of Animal Ecology, 81(6), 1171–1182. https://doi.org/10.1111/j.1365-2656.2012.01997.x

Sawyer, H., Merkle, J.A., Middleton, A.D., Dwinnell, S.P., & Monteith, K.L. (2019). Migratory plasticity is not ubiquitous among large herbivores. Journal of Animal Ecology, 88(3), 450–460. https://doi.org/10.1111/1365-2656.12926

Schaub, M., Gimenez, O., Schmidt, B.R., & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture-recapture framework. Ecology, 85(8), 2107–2113. https://doi.org/10.1890/03-3110

Skov, C., Chapman, B.B., Baktoft, H., Brodersen, J., Brönmark, C., Hansson, L.-A., ..., Nilsson. P. A. (2013). Migration confers survival benefits against avian predators for partially migratory freshwater fish. Biology Letters, 9(2), 20121178. https://doi.org/10.1098/rsbl.2012.1178

Székely, T., Weissing, F.J., & Komdeur, J. (2014). Adult sex ratio variation: implications for breeding system evolution. Journal of Evolutionary Biology, 27(8), 1500–1512. https://doi.org/10.1111/jeb.12415

Ummenhofer, C.C., & Meehl, G.A. (2017). Extreme weather and climate events with ecological relevance: a review. Philosophical Transactions of the Royal Society B, 372(1723), 20160135. https://doi.org/10.1098/rstb.2016.0135

Welbergen, J.A., Klose, S.M., Markus, N., & Eby, P. (2007). Climate change and the effects of temperature extremes on Australian flying-foxes. Proceedings of the Royal Society B, 275(1633), 419–425. https://doi.org/10.1098/rspb.2007.1385

Widemo, F., & Sæther, S.A. (1999). Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. Trends in Ecology and Evolution, 14(1), 26–31. https://doi.org/10.1016/S0169-5347(98)01531-6

Wysujack, K., Greenberg, L.A., Bergman, E., & Olsson, I.C. (2009). The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish, 18(1), 52–59. https://doi.org/10.1111/j.1600-

0633.2008.00322.x

Zúñiga, D., Gager, Y., Kokko, H., Fudickar, A.M., Schmidt, A., Naef-Daenzer, B., ... Partecke, J. (2017). Migration confers winter survival benefits in a partially migratory songbird. eLife, 6, e28123. https://doi.org/10.7554/eLife.28123