








## RESEARCH ARTICLE

# Early-life variation in migration is subject to strong fluctuating survival selection in a partially migratory bird

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## Abstract

1. Population dynamic and eco-evolutionary responses to environmental variation and change fundamentally depend on combinations of within- and among-cohort variation in the phenotypic expression of key life-history traits, and on corresponding variation in selection on those traits. Specifically, in partially migratory populations, spatio-seasonal dynamics depend on the degree of adaptive phenotypic expression of seasonal migration versus residence, where more individuals migrate when selection favours migration.
2. Opportunity for adaptive (or, conversely, maladaptive) expression could be particularly substantial in early life, through the initial development of migration versus residence. However, within- and among-cohort dynamics of early-life migration, and of associated survival selection, have not been quantified in any system, preventing any inference on adaptive early-life expression. Such analyses have been precluded because data on seasonal movements and survival of sufficient young individuals, across multiple cohorts, have not been collected.
3. We undertook extensive year-round field resightings of 9359 colour-ringed juvenile European shags *Gulosus aristotelis* from 11 successive cohorts in a partially migratory population. We fitted Bayesian multi-state capture-mark-recapture models to quantify early-life variation in migration versus residence and associated survival across short temporal occasions through each cohort's first year from fledging, thereby quantifying the degree of adaptive phenotypic expression of migration within and across years.
4. All cohorts were substantially partially migratory, but the degree and timing of migration varied considerably within and among cohorts. Episodes of strong survival selection on migration versus residence occurred both on short timeframes within years, and cumulatively across entire first years, generating instances of instantaneous and cumulative net selection that would be obscured at coarser

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temporal resolutions. Further, the magnitude and direction of selection varied among years, generating strong fluctuating survival selection on early-life migration across cohorts, as rarely evidenced in nature. Yet, the degree of migration did not strongly covary with the direction of selection, indicating limited early-life adaptive phenotypic expression.

5. These results reveal how dynamic early-life expression of and selection on a key life-history trait, seasonal migration, can emerge across seasonal, annual, and multi-year timeframes, yet be substantially decoupled. This restricts the potential for adaptive phenotypic, microevolutionary, and population dynamic responses to changing seasonal environments.

#### KEYWORDS

adaptive phenotypic plasticity, cohort, European shag *Gulosus aristotelis*, fluctuating selection, juvenile survival, multi-state capture-mark-recapture, partial seasonal migration, viability selection

## 1 | INTRODUCTION

As climate change acts to increase environmental variability, population persistence depends on timely expression of key phenotypes that mitigate negative environmental impacts on fitness (Chevin et al., 2010; Chevin & Hoffmann, 2017; Fox et al., 2019; Ghalambor et al., 2007; Hoffmann & Sgró, 2011). Specifically, environmental variation may generate substantial phenotypic variation that can experience strong selection, which can itself vary temporally in both magnitude and direction (Bell, 2010; Siepielski et al., 2009). Varying phenotypic expression can then aid population persistence if particular phenotypes are expressed and positively selected for in the same timeframe (i.e. right phenotype at the right time). Such variation arising within genotypes represents adaptive phenotypic plasticity (Edelaar et al., 2017; Ghalambor et al., 2007). Demonstrating such adaptive variation, and predicting overall system outcomes, then requires quantifying temporal variation in the expression of key phenotypes and in selection on those phenotypes and evaluating the degree of temporal congruence between phenotypic expression and selection. However, these interconnected objectives are still rarely achieved (de Villemereuil et al., 2020; Merilä & Hendry, 2014; Reid et al., 2020).

Useful inferences require focusing on relevant traits, life-history stages, and timeframes of selection (Chevin & Hoffmann, 2017; Lande, 2014; Tufto, 2015). Many key traits that mitigate environmental challenges are initially expressed as juveniles, and could be subject to strong and varying viability selection (i.e. where survival probabilities vary with phenotype; Jebb et al., 2021; Milner et al., 1999). Very early-life stages can thereby shape later-life phenotypic distributions and resulting population outcomes (Lindström, 1999). Further, in seasonal environments, juveniles inevitably experience rapidly changing conditions through initial months (e.g. summer to winter), potentially driving phenotypic plasticity and/or changing forms or magnitudes of selection. Congruence or divergence between labile

phenotypes and selection, and any resulting (mal)adaptive phenotypic plasticity, could then arise on relatively short timeframes both within and among cohorts experiencing different early-life environmental conditions. Yet, while one leading empirical study quantified temporal covariation between trait expression and selection in wild populations (de Villemereuil et al., 2020), most empirical and theoretical efforts focus on annual timeframes and adult traits (e.g. de Villemereuil et al., 2020; Lande, 2014; Tufto, 2015). Attempts to infer overall population and eco-evolutionary outcomes will therefore be incomplete, and potentially misleading, if within-year and among-year dynamics of early-life phenotypic variation and selection are not considered (e.g. Jebb et al., 2021; Kasumovic, 2013; Mojica & Kelly, 2010).

One key trait through which many animals respond to seasonally deteriorating environments is seasonal migration (i.e. reversible intra-annual movements, hereafter 'migration'). Migration is commonly facultative, where some individuals within a focal breeding population remain resident year-round, while other individuals migrate away through the non-breeding season and therefore experience different seasonal environmental conditions (Chapman et al., 2011). Such 'partial migration' is taxonomically widespread (Berg et al., 2019; Buchan et al., 2020; Chapman et al., 2012; Gowan et al., 2019; Grayson et al., 2011). Further, the occurrence and timing of migration departures can vary within and among years and cohorts in diverse systems (Eggeman et al., 2016; Fudickar et al., 2013; Gowan et al., 2019; Grayson et al., 2011; Reid et al., 2020), largely representing phenotypic plasticity. Such variation may be subject to selection, of magnitudes and directions that could also vary within and among cohorts. Partial migration could therefore drive joint spatial and seasonal eco-evolutionary dynamics through coupled within-cohort and among-cohort temporal dynamics of phenotypic expression and selection (Reid et al., 2018, 2020).

However, despite the potentially major role that phenotypic dynamics of early-life migration could play in driving system responses

to changing seasonal environments, leading studies on variation in migration and associated selection in partially migratory systems focus on adults (Acker, Daunt, Wanless, Burthe, Newell, Harris, Gunn, et al., 2023; Eggeman et al., 2016; Grayson et al., 2011; Reid et al., 2020). Yet, migratory phenotypes are commonly first expressed and developed as juveniles, before becoming relatively canalized in adults (Gowan et al., 2019; Grist et al., 2014; Lok et al., 2011; Péron & Grémillet, 2013; Sergio et al., 2014; Vansteelant et al., 2017; Witczak et al., 2024). Rapid changes in the phenotypic expression of migration versus residence, likely representing plasticity, might consequently be greater in juveniles than subsequently and could be adaptive or maladaptive. Studies on tractable fully migratory species are now quantifying early-life development of migration, focusing on variation in routes and destinations (e.g. Lok et al., 2011; Péron & Grémillet, 2013; Vansteelant et al., 2017; Wynn et al., 2022). However, none have quantified very early-life temporal dynamics of the occurrence of migration and associated selection in partially migratory populations, where within-cohort and among-cohort variation and the resulting potential for (mal)adaptive plasticity might be strongly manifested. This limitation impedes any attempt to comprehensively predict phenotypic and eco-evolutionary dynamic responses to changing seasonal environments in partially seasonally mobile systems.

Progress requires quantifying the spatial locations and associated survival of large numbers of potentially mobile juveniles on fine temporal scales throughout the months following birth, encompassing multiple cohorts within a partially migratory population. Such datasets have not previously been collected. This is not least because juveniles in many taxa are too small or underdeveloped to deploy tracking devices, technically feasible deployments may be too detrimental given the limited physical or foraging capabilities of young individuals, and high mortality rates and/or natal dispersal impede retrieval of passive (non-transmitting) devices (Hazen et al., 2012; Shillinger et al., 2012).

To circumvent these challenges, we undertook extensive surveys of a field-observable partially migratory population of European shags *Gulosus aristotelis* (hereafter 'shags') to obtain year-round resightings of 9359 colour-ringed juveniles from 11 cohorts, encompassing the known non-breeding season range. We then fitted Bayesian multi-state capture-mark-recapture (MS-CMR) models to quantify three key aspects of temporal variation in migration and associated survival selection within and across the first year from fledging.

First, to reveal the within- and among-cohort temporal dynamics of early-life partial migration, we quantified variation in departure and return probabilities occurring on short within-year timescales within each cohort. We thereby quantified the net emerging variation in phenotypic expression of seasonal migration versus residence through the months following fledging, and quantified the pattern and magnitude of variation among cohorts.

Second, to reveal the within- and among-cohort temporal dynamics of early-life selection on migration, we estimated survival probabilities of migrants and residents through successive short

time intervals following fledging. We thereby quantified the directions and magnitudes of survival selection occurring on short timescales, and emerging cumulatively across the first year from fledging, and thus quantified the pattern and magnitude of variation in selection manifested within and among cohorts.

Third, to reveal the degree of adaptive phenotypic expression of early-life migration, we quantified the degree to which increased expression of migration was aligned with episodes of selection for migration, both within and among cohorts. Together, our new data, analytical approaches, and multifaceted results provide new empirical insights into how dynamic patterns of early-life phenotypic variation and associated selection can arise, fluctuate, and accumulate within and among successive cohorts, thereby shaping population responses to changing seasonal environmental conditions.

## 2 | METHODS

### 2.1 | Study system and data collection

A shag population breeding on the Isle of May (hereafter 'IoM') National Nature Reserve, Scotland (56°11'5.40" N, 2°33'16.19" W), is well suited to quantifying variation in early-life migration and selection. Specifically, shags are pursuit-diving seabirds that, given their partially wettable plumage, must return to land every day to dry and thermoregulate. This restricts their year-round distribution to coastal habitats. Colour-ringed individuals, including juveniles, can consequently be directly resighted throughout the year, initially at their natal locations and then at subsequent autumn and winter roost sites (Acker, Daunt, et al., 2021; Grist et al., 2014).

During the 2010–2020 breeding seasons (April–August), intensive reproductive monitoring on IoM meant that ~95% of fledged chicks were ringed with uniquely coded metal and colour rings (mean  $856 \pm 188$  SD chicks ringed per year, mean fledging date July  $16 \pm 11$  SD days). During the 2010–2022 non-breeding seasons (September–March) extensive surveys were undertaken to locate colour-ringed individuals (field-identifiable at  $\leq 150$ m without recapture), and hence identify current residents (primarily defined as individuals that roost overnight on IoM) and seasonal migrants (defined as individuals that had moved elsewhere, Supporting Information S1, Acker, Daunt, et al., 2021). Core surveys focussed on known major roost sites along the north-eastern Scottish coast, including IoM, which were visited every 1–2 weeks as far as feasible (Supporting Information S1, Acker, Daunt, et al., 2021; Grist et al., 2017, 2014). During each survey, observers recorded identities of all visible colour-ringed shags. More geographically extensive sightings were collected through occasional visits to other roost sites, alongside substantial 'citizen science' contributions (Supporting Information S1, Acker, Daunt, et al., 2021). This huge effort generated 17,460 observations of fledged individuals during their first year, plus 55,540 subsequent resightings of surviving >1-year-old individuals prior to or following recruitment (typically when 3 years old). Since natal dispersal distances are typically very short compared with seasonal migration

distances (90.4% of surviving individuals bred on IoM and a further 6.1% bred  $\leq 50$  km away; Barlow et al., 2013), longer-distance pre-recruitment movements can be clearly interpreted as migration (typically 100–500 km). Ringing and fieldwork activities were licenced by the British Trust for Ornithology and NatureScot (permits A400 and A4607). No further ethical approval was required.

## 2.2 | Model design

We devised a MS-CMR model to estimate migration and survival probabilities through the year from fledging to the first summer (i.e. to age 1 year) given our spatially variable resighting data. We envisage sequences of discrete 'occasions', between which individuals can survive and move between locations, with probabilities that depend on an individual's current location. The possible outcomes (alive at some location or dead) represent different states, which can be observed with some detection probability. Such models address the biases in estimates of migration and survival probabilities that would otherwise arise given that surviving individuals are not always resighted (in which case current states are unknown; Acker, Daunt, et al., 2021; Gourlay-Larour et al., 2014; Gowan et al., 2019; Grayson et al., 2011).

For current purposes, we defined four states: alive as resident (R), alive in migrant states 1 and 2 ( $M_1$  and  $M_2$ , representing locations that were and were not intensively surveyed respectively), and dead (D; Figure 1; Supporting Information S1). Here,  $M_1$  and  $M_2$  were distinguished solely to account for differences in detection probability, thereby handling heterogeneity that could otherwise bias estimated migration and survival probabilities.

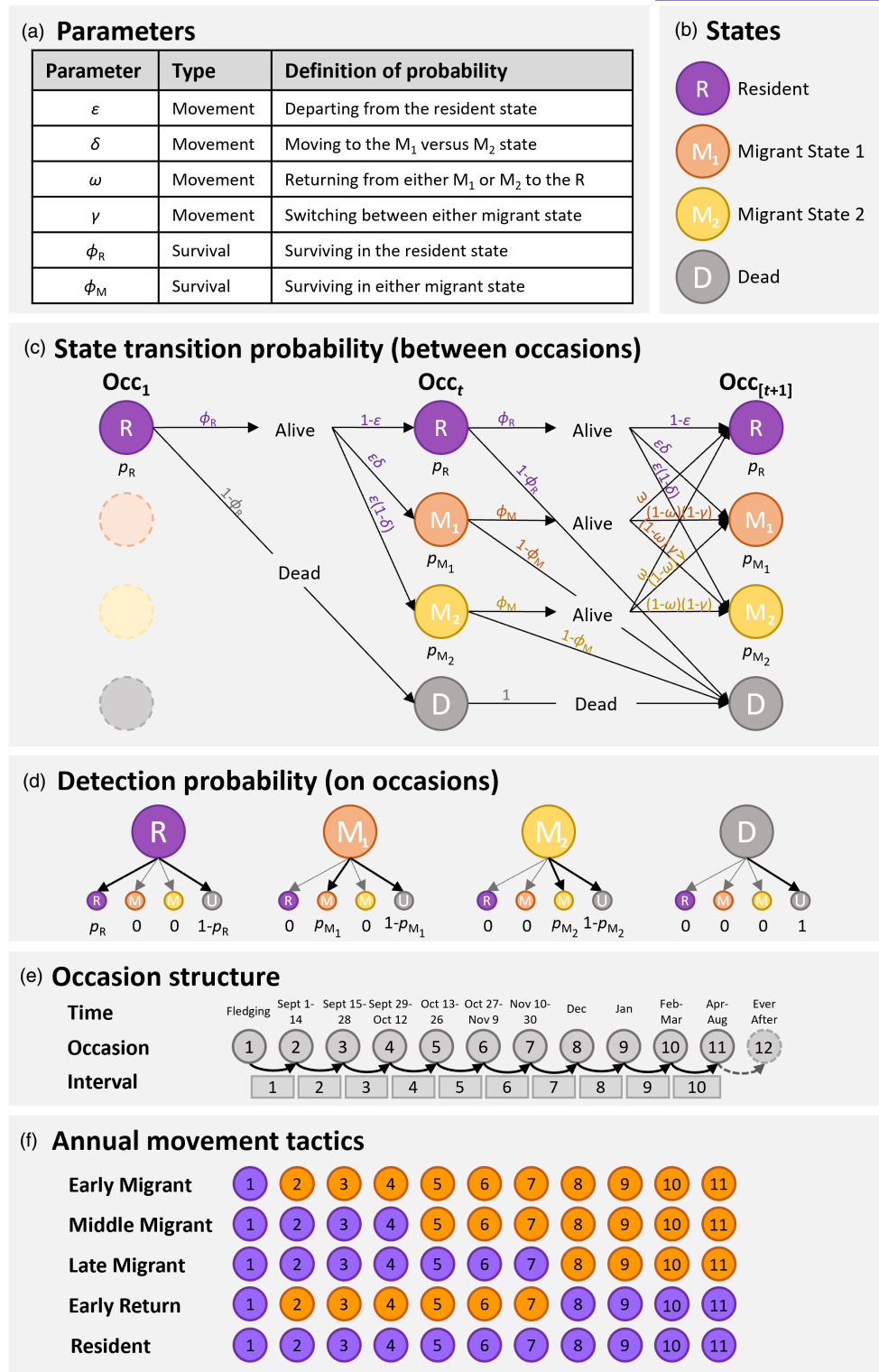
The first annual occasion comprised the breeding season, when all focal ringed chicks were on IoM, and hence in state R. Subsequently, conditional on survival through the intervals between occasions, individuals in R can remain resident or move to  $M_1$  or  $M_2$ , while individuals in  $M_1$  or  $M_2$  can remain in their current state, switch to the other migrant state, or return to R. These possible movements were formulated through combinations of four parameters (Figure 1), defined as the probabilities of departing from R ( $\epsilon$ ), moving to  $M_1$  versus  $M_2$  conditional on departing ( $\delta$ ), returning from  $M_1$  or  $M_2$  to R ( $\omega$ ), and switching between  $M_1$  and  $M_2$  conditional on remaining a migrant ( $\gamma$ ). We estimated separate survival probabilities for individuals that started each interval in R ( $\phi_R$ ) versus  $M_1$  or  $M_2$  ( $\phi_M$ ; Figure 1). Since  $M_1$  and  $M_2$  were distinguished based on known differences in surveying intensity, not explicitly based on location or ecology, we had no strong expectation that movement or survival probabilities would differ. We therefore constrained  $\phi_M$  to be the same for individuals in  $M_1$  and  $M_2$ ,  $\omega$  to be the same for individuals that could depart from  $M_1$  and  $M_2$ , and  $\gamma$  to be the same for individuals that could switch between  $M_1$  and  $M_2$  in both directions. On each occasion, individuals had distinct probabilities of being detected depending on their current state (Figure 1d, denoted  $p_R$ ,  $p_{M1}$ , and  $p_{M2}$  for states R,  $M_1$ , and  $M_2$ , respectively). Since we only used live resightings, the probability of observing dead individuals is zero.

To estimate survival and movement probabilities on relatively fine temporal scales, we divided the biological year into 11 occasions (i.e. resighting time periods), generating 10 intervals for parameter estimation (Figure 1e). Occasions were defined as a pragmatic balance between minimizing durations versus ensuring relatively high detection probabilities across R and  $M_1$  on all occasions for all cohorts (Supporting Information S2). This maximizes precision on estimated timings of movements and mortality, while allowing parameter estimation. Exploratory analyses based on knowledge of fieldwork efforts generated a robust structure with five initial 2-week occasions, followed by one 3-week occasion, two 1-month occasions, and one 2-month occasion up to the first summer (Figure 1e; Supporting Information S2). While MS-CMR models assume that occasions are instantaneous, they are robust to longer occasions such as ours (given approximately constant detection and survival probabilities within occasions; O'Brien et al., 2005).

We specified occasion- and cohort-specific movement, survival, and detection parameters (Figure 1a,e), thereby defining fully time-dependent models and allowing us to quantify fine-scale temporal variation. However, for the transition from the first (to second) occasion when all individuals were initially resident  $\phi_M$ ,  $\omega$ , and  $\gamma$  are undefined (and not estimated). Further, because survival and detection probabilities cannot be distinguished in the final time-step of fully time-dependent capture-mark-recapture models (Lebreton et al., 1992), we added a 12th occasion to specify whether an individual was ever observed after its first year ('ever after', Figure 1e). While parameters pertaining to the 'ever after' occasion are not individually identifiable, modelling their combination ensures that all focal movement and survival probabilities through the year from fledging are identifiable and hence can be estimated (i.e. intervals through the 1st–11th occasions, Supporting Information S2).

## 2.3 | Analyses

We used the field resighting data to create state-specific encounter histories for 9359 fledglings that were colour-ringed on IoM during 2010–2020 (i.e. 11 cohorts), comprising the 11 defined within-year occasions plus the 12th 'ever after' occasion (Figure 1e; Supporting Information S2). Since fledgling sexes were typically unknown, we did not model sex effects. However, migration versus residence is not strongly sexually dimorphic in adult shags in the focal system (Acker, Daunt, et al., 2021; Acker, Daunt, Wanless, Burthe, Newell, Harris, Gunn, et al., 2023). We coded and analysed our model in STAN v2.21.0, a probabilistic programming language for Bayesian inference using 'Hamiltonian' Markov chain Monte Carlo ('MCMC'; Carpenter et al., 2017) called from R v4.1.2 (R Core Team, 2021). For simplicity, each cohort was analysed in a separate model, generating fully cohort-specific parameter estimates. This does not entail any loss of information because there are no shared data or occasions across the first years of different cohorts. Full annotated code, data, and numerical results are archived in the Dryad repository (Ugland et al., 2024).



**FIGURE 1** Summaries of (a) nine model parameters, (b) four defined states, (c) probabilities of transitioning between states during intervals between consecutive occasions, comprising survival and movement, (d) event probabilities of being detected on each occasion, (e) timings of 11 modelled within-year occasions plus the twelfth 'ever after' occasion, and of the 10 intervening intervals (time up to: 1: Early September, 2: Late September, 3: Early October, 4: Late October, 5: Early November, 6: Late November, 7: December, 8: January, 9: February–March, 10: First summer), and (f) five focal tactics used to estimate annual survival. On (c), coloured circles correspond to states defined in (b), and arrows show transition probabilities defined by parameters listed in (a). (d) shows the detection probability in each state (small circles) conditional on being alive in that state (large circles) on any occasion. Arrows on (e) highlight that movement and survival parameters are estimated through intervals between occasions, while detection is estimated on each occasion. On (f), purple and orange denote whether individuals were resident or migrant, respectively on each occasion.

We specified vague uniform priors with range 0–1 on all parameters, except for survival and  $M_2$  detection probabilities, and for September–October detection probabilities for the 2011 cohort. Mean shag survival probability from fledging to age 1 year was previously estimated as 0.51 in our system ( $\pm 0.04$  SE; Frederiksen et al., 2008). This implies that survival probabilities over any successive short intervals within the first year must typically be much higher. We therefore specified subjective (informative) priors on  $\phi_R$  and  $\phi_M$ , as Beta(10,0.9) distributions (Supporting Information S3). Further, since we knew that detection probabilities for the non-intensively surveyed  $M_2$  migrants would be low, we specified Beta(0.5,6) priors on  $p_{M_2}$  (Supporting Information S3). Finally, due to known low surveying intensity in September 2011, we specified a Beta(0.5,6) prior for  $p_R$  and constrained  $\varepsilon$  to be the same across the first three intervals.

Posterior distributions were sampled using four MCMC chains, each including 1000 warmup iterations followed by 4000 monitored iterations, generating 16,000 posterior samples in total. We summarized posterior distributions of model parameters as posterior means and 95% credible intervals (95% CIs). MCMC diagnostics revealed no major challenges with posterior sampling ( $\hat{R} < 1.01$ , effective sample sizes of key primary parameters  $> 1000$ , Supporting Information S4). Our models and assumptions regarding parameter constraints well captured the variation of interest, as evidenced by thorough examinations of model validity and fit. These included fitting our models to simulated data, posterior predictive checks, and validating estimates of annual survival probabilities computed as products of occasion-specific survival probabilities estimated within our full Bayesian multi-state models against direct maximum likelihood estimates of annual probabilities (Supporting Information S4).

To further summarize key parameters (namely,  $\varepsilon$ ,  $\omega$ ,  $\phi_R$ , and  $\phi_M$ ) across all cohorts, we computed the posterior distributions (and hence the posterior mean and 95% CI) of the interval-specific grand means and variances (hereafter termed 'grand means' and 'grand variances'), by computing the mean and variance for all relevant intervals across the 11 cohorts. Finally, since the specified occasions (and hence intervals) varied in duration (Figure 1e), raw estimates of  $\varepsilon$ ,  $\omega$ ,  $\phi_R$ , and  $\phi_M$  are not all directly comparable across intervals as estimates per unit time. Hence, to allow approximate comparisons we rescaled these probabilities to standard 2-week units (Supporting Information S5).

## 2.4 | Derived biological quantities

To quantify overall magnitudes of interval-specific migration and associated survival selection, and to scale up these effects across the sequences of occasions and intervals within each cohort, we computed four sets of derived quantities from the primary model parameters to quantify key biological effects.

First, we computed the posterior distribution of the 'migratory fraction' ( $m$ ) for each occasion, defined as the expected proportion

of surviving individuals that are migrant (i.e. away from IoM). The full posterior distribution of  $m$  was calculated by combining relevant  $\varepsilon$ ,  $\omega$ ,  $\phi_R$ , and  $\phi_M$  probabilities for each occasion and cohort (Supporting Information S6). We also computed posterior distributions of the grand mean and grand variance of  $m$  across all 11 cohorts.

Second, we quantified the directions and magnitudes of survival selection on seasonal migration versus residence (i.e. the degree to which one phenotype has higher survival probability than the other) by computing posterior distributions of the difference between  $\phi_M$  and  $\phi_R$  (survival difference ' $\Delta = \phi_M - \phi_R$ ') for each interval for each cohort. Here, positive values indicate that migrants had higher survival than residents, while negative values indicate the converse. 95% CIs that do not include zero provide evidence of selection. Additionally, to further visualize the degree of evidence for fine-scale differences in survival, we computed the posterior probability that  $\Delta$  exceeded zero. Here, values close to 1 or 0 provide strong evidence for selection for migration or residence respectively, while values close to 0.5 imply no evidence of selection.

Third, to scale up from the estimated interval-specific survival probabilities to overall annual survival probabilities (i.e. through the first year from fledging) and resulting selection, we multiplied through sequences of interval-specific  $\phi_R$  and  $\phi_M$  chosen to represent biologically relevant migratory 'tactics' among all possible temporal sequences of occasions spent as resident versus migrant (Figure 1f). Specifically, we chose 5 of the 1024 possible tactics that our 11-occasion structure yields. Since our model formulation and parameterization impose no a priori constraints on transitions between occasions, any of these tactics, including repeated switching between the resident and migrant states could in principle emerge. However, given the encounter history data, some transitions and hence tactics were estimated by our model to be very unlikely. To illustrate the resulting variation, for each cohort we first calculated the probability that a surviving individual would follow each possible tactic, then selected five biologically meaningful tactics that commonly occurred across the cohorts (Supporting Information S7). These comprised the two pure phenotypic tactics (Resident: individuals that remained at IoM through all 11 occasions; Early Migrant: individuals that were migrant through occasions 2–11) and three intermediate tactics (Middle Migrant, Late Migrant, and Early Return, which were migrant through occasions 5–11, 8–11, and 2–7 respectively; Figure 1f). These tactics are hypothetical routes through the 11 occasions and were not assigned to real individuals. Resulting annual survival estimates for each tactic assume that survival between consecutive occasions entirely depends on an individual's starting state (resident or migrant) with no further memory (i.e. first-order Markovian, as is standard for MS-CMR analyses; Acker, Daunt, et al., 2021).

Fourth, to quantify the temporal congruence between the degree of migration and the magnitude and direction of selection, and hence test for adaptive phenotypic expression, we computed the association between the migratory fraction  $m$  and survival difference  $\Delta$  both within and among cohorts. To quantify the within-cohort association, we computed the posterior distributions of the

regression of  $\Delta$  against  $m$  across all intervals within each cohort (i.e. September–August; [Supporting Information S8](#)). For the among-cohort association, we first computed the posterior distributions of the regression of  $\Delta$  against  $m$  within each interval across all cohorts (i.e. 2010–2020; [Supporting Information S8](#)). We also computed the posterior distributions of the regression of annual  $\Delta$  ( $\Delta_A$ : defined as the difference in annual survival probability between the early migrant and resident tactics) against  $m$  in mid-winter (i.e. the mean across occasions 8–9, encompassing December–January; [Figure 1e](#)) across the 11 cohorts. We focussed on these occasions because the greatest among-cohort variation in  $m$ , and the greatest evidence of selection, was observed in this period (see [Section 3](#)). Given our formulations of  $m$  and  $\Delta$ , positive associations indicate adaptive expression (i.e. greater expression of migration coincides with selection for migration).

We focus on presenting estimates of the key biological parameters of interest, namely cohort- and interval-specific  $\varepsilon$ ,  $\omega$ ,  $\phi_R$ ,  $\phi_M$ ,  $m$ , and  $\Delta$ . All parameter estimates, including those for the additional parameters that are structural parts of our MS-CMR models but not of current direct biological interest (namely  $\delta$ ,  $\gamma$ ,  $p_R$ ,  $p_{M1}$ , and  $p_{M2}$ ), are shown in [Supporting Information S9](#). Throughout, we expected that some primary and derived parameters would be estimated with considerable uncertainty. For example,  $\varepsilon$  and  $\omega$  when many or few individuals are already migrant respectively, and all parameters when many individuals are already dead, leaving few individuals in the resident and/or migrant states. In such circumstances, strong inferences on parameter values cannot be drawn. However, such uncertainty does not necessarily impede overall population-level inferences, as probabilities applying to few individuals have small population-level effects.

### 3 | RESULTS

#### 3.1 | Dynamics of early-life migration

Across all 11 cohorts, the grand posterior mean probability  $\varepsilon$  of departing from the resident state (i.e. breeding area) straight after the natal breeding season (i.e. the first interval) was 0.44 [95% CI: 0.36, 0.51]. Hence, on average, almost half of each juvenile cohort had already migrated by early September ([Figure 2a](#), with departures from early-mid-August). After scaling  $\varepsilon$  to 2-week time units, grand mean estimates through the rest of the biological year were between 0.15 and 0.25, decreasing to 0.07 [0.03, 0.11] during the final interval up to the first summer ([Figure 2a](#)). Some degree of departure therefore occurred throughout autumn and winter. However, there was substantial among-cohort variation, especially in late winter ([Figure 2a](#); [Supporting Information S10](#)). Some cohorts had particularly high or low  $\varepsilon$  through some intervals. Notably,  $\varepsilon$  was 0.62 [0.25, 0.92] and 0.70 [0.28, 0.94] up to early and late October respectively for the 2012 cohort, and 0.71 [0.38, 0.95] in February–March for the 2020 cohort. Conversely,  $\varepsilon$  was generally low for the 2014 cohort, with posterior means below 0.05 up to early November

(0.03 [0.00, 0.13]), January (0.03 [0.00, 0.13]), and February–March (0.04 [0.00, 0.15]).

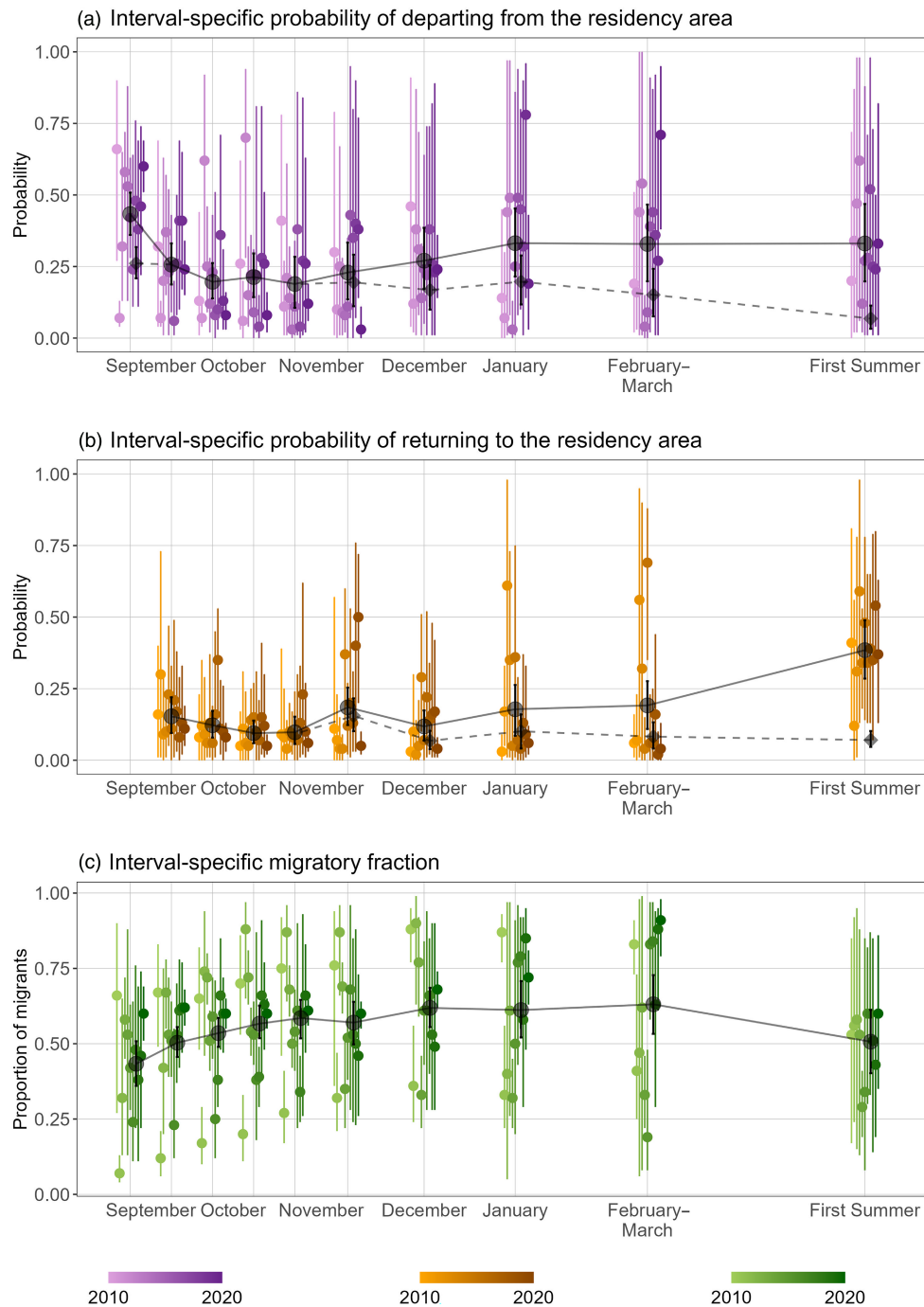
Grand mean probabilities  $\omega$  of returning from either migrant state to the resident state were relatively low across all cohorts until the final interval, ranging between 0.07 and 0.16 after scaling to 2-week time units ([Figure 2b](#)). However, there was again considerable among-cohort variation, particularly in late winter ([Figure 2b](#); [Supporting Information S10](#)). The 2014, 2018, and 2019 cohorts had relatively high  $\omega$  up to early November (posterior means  $\geq 0.37$ ). While  $\omega$  was low for most cohorts up to February–March (0.19 [0.11, 0.28]), values for the 2015 cohort were notably high (0.69 [0.35, 0.88]).

Accordingly, the grand mean migratory fraction  $m$ , which reflects the combined temporal sequence of departure and return probabilities, showed that all cohorts were substantially partially migratory, as around half the individuals that were estimated to have survived at any given time were typically migrants, increasing slightly in mid-winter ([Figure 2c](#)). However,  $m$  varied substantially among cohorts, especially in winter. For example, >72% of the 2010, 2016, 2017, 2019, and 2020 cohorts were migrant between December and up to February–March, while <50% of the 2011, 2012, 2014, and 2015 cohorts were migrant in the same period. Through the autumn  $m$  was less variable, with grand variances between fledging and up to late November <0.045 compared with the winter, with grand variances of 0.07 [0.039, 0.096] up to January and 0.09 [0.057, 0.125] up to February–March ([Supporting Information S10](#)).

#### 3.2 | Dynamics of survival selection

Interval-specific grand posterior mean survival probabilities for residents  $\phi_R$  and migrants  $\phi_M$  were generally high through the autumn (>0.92) up to late November, then decreased through the winter (>0.85; [Figure 3a,b](#)). Scaled 2-week estimates were generally uniformly high, though some instances of notably low  $\phi_R$  or  $\phi_M$  occurred ([Figure 3a,b](#)). Most conspicuously,  $\phi_R$  was 0.59 [0.47, 0.71] for the 2020 cohort through the interval up to February–March, and 0.61 [0.38, 0.87] and 0.60 [0.41, 0.83] for the 2017 and 2015 cohorts respectively up to the first summer ([Figure 3a](#)). Meanwhile, low  $\phi_M$  occurred in the interval up to January for the 2018 and 2012 cohorts (0.68 [0.52, 0.85] and 0.62 [0.37, 0.96] respectively) and up to the first summer for the 2017 and 2013 cohorts (0.68 [0.56, 0.81] and 0.64 [0.32, 0.98] respectively; [Figure 3b](#)).

Correspondingly, there was substantial within- and among-cohort variation in the interval-specific survival difference  $\Delta$ , and hence in the magnitude and direction of survival selection on migration. Posterior means of  $\Delta$  were generally close to zero from fledging up to late November, indicating little or no autumn selection ([Figure 3c](#)). Yet, the proportions of posterior estimates above zero were commonly slightly below 0.5 (65% of posterior estimates from intervals 2–6; [Figure 3d](#)). Accordingly, if anything, the evidence indicates some consistently weak selection against migration in autumn.



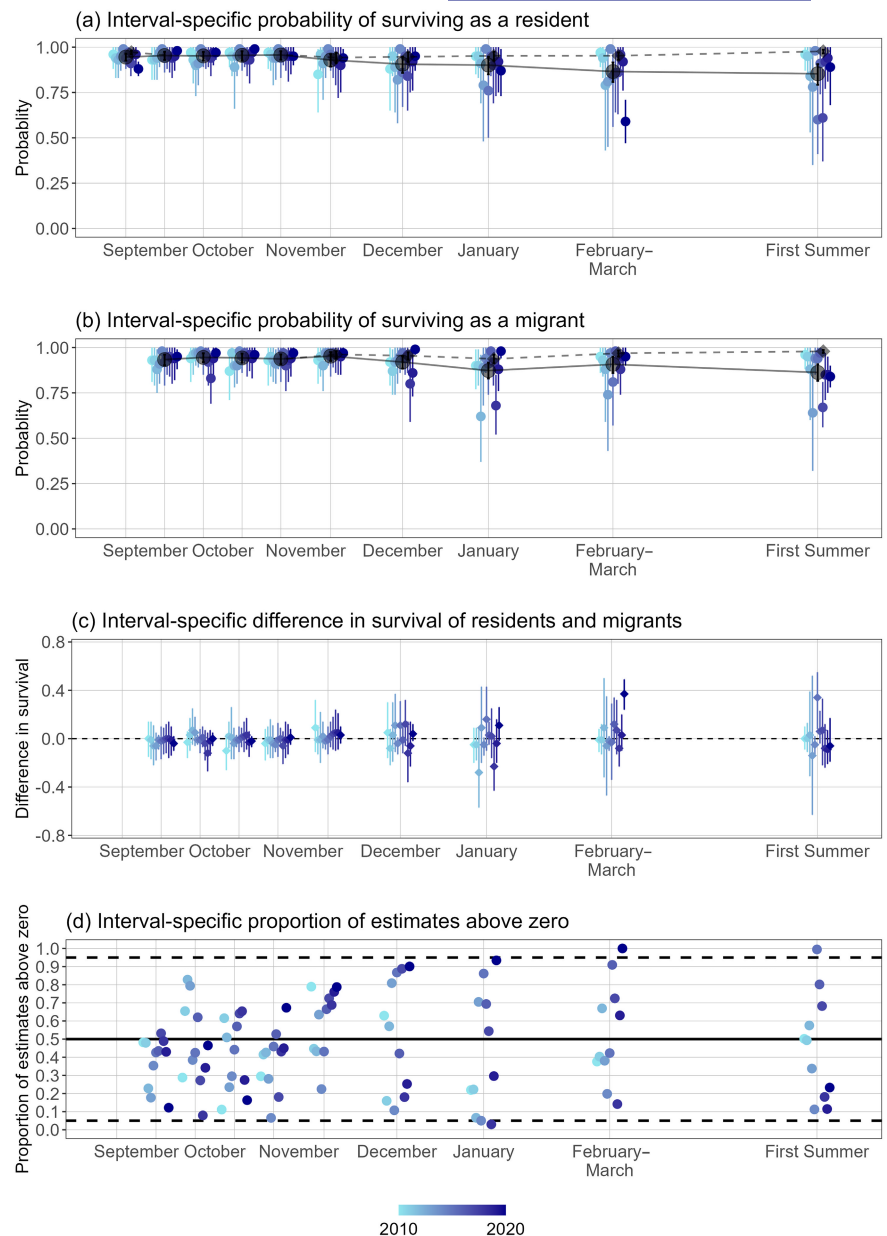
**FIGURE 2** Interval-specific probabilities of (a) departing from and (b) returning to the residence state, culminating in (c) the proportion of individuals that are away (i.e. the migratory fraction) at the end of each interval. Points are posterior means for each of the 11 focal cohorts (light to dark shading denotes cohorts hatched in 2010–2020) with 95% CI. X-axis labels correspond to occasions at the ends of focal intervals. Return probabilities are not estimated in the interval following the first occasion, because all individuals were resident. Some estimates are accompanied by substantial uncertainty, and hence not interpreted. Larger black points are posterior means (circles, solid line) and scaled estimates of means to two-week time units (diamonds, dashed line, panels (a) and (b)) across all cohorts with corresponding 95% CIs. Primary estimates of all modelled movement, survival, and detection parameters are shown in [Supporting Information S9](#).

Subsequently, clear episodes of strong selection occurred on short timescales during winter, in different directions in different cohorts (i.e. representing fluctuating selection between episodes, [Figure 3c,d](#)). Specifically, the 2018 cohort experienced strong selection for residence in the interval up to January ( $\Delta = -0.23$

$[-0.43, 0.01]$ ), while the 2020 and 2015 cohorts experienced strong selection for migration up to February–March and up to the first summer, respectively ( $\Delta = 0.37$   $[0.24, 0.49]$  and  $0.34$   $[0.08, 0.55]$ ). Although the posterior mean of  $\Delta$  for the 2012 cohort in the interval up to January was also strongly negative, the 95% CI was wide



**FIGURE 3** Interval-specific estimates of (a) survival probabilities of residents, (b) survival probabilities of migrants, (c) the migrant-resident difference  $\Delta$  (positive and negative values indicate higher migrant and resident survival respectively; 95% CIs that do not overlap zero show strong evidence for interval-specific selection), and (d) the posterior probability that  $\Delta$  exceeds zero (values closer to 1 or 0 indicate higher migrant or resident survival respectively, where dashed lines at 0.05 and 0.95 visualize 90% CI). Points are posterior means for each of the 11 focal cohorts (dark to light shading denotes cohorts hatched in 2010–2020) with 95% CI. X-axis labels correspond to occasions at the ends of focal intervals. On (a) and (b) larger black points are posterior means (circles, solid line) and scaled estimates to 2-week time units (diamonds, dashed line) across all cohorts with corresponding 95% CI. Migrant survival probabilities are not estimated in the interval following the first occasion because all individuals were resident. Some estimates are accompanied by substantial uncertainty, and hence not interpreted.



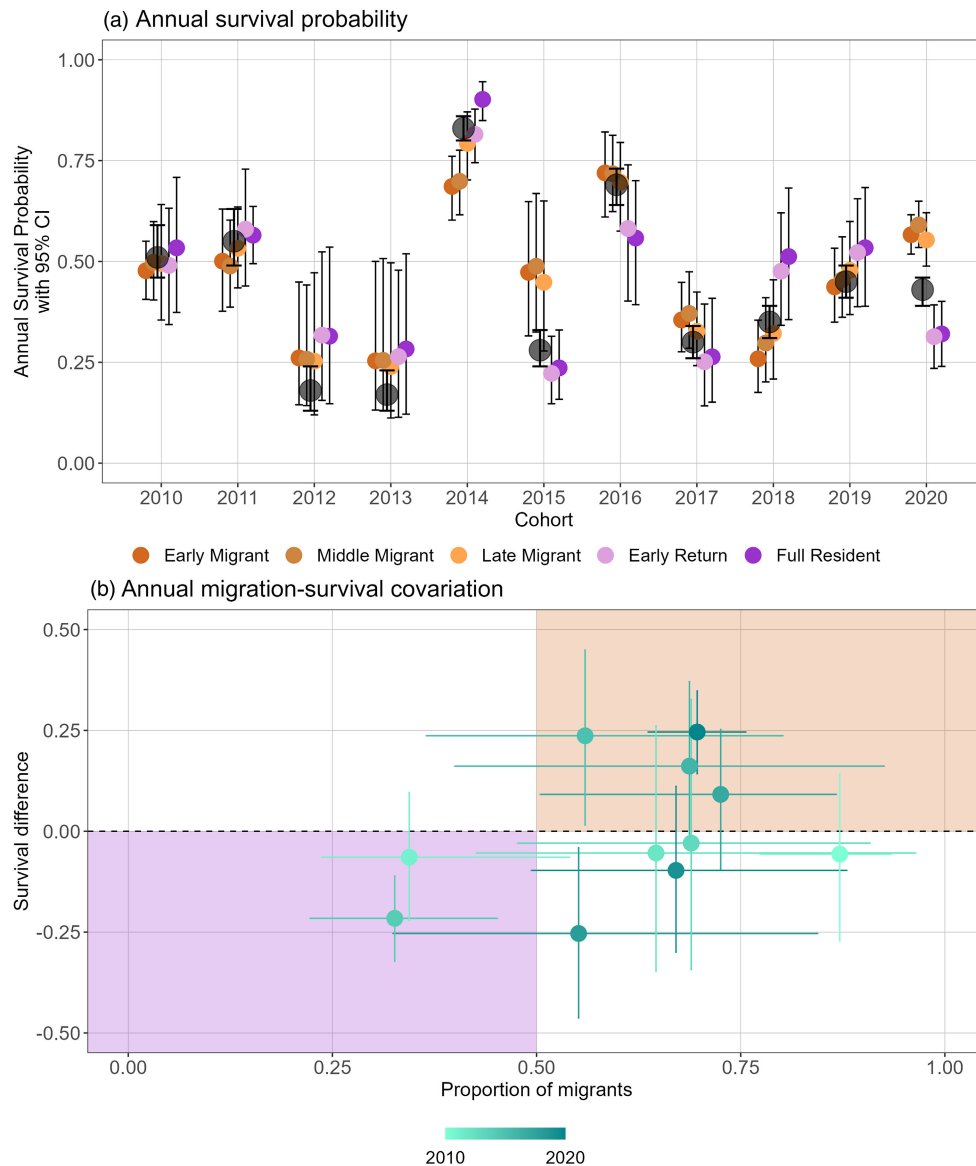
(partly due to previous mortality) and spanned zero, meaning there was no strong evidence of selection.

### 3.3 | Annual survival selection

Annual survival probabilities computed for the five focal tactics (Figure 1f) showed that the magnitude and direction of survival selection on the occurrence and timing of migration varied dramatically among cohorts, generating annual-level fluctuating selection (Figure 4a). For the 2015, 2016, and 2020 cohorts, annual survival probabilities for full residents and early returners were considerably lower than for the other tactics (Figure 4a). Conversely, for the 2014 and 2018 cohorts, annual survival probabilities for full residents, and to some degree early returners, were considerably higher (Figure 4a). These differences reflected episodes of strong

winter selection for migration in 2015 and 2020 and against migration in 2018 (Figure 3). In contrast, for the 2014 cohort, higher annual survival of residents arose because  $\phi_R$  slightly, but consistently, exceeded  $\phi_M$  across multiple intervals (Figure 3). Similarly, the 2016 cohort had on average marginally higher migrant survival across the autumn and winter (Figure 3). Annual survival probabilities did not vary among the focal tactics for the other cohorts (Figure 4a), with uncertainty in 2012 and 2013 caused by substantial mid-winter mortality.

Evidently, the direction and magnitude of selection were not tightly associated with overall annual survival probability across cohorts, which itself varied from  $<0.20$  in 2012 (0.18 [0.13,0.24]) and 2013 (0.17 [0.13,0.23]) to 0.83 [0.80,0.86] in 2014 (Figure 4a). For example, selection for residence occurred in years with high and low annual survival probabilities (2014 vs. 2018), as did selection for migration (2016 vs. 2015).



**FIGURE 4** (a) Estimated first-year survival probabilities for five focal tactics for the 11 focal cohorts. Coloured points show posterior means with 95% CI. Black points show overall annual survival probabilities that were additionally estimated directly for each cohort (Supporting Information S4: Figure S5). (b) Annual survival difference  $\Delta_A$  versus the mid-winter migratory fraction  $m$  for the 11 focal cohorts (light to dark shading denotes cohorts hatched in 2010–2020) with 95% CI. The top right (orange) quadrant indicates  $\geq 50\%$  migrants and  $\Delta_A$  favouring migrants, while the lower left (purple) quadrant indicates  $\geq 50\%$  residents and  $\Delta_A$  favouring residents, denoting the parameter space representing adaptive phenotypic expression.

### 3.4 | Association between survival selection and migratory fraction

The existence of substantial within- and among-cohort variation in both the migratory fraction  $m$  and the magnitude and direction of survival selection  $\Delta$  generates substantial opportunity for (mal) adaptive phenotypic expression of seasonal migration. However, there was no consistent association between  $\Delta$  and  $m$  across cohorts within each interval, nor any consistent association between  $\Delta$  and  $m$  across intervals within each cohort (Supporting Information S8). The mid-winter  $m$  (i.e. December–January), if anything, tended to be positively associated with  $\Delta_A$  (posterior mean regression slope

0.25 [−0.19, 0.68]). However, the evidence for such a relationship was weak, and 5 out of the 11 cohorts were predominantly migrant in winters when selection favoured residents (Figure 4b). Consequently, there was no strong evidence of immediately adaptive phenotypic expression of migration within or among cohorts.

## 4 | DISCUSSION

Understanding and predicting responses of potentially mobile populations to changing seasonal environments requires quantifying variation in the expression of early-life seasonal migration versus

residence, and in associated survival selection, emerging within and among multiple cohorts. However, these attributes have not previously been quantified in any partially migratory system, precluding any inference on magnitudes of (mal)adaptive migratory plasticity and resulting spatio-seasonal dynamics. Insights require advanced analyses of seasonal movements and survival across multiple cohorts of potentially mobile juveniles, but such data have not previously been collected. Our MS-CMR analyses of geographically extensive colour-ring resightings from 11 cohorts of juvenile European shags demonstrate substantial within- and among-cohort variation in the expression of migration, and in the timing, magnitude, and direction of survival selection, through the year following fledging. Yet, despite evidence of temporal variation in the degree of migration versus residence and of fluctuating survival selection, increased expression of migration was not tightly coupled with selection for migration, providing no evidence of immediately adaptive (or strongly maladaptive) early-life variation.

#### 4.1 | Dynamics of early-life migration

Juvenile shags were substantially partially migratory, with grand means of 50%–60% of individuals estimated to be migrant through the year following fledging (Figure 2c). These migratory fractions slightly exceed those estimated for adult shags in the focal population (30%–60%, grand mean 44% [21%,76%], Acker, Daunt, et al., 2021). Such decreased migration from sub-adult to adult stages occurs in other partially migratory species, including major shifts from predominant migration to predominant residence following recruitment (Gowan et al., 2019; Holte et al., 2017; Smith & Nilsson, 1987; Witczak et al., 2024, but see Eggeman et al., 2016). Within-individual shifts could reflect changing physical dominance, with younger individuals more likely to be displaced, and/or lower costs of departure such as no breeding-site loss (Smith & Nilsson, 1987, but see Boyle, 2008). Yet, while ontogeny of migration has been examined in fully migratory systems where juveniles have a refinement period before becoming canalized as adults (Péron & Grémillet, 2013; Sergio et al., 2014; Wynn et al., 2022), both juvenile and adult migratory fractions have rarely been rigorously quantified in partially migratory systems (but see Witczak et al., 2024).

Migratory fractions also varied substantially among juvenile shag cohorts (e.g. posterior means ranged 33%–90% in January; Figure 2c), resulting from substantial temporal variation in departure and return probabilities within and among cohorts (Figure 2a,b). Such variation among consecutive cohorts likely primarily reflects phenotypic plasticity. Since adult shags generally survive to breed in multiple years (mean:  $2.9 \pm 2.2$  SD), consecutive cohorts are offspring of many of the same parents, precluding substantial genetic change between cohorts. Further, quantitative genetic analyses of adults showed only small microevolutionary shifts towards increased migration across years through the study period (Acker, Daunt, Wanless, Burthe, Newell, Harris, Swann, et al., 2023). Accordingly, future analyses with more years of data should aim to identify biotic

and/or abiotic environmental drivers of departure and return probabilities across the geographical system, and explicitly quantify underlying reaction norms. However, typically almost 50% of juvenile shags had already migrated by early September (with movements commonly occurring in late August following fledging in July). Initial migration may therefore be substantially 'pre-emptive', occurring largely in advance of, not directly in response to, major seasonal environmental impacts such as decreasing sea temperatures and the arrival of autumn and winter storms.

#### 4.2 | Dynamics and implications of survival selection

Our analyses showed that the timing, direction, and magnitude of early-life survival selection on seasonal migration versus residence was highly dynamic, with varying short-term and cumulative effects. Survival selection on migration versus residence through the autumn following fledging (i.e. September–November) was generally very weak, yet the posterior mean estimates commonly tended towards higher survival of residents than migrants (Figure 3). Such consistent incremental effects can generate strong overall selection when scaled up over a whole year, even without any detectable short-term episodes of selection. Indeed, high annual survival probability for the full resident tactic in 2014 emerged because  $\phi_R$  was consistently slightly higher than  $\phi_M$  across all intervals through the first year. Incremental effects also generated higher annual survival for the early migrant tactic in 2016. However, in some years, such incremental effects were dwarfed by distinct episodes of strong winter selection, comprising strong selection against residents in 2020 and 2015, and strong selection against migrants in 2018 (Figure 3).

Considering the five focal migratory tactics then highlights how combinations of weak and strong selection occurring on short timeframes can scale up to generate selection on migration timing. For example, in years with consistent weak selection in either direction (e.g. 2014, 2016), survival probabilities for the three intermediate tactics were correspondingly intermediate between full residents and early migrants. Conversely, in years with episodes of strong selection (2015, 2018, 2020), tactic-specific annual survival probabilities diverged according to the timing of selection (Figure 4a). Hence, by considering relatively fine temporal scales, our analyses reveal two different routes to strong annual-level selection, through effectively instantaneous or consistent incremental mortality. This highlights how relatively benign years, versus years with environmental conditions that cause discrete episodes of substantial non-random mortality, can affect overall selection landscapes on the full temporal distributions of phenotypic expression. The distinction between these routes would be obscured if selection were solely estimated at the annual level, which would also impede the identification of environmental drivers of selection. Further, our results highlight how pooling data from multiple years or cohorts, as often done by studies that aim to quantify costs of migration (Buchan et al., 2020), could conceal dynamic

patterns of selection that are not consistent across years in timing or direction (Chevin & Hoffmann, 2017). Our analyses therefore emphasize the need to quantify selection at fine temporal scales, capturing variation both within and among years.

Our evidence that annual juvenile survival probabilities can differ by up to 0.25 in either direction (e.g. strong selection for migration in 2015 and 2020, and strong selection for residence in 2014 and 2018; Figure 4), and that juveniles were substantially partially migratory ( $0 < m \ll 1$ , Figure 2c), implies that observed episodes of strong occasion-specific and annual selection will directly and non-trivially alter population composition within juvenile cohorts, and hence alter current seasonal distributions of individuals. Further, strong selection acted in both directions, constituting fluctuating selection.

Robust evidence of strong temporally fluctuating selection is still relatively rare for any trait in nature (de Villemereuil et al., 2020; Morrissey & Hadfield, 2012). Examples often involve strongly varying environmental conditions (e.g. selection on group size during droughts in cliff swallows, *Petrochelidon pyrrhonota*; Brown et al., 2016, and on boldness due to food availability in Siberian chipmunks, *Tamias sibiricus*; Le Cœur et al., 2015). Fluctuating selection on migration versus residence also occurred in adult shags in the focal system, where annual fitness (comprising combined survival and subsequent reproductive success) of residents exceeded that of migrants in most years, but migrants substantially outperformed residents in years with extremely stormy winters (Acker, Burthe, et al., 2021). Two such winters, 2012–13 and 2017–18, showed very strong survival selection against residence ( $\Delta \approx 0.2$ ; Acker, Burthe, et al., 2021; Acker, Daunt, et al., 2021). Notably, our current results reveal that these storm-induced selection events in adults did not coincide with analogous selection events in juveniles. Rather, selection against residence was weak for the 2017 cohort, and effectively absent for the 2012 cohort (Figure 4a). Conversely, years with strong selection in juveniles (2014–2016 and 2018 cohorts) showed little or no selection in adults (Acker, Daunt, et al., 2021). Our results therefore show that environmentally induced selection on migration is strongly age-specific.

These notable age-specific outcomes can be partly rationalized because the extreme storms caused relatively high mortality across all adults, but particularly residents, causing selection. Our results show that these same events caused even higher mortality across all juveniles regardless of migratory tactic (Figure 4a), perhaps because juveniles are less able to tolerate rough conditions, thereby largely eliminating rather than generating potential for selection (e.g. Chevin & Hoffmann, 2017). Meanwhile, the higher overall juvenile survival probabilities in other winters increased the potential for selection, although the exact environmental drivers of observed incremental and instantaneous selection events remain to be identified.

Episodes of strong temporally varying selection on juvenile migration could shape evolutionary outcomes both by inducing short-term microevolutionary shifts in opposite directions and by altering the distributions of adult phenotypes and genotypes that are available for subsequent selection (e.g. Jebb et al., 2021;

Kasumovic, 2013). Such effects could help maintain additive genetic variation underlying liability to migrate and the resulting potential for future microevolution. However, recent quantitative genetic analyses of migration versus residence in our system revealed moderate additive genetic variance and heritability in juvenile liability to migrate in autumn (i.e. Mid-August–October), but smaller values in winter (i.e. November–March; Fortuna et al., 2024). Hence, the episodes of strong phenotypic selection that we demonstrate occurred at times when relatively little additive genetic variance was expressed. Selection and expression of additive genetic variation were therefore somewhat temporally decoupled within the first year, restricting microevolutionary responses. This further emphasizes the need to estimate selection (and genetic variation) on short seasonal as well as annual timescales, since expected rates of microevolutionary change could otherwise be substantially overestimated.

### 4.3 | Covariation between migration and selection

The substantial within- and among-cohort variation in migratory fraction, and in the magnitude and direction of survival selection, generates substantial potential for adaptive phenotypic expression if juvenile shags express migration or residence at times when these phenotypes are positively selected. However, we found no evidence of strong associations between interval-specific migratory fraction and selection estimates, either within or among cohorts. Further, the among-cohort relationship between mid-winter migratory fraction and annual selection across cohorts was weak (Figure 4b), and >50% of surviving juveniles were typically migrant, even in years when selection strongly favoured residence.

Decoupling of phenotypic expression and selection of labile traits might be expected in highly variable and unpredictable environments, where individuals cannot enact phenotypic plasticity in time to match environmental changes, especially if plasticity is costly (Lande, 2014; Tufto, 2015). This could apply in our system, where migration versus residence is substantially enacted in late summer before conditions in the residence and/or migrant areas could severely deteriorate, and mid-winter movements could have survival costs (e.g. Acker, Daunt, Wanless, Burthe, Newell, Harris, Gunn, et al., 2023), especially when enacted in poor environmental conditions. Such pre-emptive partial migration could then represent some degree of bet-hedging, increasing the probability of lineage survival in highly stochastic environments (e.g. Tufto, 2015).

However, there could still be adaptive reasons why juvenile shags migrate. This could occur if juvenile winter location shapes adult winter location, for example, through site familiarity, and if there is strong selection for migration in adults. Such selection does occur in the focal system, but only in extremely stormy winters (Acker, Burthe, et al., 2021; Acker, Daunt, et al., 2021). Future analyses should therefore aim to quantify the progression of migration versus residence, and the use of key migrant destinations, through successive winters spanning the transition from juvenile to adult; quantify associated selection and selection on plasticity (i.e. on within- and

between-winter changes in location); and thereby decompose the causes of population-level phenotypic shifts in non-breeding season distributions. Such decompositions require further major analyses, which have not yet been fully attempted or achieved for any partially migratory system.

In advance of these future objectives, our current results demonstrate that substantial phenotypic variation in a key life-history trait, seasonal migration versus residence, and substantial variation in survival selection on migration, can arise on short timeframes within and among juvenile cohorts – yet can be substantially decoupled, representing limited immediately adaptive movement. These results highlight that quantifying coupled variation in phenotypes and fitness components on both seasonal and annual timescales will be necessary to understand and predict population outcomes in increasingly variable environments.

### AUTHOR CONTRIBUTIONS

Overarching objectives were conceived by Jane M. Reid and Francis Daunt. Data extraction and analyses were conceived and implemented by Cassandra R. Uglund, Jane M. Reid, and Paul Acker, with input from Rita Fortuna and Thomas R. Haaland. Long-term data were collected and collated by Mark A. Newell, Sarah J. Burthe, Francis Daunt, Sarah Wanless, Michael P. Harris, Carrie Gunn, Timothy I. Morley, Robert L. Swann, and Jane M. Reid. The manuscript was drafted by Cassandra R. Uglund with input from Jane M. Reid. All authors contributed to conceptual development and manuscript editing.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.r4xgxd2mf> (Uglund et al., 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1:** Details of resighting methods and state definitions.

**Appendix S2:** Details of occasion structure and encounter history creation.

**Appendix S3:** Details of prior choices and model constraints.

**Appendix S4:** Details of model checking and validation.

**Appendix S5:** Details of re-scaled occasions.

**Appendix S6:** Details of the migratory fraction.

**Appendix S7:** Details of annual survival tactics.

**Appendix S8:** Details of the covariance between migratory fraction and selection.

**Appendix S9:** Results figures for cohort-specific model parameters.

**Appendix S10:** Details of parameter variances.

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