PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Fortuna R *et al*. 2026 Temporal dynamics of selection on early-life phenotypic plasticity in seasonal migration versus residence. *Proc. R. Soc. B* **293**: 20251063.
https://doi.org/10.1098/rspb.2025.1063

Received: 22 April 2025
Accepted: 5 December 2025

Subject Category:
Evolution

Subject Areas:
evolution, ecology

Keywords:
adaptive plasticity, cost of plasticity, dichotomous trait, fitness, labile trait, multi-state capture–mark–recapture model, partial migration, phenotypic flexibility, reversible plasticity, survival

Author for correspondence:
Jane M. Reid
e-mail: jane.reid@abdn.ac.uk

Temporal dynamics of selection on early-life phenotypic plasticity in seasonal migration versus residence

Rita Fortuna[1], Paul Acker[1], Cassandra R. Ugland[1], Sarah J. Burthe[2], Carrie Gunn[2], Michael P. Harris[2,†], Josie H. Hewitt[2], Timothy I. Morley[3], Mark A. Newell[2], Robert L. Swann[4], Erin A. Taylor[2], Sarah Wanless[2], Francis Daunt[2] and Jane M. Reid[1,3]

[1]Department of Biology, Faculty of Natural Sciences, Norwegian University of Science and Technology, Trondheim, Norway
[2]UK Centre for Ecology and Hydrology, Edinburgh, UK
[3]School of Biological Sciences, University of Aberdeen, Aberdeen, UK
[4]Highland Ringing Group, Tain, Ross-shire, UK

RF, 0000-0002-6049-3690; PA, 0000-0002-3815-772X; CRU, 0009-0009-8686-6473; SJB, 0000-0001-8871-3432; JHH, 0009-0005-7838-8396; SW, 0000-0002-2788-4606; FD, 0000-0003-4638-3388; JMR, 0000-0002-5007-7343

The form, magnitude and temporal dynamics of selection on phenotypic plasticity will fundamentally shape eco-evolutionary responses to environmental variation, but such attributes have not been fully conceptualized or quantified in nature. We provide a general framework that conceptualizes the dynamics of selection on phenotypic plasticity in labile dichotomous traits, which commonly shape behaviour and life history. Specifically, we highlight distinctions between selection on expressed plasticity and selection on resulting phenotypes, effects of phenotypic switches in opposite directions, and the full selection dynamics emerging across temporal sequences of environmental conditions. To enact this framework, we quantified selection on early-life plasticity in the ecologically critical trait of seasonal migration versus residence, by fitting a novel multi-state model to spatio-seasonal resighting data from 13 newly fledged cohorts of partially migratory European shags (*Gulosus aristotelis*). We demonstrate strong and consistent directional selection against early-life plasticity, manifested as substantially lower juvenile survival after phenotypic switches from resident to migrant, but not after reverse switches from migrant to resident. Yet, evident short-term costs translated into weaker and fluctuating selection on plasticity given sequences of phenotypes expressed throughout initial months. We thereby reveal how complex forms of selection against early-life plasticity can arise yet be rapidly attenuated in nature.

1. Introduction

Phenotypic plasticity, as manifested when a genotype or individual expresses different phenotypes in different environments, mediates critical responses to rapid environmental changes [1–4]. When plasticity allows expression of a phenotype that increases individual survival and/or reproductive success (and hence fitness), the resulting phenotype will experience positive selection within a population [5–7]. However, rather than solely acting on expressed phenotypes, selection could also act on the expression of phenotypic plasticity itself. This could occur if the process of changing phenotype induces lower

---

[†]Deceased December 2023

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8230368.

THE ROYAL SOCIETY
PUBLISHING

(or higher) fitness than retaining a constant phenotype [1,8–10]. The magnitude and direction of selection on phenotypic plasticity, and how such attributes vary with environmental conditions, will fundamentally affect the evolutionary dynamics of plasticity, and hence shape the phenotypic responsiveness of populations experiencing environmental changes [1,3,5,11]. However, the forms, magnitudes and dynamics of selection on plasticity are rarely fully conceptualized or quantified, especially in wild populations [12–14], impeding comprehensive prediction of eco-evolutionary outcomes [3,15].

One component of selection on phenotypic plasticity could emerge if individuals that newly express a phenotype via plasticity have higher or lower subsequent fitness than individuals that have expressed that phenotype consistently across preceding timepoints and environments (i.e. phenotypic consistency [8,16,17]). Here, quantifying selection on phenotypic plasticity versus consistency requires distinguishing fitness effects of plasticity from fitness effects of the resulting phenotype. This can be achieved by jointly considering individuals' previous and currently expressed phenotypes (figure 1).

Such fitness effects of plasticity could be particularly strong and dynamic for labile traits that are repeatedly expressed as discrete dichotomous phenotypes, which includes key environmentally sensitive behavioural and life-history traits (e.g. stay versus move; breed versus skip reproduction; freeze versus fly to avoid predation; bask versus seek shade to thermoregulate [18–22]). Here, phenotypic plasticity is expressed as reversible switches between the two alternative phenotypes (which has also been termed 'phenotypic flexibility' [23,24]). Such phenotypic switches could entail substantive fitness effects beyond those associated with the resulting phenotype (figure 1a–c). For example, such effects could stem from inherent ecological risks and/or energetic demands of major physiological or behavioural transitions [25,26]. Furthermore, beyond distinguishing fitness effects of plasticity from fitness effects of resulting phenotypes, fully quantifying the form, dynamics and consequences of selection on expressed plasticity in dichotomous traits requires four additional considerations.

First, the fitness consequences of expressing plasticity might differ between the two directions of phenotypic switch (figure 1a–c). This could occur, for example, if switching in one direction (e.g. transitioning from phenotype A to phenotype B) entails greater or longer-term physiological and/or energetic challenges than switching in the other direction (e.g. transitioning from phenotype B to phenotype A; figure 1a–c). Second, the fitness consequences of a phenotypic switch in either direction could vary with the timing of the switch and/or with prevailing environmental conditions, for example if energetic costs of switching between phenotypes A and B are environment-dependent (figure 1a–c) [10,16]. Overall fitness effects of phenotypic switches, and resulting selection, might therefore vary across successive timepoints within cohorts of individuals, and/or vary among cohorts experiencing different environmental conditions (figure 1b,c). Consequently, third, more complex fitness outcomes and resulting forms of selection could emerge over longer timeframes that encompass multiple episodes of phenotypic expression and potential switching between timepoints (hereafter termed 'phenotypic sequences'; figure 1d). For instance, if expressing alternative phenotypes in different environments is advantageous, individuals that switched phenotypes between timepoints (i.e. expressed a plastic phenotypic sequence) could have higher cumulative fitness than individuals that did not switch (i.e. expressed a canalized phenotypic sequence; figure 1d). Importantly, this could occur even when there are immediate costs of switching, ultimately generating overall selection for phenotypic plasticity over canalization (figure 1d). Yet, fourth, the evolutionary implications of such selection will also depend on the prevalence of plastic versus canalized phenotypic sequences expressed within and across cohorts (figure 1d). Here, high or low fitness of rare phenotypic sequences (figure 1d) may have little immediate impact on phenotypic or evolutionary dynamics. Predicting eco-evolutionary outcomes of plastic responses to environmental changes therefore requires quantifying the full fitness dynamics and prevalence of phenotypic plasticity versus consistency within and across successive episodes of expression (figure 1), but this is rarely achieved [24,27–29].

One labile dichotomous trait that can substantially affect fitness is seasonal migration versus residence, as facultatively expressed in partially migratory populations (including many birds, fish, mammals, amphibians [21,30]). Here, some individuals stay resident at their breeding locations while other individuals temporarily migrate away at different times through the seasonal progression from breeding to non-breeding season [21,30–32]. Hence, occurrences of migration represent plastic individual switches from resident to migrant, for example in response to seasonal changes in daylength, population density, food abundance and/or weather [30,33–35]. Furthermore, particularly given short-distance migration, migrants can potentially return at different times during the non-breeding season, and therefore express a plastic switch from migrant to resident [21]. Resulting variation in location and timing exposes individuals to differing environmental conditions which could affect their survival and/or reproduction, potentially generating strong selection on phenotypic expression of migration versus residence [36–40].

Yet, beyond selection on phenotypes, there is also potential for selection on plasticity in migration versus residence. This would occur if switching between resident and migrant within or between non-breeding seasons causes different survival (or subsequent reproduction) from consistently expressing residence or migration [40,41]. Such effects could be particularly likely following early-life switches by naive juveniles through their first seasonal transitions after the natal period. Here, for example, initial unfamiliarity with new non-breeding season destinations may cause inefficient or risky use of local resources [42–45]. In turn, any resulting early-life selection against plasticity in migration versus residence could constrain population capacity for plastic responses, generating canalized populations that are less responsive to changing environments [21,46,47]. Yet, despite such potential for early-life fitness effects, no studies have quantified selection on early-life plasticity in migration versus residence, precluding inferences on future phenotypic variation and resulting spatio-seasonal population and evolutionary dynamics [21,48,49].

Accordingly, to enact our conceptual framework (figure 1), we quantified differences in survival (and hence survival selection) given expression of phenotypic plasticity or consistency in early-life seasonal migration versus residence. We did this by devising and fitting a novel multi-state capture-mark-recapture (MS-CMR) model to spatio-seasonal ring-resighting data from 13 newly fledged cohorts of European shags (*Gulosus aristotelis*; hereafter 'shags'). We first quantified short-term survival differences between juveniles that consistently expressed versus plastically switched from resident to migrant (and vice

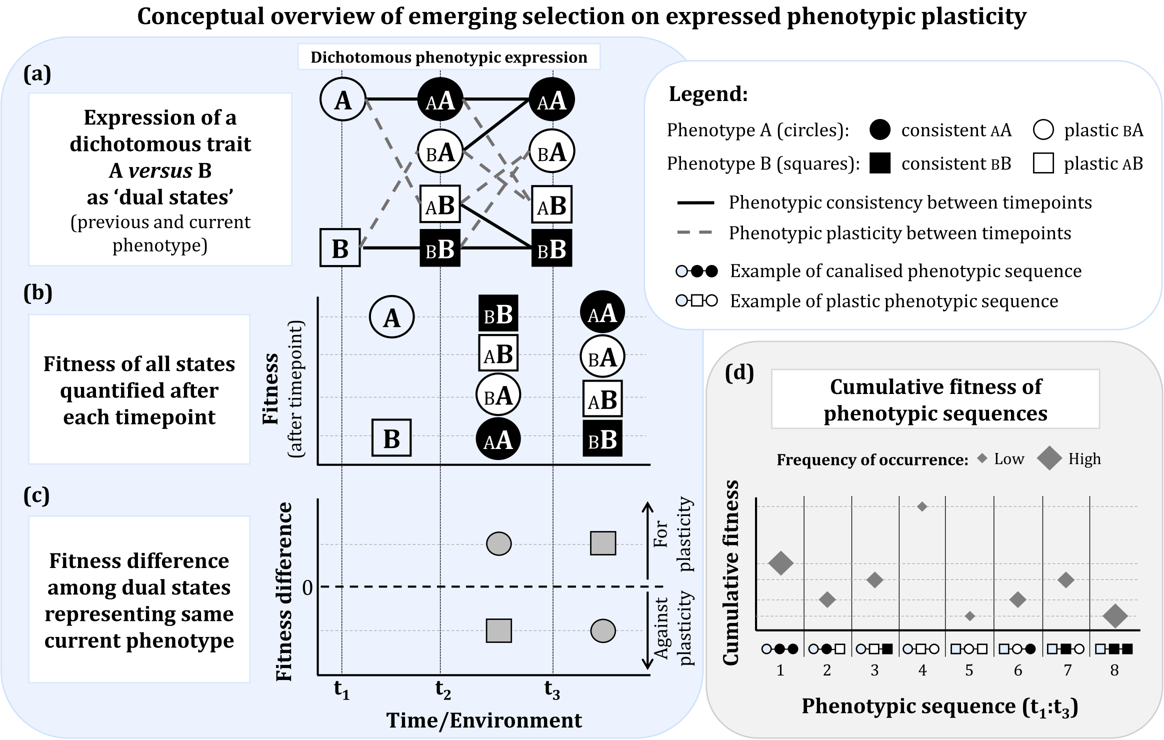

Figure 1. Conceptualization of selection on expressed phenotypic plasticity, envisaging a labile dichotomous trait. (a) Individuals can express either of two discrete phenotypes—A (circles) and B (squares)—along any temporal sequence of environments (timepoints t_1 to t_3). At t_1, only currently expressed phenotypes are known, while at t_2 and t_3 preceding and current phenotypes are shown (first and second letters of the 'dual states' respectively). Here, current phenotypes A and B each comprise two groups of individuals: those that expressed that phenotype consistently from the previous timepoint (black states AA and BB), and those that expressed it through a plastic phenotypic switch from the previous timepoint (white states BA or AB). Solid and dashed lines between timepoints show all possible transitions between states, representing phenotypic consistency and plasticity, respectively. (b) Hypothetical fitness of each (dual) state, quantified after each timepoint (i.e. following expression of phenotypic plasticity or consistency). (c) Resulting fitness differences between plastic and consistent expression of phenotype A (grey circles) and phenotype B (grey squares) after each timepoint, with non-zero differences representing selection on expressed phenotypic plasticity. After t_1, any selection on plasticity cannot be distinguished from selection on current phenotypes. After t_2, fitness differences vary with the direction of phenotypic switch, with higher fitness for phenotypic switches from B to A (implying selection for such plasticity), and lower fitness for phenotypic switches from A to B (implying selection against such plasticity), when compared with consistent expression of A or B, respectively. After t_3, fitness differences are in the opposite directions from the previous timepoint, implying that fitness consequences of phenotypic switches vary with the time and/or environment of expression. (d) Resulting cumulative fitness (*y*-axis) of each canalized or plastic phenotypic sequence expressed from t_1 to t_3 (denoted by sequences of circles/squares numbered 1–8 on the *x*-axis). Cumulative fitness values result from the fitness stemming from each state, at each sequential timepoint (panel (b)). Diamond sizes denote the hypothetical frequency of occurrence of each phenotypic sequence. This example implies strong selection both for and against phenotypic sequences that exhibit greatest plasticity across environments (sequences 4 and 5), depending on the resulting phenotypes expressed. Yet such selection may have little immediate impact on future phenotypic expression, as these sequences have low frequencies of occurrence.

versa) at consecutive timepoints during the months following fledging. We hence estimated magnitudes of survival selection on expression of early-life phenotypic plasticity, and estimated among-cohort variation. To infer population-level consequences of observed selection episodes, we also estimated proportions of individuals that did and did not express plastic switches. Finally, we quantified longer-term cumulative survival across the focal timepoints given plastic or canalized sequences of expression of the alternative phenotypes (figure 1). We demonstrate episodes of notably strong and consistent directional survival selection against plastic switches from resident to migrant, but not vice-versa. Moreover, we show how such effects can translate into substantial among-cohort variation in the strength and direction of selection on longer-term plastic versus canalized phenotypic sequences. We thereby reveal the temporal dynamics of early-life selection on plasticity in seasonal migration versus residence, and highlight how such dynamics could shape overall capacity for adaptive phenotypic variation.

2. Material and methods

(a) System and data collection

A partially migratory shag population breeding on Isle of May National Nature Reserve (hereafter 'IoM') in Scotland (56°11′ N, 2°33′ W) provides a highly relevant and tractable system to quantify survival selection on early-life plasticity in migration versus residence. Partial migration occurs within all life stages, with individuals expressing varying (and hence plastic) resident and/or migrant phenotypes during the non-breeding season (late August–March [41,44]). In particular, newly fledged juveniles can stay resident at their natal colony (IoM) or migrate. Such movements can occur soon after fledging (i.e. August–September), or later via switches from residence to migration through their first autumn–winter (October–December [44]). Accordingly, temporal data can be collected on individuals' locations, thereby tracking resident versus migrant phenotypes expressed at different timepoints from fledging through autumn–winter. This allows survival comparisons between current migrants that recently switched from resident to migrant and current migrants that expressed migration consistently across the focal timepoints. Additionally, since some juveniles return from migration to residence through autumn–winter [44], survival can also be compared between recently returned and consistent residents. Survival selection on expression of phenotypic plasticity can consequently be distinguished from survival selection on currently expressed phenotypes, for both possible directions of phenotypic switch (figures 1 and 2). Since seasonal migration is only expressed during the non-breeding season, and shags do not typically first breed until age 3 years, such survival comparisons represent the total direct selection on the focal episodes of phenotypic plasticity. There is no scope for reproductive selection, except through indirect carry-over effects manifested with time lag of more than 2 years, and conditional on survival to adulthood.

To obtain the required data, during the 2010–2022 breeding seasons (April–August; 13 cohorts), all breeding attempts on IoM were monitored. Over 95% of fledglings were marked with uniquely coded colour rings field-readable from ≤150 m with a telescope (533–1064 ringed individuals per year, mean = 818). Since shags return to shore daily, marked individuals can be observed at coastal roost sites year-round, allowing direct observation of individuals' current locations and hence current status as resident or migrant. Accordingly, during the 2010–2024 non-breeding seasons, we undertook regular (approximately biweekly) resighting surveys on IoM and adjacent day roosts to detect current residents (defined as individuals roosting on IoM at night; electronic supplementary material, A1). We also undertook similar surveys at core roost sites spanning the north-east UK coast (ranging 100–500 km from IoM) to detect current migrants (defined as not returning to IoM at night; electronic supplementary material, A1). These sites are reachable from IoM within 1–2 days by juvenile shags, and encompass their main winter range [37,44,50]. Ad hoc resightings at other sites (spanning approx. 800 km from IoM) were also collected, including citizen science contributions (electronic supplementary material, A1). Overall, this major effort generated 32 376 first-year resightings spanning 10 788 colour-ringed juveniles fledged during 2010–2022. Since natal dispersal from IoM is uncommon and short-distance (approx. 95% of individuals recruit to IoM or nearby colonies [51]), longer distance early-life movements can be validly interpreted as migration [44,52].

Ringing was licensed by the British Trust for Ornithology (permits A400, A4607). Fieldwork on IoM was annually licensed by NatureScot.

(b) Multi-state capture-mark-recapture model with dual states

We devised a novel MS-CMR model to estimate survival probabilities of current resident and migrant individuals, conditional on their preceding phenotype (i.e. with 'dual states' defining the individual's preceding and current phenotypes [53]). These focal probabilities were estimated from the resighting data, while accounting for spatial and temporal variation in detection probabilities (figure 2a; electronic supplementary material, A2). Fitness effects of phenotypic plasticity, and resulting components of selection, were estimated as the differences in survival between consistent and plastic expression of residence, and between consistent and plastic expression of migration, through two focal time periods. These time periods span juveniles' first transition from the natal breeding season to autumn–winter (figure 2a), encompassing known periods of juvenile movement (mostly from August–December) and substantial winter mortality [44].

To achieve these objectives within a discrete-time MS-CMR model, we defined five primary 'occasions' spanning the natal breeding season (June–July, when chicks are typically ringed before fledging) to the following March (approx. 8 months post-fledging; figure 2). Phenotypes (represented as 'states') are expressed at each occasion, while survival and movement probabilities are estimated for intervals between consecutive occasions (figure 2b). Occasion durations varied to ensure adequate detection probabilities at resident and migrant sites, given temporal variation in field resighting efforts (figure 2a,b; electronic supplementary material, A1) [52].

Occasion 1 comprises the natal period (June–mid August), when all fledglings are on IoM, and hence in the 'resident' R state. In the interval between the first and second (mid-August–September) occasions, individuals that survive (with probability ϕ) can transition to the new migrant 'ʀM' state with probability ε of departing from IoM, or remain resident 'ʀR' with probability $1-\varepsilon$ of not departing (figure 2a–c; electronic supplementary material, A2). In these initial 'dual states', the small first and large second letters denote the phenotypes expressed at the preceding and current occasions respectively. From occasion 2 to 3 (October), individuals survive with probability ϕ that depends on their dual state (ʀR or ʀM). However, at this point, any difference in survival between the dual states and resulting selection on plasticity cannot be distinguished from selection on currently expressed phenotypes (R or M). This is because the required comparator states 'ᴍR' and 'ᴍM' do not exist at occasion 2 (figures 1 and 2), since all residents have been consistently resident since occasion 1, and all migrants have just switched from residence (and cannot have been migrant previously).

We therefore define two further occasions between which plastic and consistent phenotypic expression can be distinguished, and subsequent survival estimated. Here, surviving residents from occasion 2 can again remain resident or migrate, and hence enter updated dual states ʀR or ʀM, respectively, at occasion 3 (figure 2b). Meanwhile, surviving migrants from occasion 2 can potentially return home with probability ω and hence enter state ᴍR, or remain migrant with probability $1-\omega$ and hence enter state ᴍM (figure 2b). Survival from occasion 3 to 4 (November–December) can then be compared between current migrants that were and were not already migrants on the preceding occasion (ᴍM versus ʀM), and between current residents that were and were not previously resident (ʀR versus ᴍR; figure 2b). All else being equal, resulting survival differences represent survival

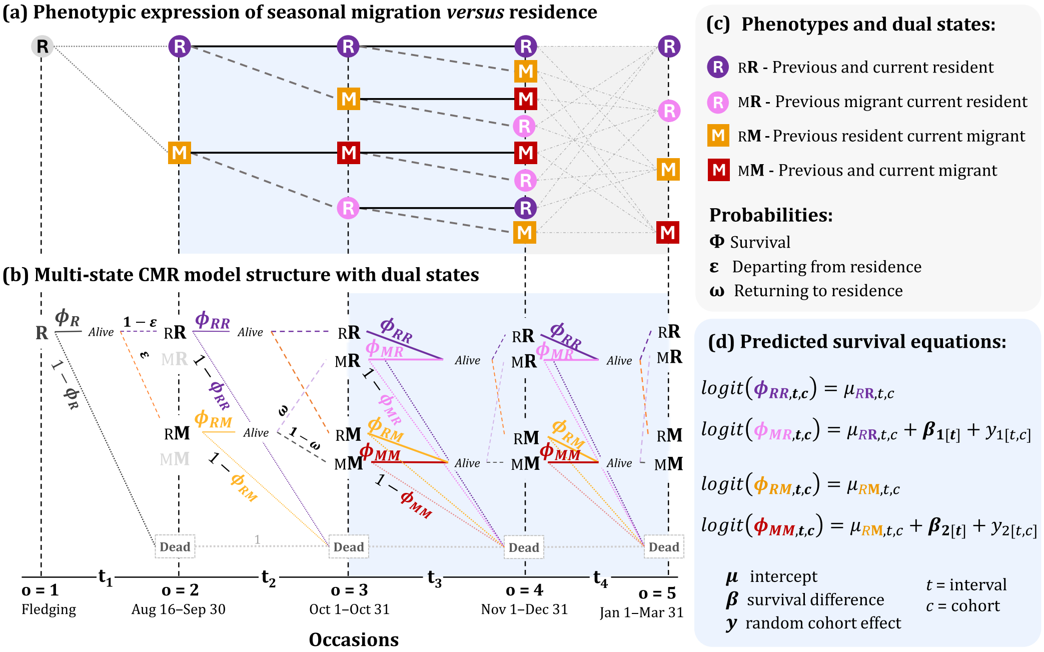

Figure 2. Conceptual and technical overview of the multi-state capture-mark-recapture (MS-CMR) model with 'dual states' used to estimate survival effects of expressed phenotypic plasticity in seasonal migration versus residence. (*a*) Representation of migrant (squares, M) and resident (circles, R) phenotypes expressed through five occasions (from fledging to March of the following year), generating phenotypic sequences through autumn–winter that incorporate episodes of phenotypic plasticity (dashed lines) and/or consistency (solid lines, analogous to figure 1a). Current residents can be previously resident (consistent rR, purple) or previously migrant (plastic mR, pink). Similarly, current migrants can be previously migrant (consistent mM, red) or previously resident (plastic rM, yellow). Intervals used to define the dual states for survival comparisons are shaded blue. (*b*) State-transition structure of the MS-CMR model, with coloured lines showing possible survival (solid lines) and movement (dashed lines) transitions between dual states, and their associated probabilities which are interval (*t*) and cohort (*c*) specific. The bottom time axis specifies the five occasions with start and end dates (*o*), thus varying in length, and the four intervals between occasions (t_1 to t_4; electronic supplementary material, A1). Phenotypes (and hence states) are expressed at each occasion, while survival and movement probabilities are estimated for intervals between consecutive occasions. Therefore, survival differences between focal dual states were estimated in the intervals between occasions 3–4 (t_3), and 4–5 (t_4) (blue shade in panel (*b*)). Cumulative survival of phenotypic sequences is measured between occasions 1–5 (i.e. through intervals t_1–t_4). (*c*) Summary and definitions of dual states and probabilities. (*d*) Logistic regression equations predicting survival probabilities and differences between focal dual states (i.e. mR versus rR, and mM versus rM) at t_3 and t_4, with definitions of parameters and indices. Full details of model specifications are in electronic supplementary material, A1–A2.

selection following expression of phenotypic plasticity between occasions 2 and 3. Equivalent comparisons of survival from occasion 4 to 5 (January–March) can be achieved for phenotypes and plasticity expressed between occasions 3 and 4 (assuming no protracted effects of phenotypes expressed before occasion 3; figure 2b).

The survival differences following plastic and consistent phenotypic expression (i.e. rR versus mR, and rM versus mM) were estimated across all cohorts, by fitting logistic regressions within the MS-CMR model (figure 2b–d). Specifically, for each of the two focal intervals (t_3 and t_4) and each cohort (c), we modelled the logit of survival probability for the two states that already existed at occasion 2 (rR and rM), as interval-by-cohort specific intercepts $\mu_{\mathbf{RR},t,c}$ and $\mu_{\mathbf{RM},t,c}$ (figure 2d). Then, logit-scale survival of the comparator state for residents, mR, was modelled as the sum of $\mu_{\mathbf{RR},t,c}$ and an interval-specific effect representing the difference between the rR and mR states across cohorts, $\beta_{1[t]}$ (figure 2d). Hence, positive $\beta_{1[t]}$ implies higher survival of the plastic dual state (i.e. of mR compared with rR). Similarly, the logit-scale survival of the comparator state for migrants, mM, was modelled as the sum of $\mu_{\mathbf{RM},t,c}$ and an interval-specific effect representing the difference between rM and mM across cohorts, $\beta_{2[t]}$ (figure 2d). Here, positive $\beta_{2[t]}$ implies higher survival of the consistent dual state (i.e. of mM compared with rM). To facilitate interpretation, the sign of $\beta_{2[t]}$ is switched in the Results so that positive β values always represent higher survival of the plastic states. Note that $\beta_{1[t]}$ and $\beta_{2[t]}$ quantify survival differences after expression of the migrant phenotype, and hence exclude any previous mortality incurred during migration (which is embedded within the survival probabilities estimated for the previous interval). We additionally modelled logit-scale interval-specific random cohort effects, $y_{1[t,c]}$ and $y_{2[t,c]}$ (with standard deviations $\sigma_{y1[t]}$ and $\sigma_{y2[t]}$), to quantify among-cohort variation in $\beta_{1[t]}$ and $\beta_{2[t]}$ (figure 2d).

We used the logit-scale parameter estimates to calculate interval-specific survival probabilities for each dual state. Although $\beta_{1[t]}$ and $\beta_{2[t]}$ were estimated as constant means across cohorts, among-cohort variation in the other parameters (figure 2d) allows emergence of among-cohort variation in survival probabilities of mR and mM ($\phi_{\mathbf{MR},t,c}$ and $\phi_{\mathbf{MM},t,c}$, analogous to $\phi_{\mathbf{RR},t,c}$ and $\phi_{\mathbf{RM},t,c}$). We did not model sex effects on movement or survival, since juveniles' sexes are typically unknown. However, frequencies of migration and associated selection do not differ markedly between adult females and males in our system [37,41].

We modelled full interval- and cohort-dependence in departure and return probabilities ($\varepsilon_{t,c}$ and $\omega_{t,c}$), thereby capturing the full temporal pattern of movements, and hence switches between resident and migrant. Movement probabilities were assumed equal for states representing the same current phenotype (rR and mR; rM and mM; electronic supplementary material, A2), implying no effect of preceding state on subsequent movement (figure 2b). By contrast, survival was conditional on each dual state (s) for each interval and cohort (i.e. $\phi_{s,t,c}$; figure 2b). Full details of state-transition probabilities are in electronic supplementary material, A2.

To account for occasion- and cohort-specific variation in detection between residents and migrants, alive individuals could be resighted in their current state with probabilities $p_{s,o,c}$ (i.e. observed as resident or migrant or not observed, electronic supplementary material, A2). Detection probabilities relate to individuals' current phenotype, and are assumed independent of preceding phenotypes. Dead individuals had $p = 0$. To account for spatial heterogeneity in $p_{s,o,c}$, the underlying model structure included two groups of migrant destinations that were and were not intensively surveyed (electronic supplementary material, A2; [44,52]). Finally, to ensure that all parameters through the focal occasions 1–5 were identifiable, we modelled a sixth 'ever after' occasion utilizing all subsequent individuals' resightings (electronic supplementary material, A2) [52]. Parameter estimates associated with this occasion, and the interval between occasions 5–6, are not biologically interpretable (electronic supplementary material, A2).

(c) Model analyses

We formulated individual encounter histories as occasion-specific summaries of resightings of all 10 788 colour-ringed shags, taking each individual's latest observation within each occasion after occasion 1 (electronic supplementary material, A2) [44,52].

The Bayesian MS-CMR model was implemented in Stan v. 2.26.1, using package *rstan* v. 2.26.13 [54,55] in R 4.2.2 [56]. We defined vague uniform priors spanning 0–1 for all directly estimated movement, survival and detection probabilities [52], except for a weakly informative prior implying low detection probability at non-intensively surveyed sites (electronic supplementary material, A2–A3). We specified weakly informative normal and half-student's *t* distributions for the logit-scale parameters and standard deviation priors, as typically recommended (electronic supplementary material, A3) [57]. Prior sensitivity analyses showed that differing priors generated equivalent conclusions (electronic supplementary material, A3).

We ran $n = 4$ chains each comprising 1000 warm-up and 2000 monitored iterations, yielding 8000 posterior samples for inference. Diagnostics indicated no sampling problems and satisfactory convergence, with $\widehat{R}<1.01$ and effective sample sizes $>100n$ for all parameters (electronic supplementary material, A3). Fitting our model to simulated datasets with expected $\beta = 0$ confirmed that the model and estimation did not return spurious evidence of non-zero effects (electronic supplementary material, A4).

Posterior distributions are summarized as posterior means with 95% credible intervals (95% CI). Survival differences between dual states are evidenced when 95% CIs for β exclude zero. To illustrate overall biological effects, we additionally computed grand means (and 95% CIs) of survival probabilities across cohorts, for each dual state and interval. We primarily present estimates of ϕ and β, with movement and detection probabilities summarized in electronic supplementary material, A6.

(d) Biological inferences

The longer-term effects of phenotypic plasticity expressed at a particular time will depend on the proportion of juveniles expressing plasticity, and also on the cumulative survival probability resulting from expression of plastic versus canalized phenotypic sequences across subsequent timepoints (figure 1). Accordingly, we computed and summarized the full posterior distributions of two further sets of derived parameters (electronic supplementary material, A5).

First, for each cohort, we computed the expected proportion (i.e. prevalence of expression) of each dual state among individuals alive at each occasion, given estimated values of $\varepsilon_{t,c}$, $\omega_{t,c}$ and $\phi_{s,t,c}$ up to that occasion (electronic supplementary material, A5). Second, we computed cumulative survival probabilities to occasion 5 (i.e. from fledging to the end of winter in January–March) for all possible phenotypic sequences expressed through occasions 1–4 (i.e. canalized residence and canalized migration after fledging, and all possible forms of expressed plasticity). These cumulative probabilities were calculated as the product of the cross-sectional $\phi_{s,t,c}$ values (incorporating the dual states; electronic supplementary material, A5). We then tested for overall differences in cumulative survival probability among plastic versus canalized phenotypic sequences by calculating grand posterior mean differences between pairs of sequences, and computing posterior probabilities that these differences exceeded zero ($\mathrm{P_{diff}} > 0$). Finally, we estimated the probability of occurrence of each phenotypic sequence by quantifying cumulative movement probabilities for each sequence and cohort as the product of $\varepsilon_{t,c}$ and $\omega_{t,c}$ estimates (electronic supplementary material, A5).

3. Results

(a) Survival differences between dual states

Across all 13 cohorts combined, survival probabilities were notably lower for migrants that had just switched from residence (rM) than for concurrent migrants that were already migrants at the preceding occasion (mM). Specifically, the logit-scale effect of rM relative to mM on survival between occasions 3–4 (conditional on phenotypes expressed in occasions 2 and 3) was strongly negative ($\beta_{2[t3]} = -1.48$ [−2.43,−0.64]). This demonstrates a survival disadvantage of phenotypic plasticity (figure 3b), manifested as substantially lower survival probabilities for rM than mM (grand means 0.81 [0.74,0.87] and 0.94 [0.90,0.97], respectively; figure 3a). Survival between occasions 4–5 (conditional on phenotypes expressed in occasions 3 and 4) also tended to be lower for rM than mM, although the logit-scale effect was smaller, with 95% CIs that spanned zero ($\beta_{2[t4]} = -0.45$

[−1.25,0.24]; figure 3a,b). Resulting grand mean survival probabilities for rM and mM were 0.72 [0.64,0.79] and 0.78 [0.74,0.83] respectively, and hence were lower overall (and varied more among cohorts) than for the interval between occasions 3–4 (figure 3a).

By contrast, through the same occasions and intervals, there was no evidence of survival differences between consistent residents (rR) and concurrent residents that had just returned from migration (mR). Logit-scale survival effects for intervals between occasions 3–4 and 4–5 were both positive, but the 95%CIs spanned zero ($\beta_{1[t3]}$ = 0.39 [−0.96,2.06] and $\beta_{1[t4]}$0.38 [−0.73,1.61]; figure 3b). Accordingly, survival probabilities for rR and mR were similar (figure 3a), with grand means of 0.93 [0.89,0.96] and 0.93 [0.84,0.99] respectively between occasions 3–4, and 0.73 [0.68,0.79] and 0.77 [0.63,0.90] between occasions 4–5.

Hence, overall, grand mean survival probabilities were higher for rR, mM and mR than for rM, especially between occasions 3–4 (figure 3a). This implies an episode of strong directional survival selection against plastic switches from resident to migrant, but not against return switches from migrant to resident, during juveniles' first seasonal progression through autumn–winter (figure 3a,b). Furthermore, survival effects did not vary substantially among cohorts: the interval-specific standard deviations representing among-cohort variation in the survival differences between rM and mM, and between rR and mR, were small (median σ_y ~ 0.5; electronic supplementary material, A6).

(b) Prevalence of expression of dual states

On average across cohorts, migration probability soon after fledging was approximately 0.5, generating similar grand mean proportions of rR and rM in occasion 2 (figure 4). Subsequent switches from resident to migrant meant that the proportions of rM were non-trivial in occasions 3 and 4 (grand means 0.17 [0.13,0.21] and 0.13 [0.10,0.17] respectively). Hence, the observed episodes of selection against rM (figure 3) caused non-trivial mortality. As might be expected, the probabilities of early return from migrant to resident were smaller, generating grand mean proportions of mR at occasions 3 and 4 of 0.08 [0.06,0.10] and 0.05 [0.04,0.07], respectively. Consistent expression of residence (rR) and migration (mM) between occasions were consequently common (figure 4a,b; electronic supplementary material, A6).

(c) Cumulative survival differences among phenotypic sequences

Despite evidence of lower survival following switches from resident to migrant, there were only small survival differences among longer-term phenotypic sequences (spanning approx. eight months from fledging) that included these phenotypic switches (RRMM and RRRM) versus canalized migration after fledging (RMMM; figure 5). Here, magnitudes and directions of survival differences among these sequences clearly varied among cohorts (figures 3 and 5), despite the cumulative estimation uncertainty. Specifically, cumulative survival for RRMM and/or RRRM was lower than for RMMM in several cohorts (2011, 2012, 2015, 2016, 2018 for RRRM, 2017, 2019, 2020 for RRMM; figure 5). However, these tendencies disappeared or were reversed in other cohorts (2018 for RRMM, 2010 and 2019 for RRRM, 2022 for both; figure 5). This resulted in small grand mean survival differences between RMMM and RRMM (−0.06 [−0.11,−0.02], $P_{diff>0}$=0), and even smaller differences between RMMM and RRRM that did not differ from zero (−0.03 [−0.0.9,0.04], $P_{diff>0}$=0.22; figure 5).

Hence, overall across cohorts, there is no strong evidence that one phenotypic sequence systematically had highest or lowest survival probability through occasions 1–5 (figure 5): all grand means are approximately 0.56, with the highest value for RMMM (0.59 [0.56,0.63]), and the lowest for RRMM (0.53 [0.48, 0.57]). Instead, there was strong among-cohort variation in the direction and strength of survival selection across phenotypic sequences (figure 5; electronic supplementary material, A6).

Probabilities of occurrences of the phenotypic sequences were similar across cohorts. Specifically, canalized residence (RRRR) and canalized migration following fledging (RMMM), and switching from residence to migration in October (RRMM), were the most prevalent (grand mean probabilities 0.38 [0.33, 0.43], 0.26 [0.22, 0.29] and 0.14 [0.11, 0.18], respectively; figure 5). Meanwhile, sequences that included multiple phenotypic switches were overall rare (e.g. RMMR, RMRR, RMRM and RRMR all ≤0.05; figure 5; electronic supplementary material, A6).

4. Discussion

The form, magnitude and temporal dynamics of selection on expression of phenotypic plasticity could substantively shape populations' capacities to respond to rapidly changing environments. Yet, such attributes are rarely quantified, especially for labile dichotomous traits expressed through early-life stages. We demonstrate notably strong and consistent selection against early-life expression of plasticity, manifested as reduced survival following phenotypic switches from resident to migrant in juvenile European shags. However, there was no evidence of analogous survival differences following reverse switches from migrant to resident. Furthermore, despite consistent episodic effects, selection on longer-term plastic versus canalized phenotypic sequences expressed from fledging through winter varied in direction and magnitude among cohorts, with overall weak effects of phenotypic switches on cumulative survival. These results reveal that early-life phenotypic plasticity in the ecologically critical trait of seasonal migration versus residence entails a proximate survival cost, and also demonstrate how such costs can be rapidly absorbed into longer-term fluctuating selection on canalized and plastic sequences of phenotypic expression.

By estimating survival probabilities of individuals expressing the same current phenotype but different preceding phenotypes, our MS-CMR model demonstrated that considerable proportions of juveniles experienced lower survival after switching from resident to migrant, compared to juveniles that were consistently migrant through focal occasions. The negative effect

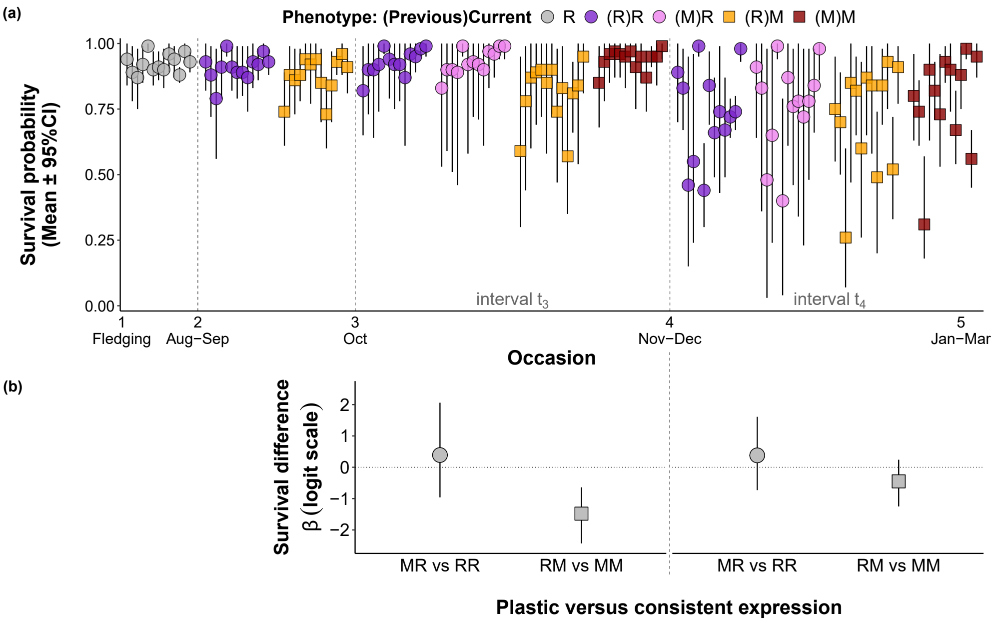

Figure 3. (a) Posterior mean survival probabilities (with 95% CIs) for each dual state, for each cohort fledged during 2010–2022 (points ordered left to right within each coloured block), through the intervals between consecutive occasions. Circles denote current residents, with grey for residents at fledging, purple for rR and pink for mR. Squares denote current migrants, with yellow for rM, and red for mM. (b) Logit-scale posterior mean survival differences (with 95% CIs) between plastic and consistent phenotypic expression, for current residents (β_1; i.e. mR versus rR, grey circles), and for current migrants (β_2; i.e. rM versus mM, grey squares) estimated for intervals t_3 and t_4. Values above and below zero respectively represent positive and negative survival effects of expressing phenotypic plasticity.

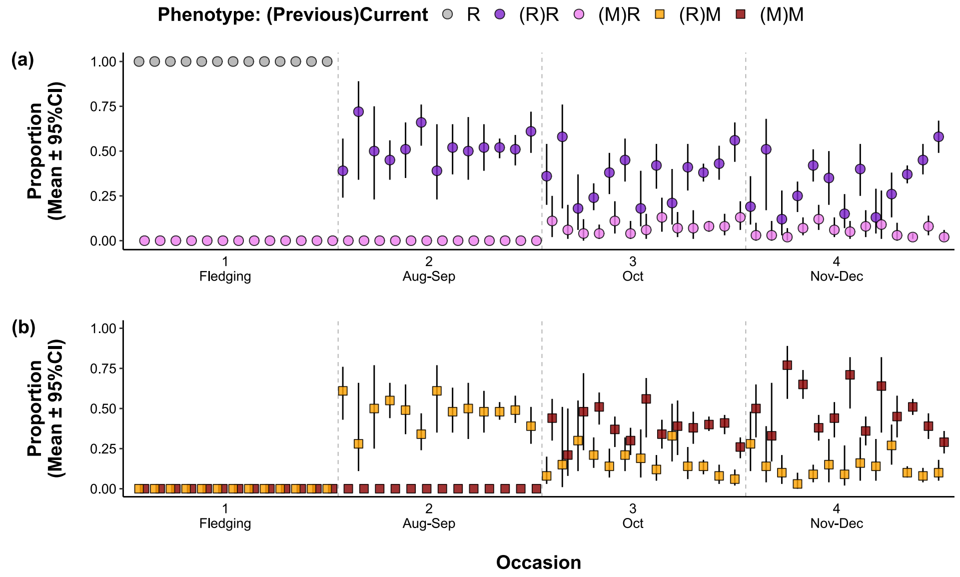

Figure 4. Posterior mean proportion of each dual state at each occasion (with 95% CIs) for cohorts fledged during 2010–2022 (coloured points ordered left to right within each occasion). (a) Proportions of rR (purple circles, with initial grey circles representing residents at fledging) and mR (pink circles). (b) Proportions of rM (yellow squares) and mM (red squares).

of switching was notably strong for survival through late autumn, with a reduction in grand mean survival probability of ca. 0.13 for plastic versus consistent migrants. Importantly, during this period, the grand mean survival probabilities of residents (regardless of preceding phenotypes) and consistent migrants are high and similar (figure 3). Our analyses therefore reveal strong survival selection against early-life expression of plastic phenotypic switches from resident to migrant, without any further selection on currently expressed phenotypes.

While dynamics of selection on plasticity are rarely quantified in wild populations, meta-analyses of available data, predominantly concerning short-term effects in experimental systems, suggest that fitness costs of plasticity are generally small and mostly detectable in 'stressful' low fitness environments [10,13]. In comparison, in our field study, negative effects

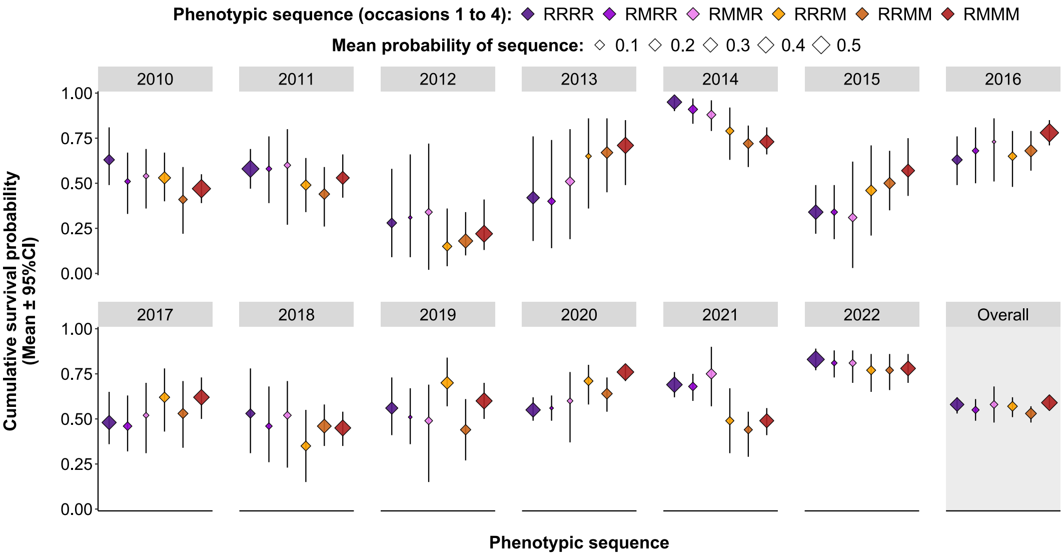

Figure 5. Posterior mean (with 95% CIs) cumulative survival probabilities from fledging to occasion 5 (approx. eight months post-fledging) for each possible phenotypic sequence expressed across occasions 1–4. Cumulative survival was estimated for each cohort (2010–2022) as the product of the respective cross-sectional survival estimates for each dual state for intervals t_1–t_4, and as a grand mean (and 95% CIs) across cohorts ('overall'). The phenotypic sequences are shown by different colours, as ordered and summarized in the legend (four-letter sequences represent the phenotypes expressed at each occasion). Diamond sizes represent the cohort-specific (or overall) mean probability of expression of each phenotypic sequence, estimated as the product of the respective cross-sectional movement probabilities for intervals t_1–t_3. Cumulative survival probabilities are not shown for extremely rare phenotypic sequences (grand mean probability of expression <0.03; electronic supplementary material, A5).

of migratory plasticity were particularly strong in autumn, when survival is generally high, and less evident through winter, when survival is overall lower due to harsher environmental conditions that impede foraging and thermoregulation (figure 3). Furthermore, observed effects were broadly consistent across cohorts, despite considerable among-cohort variation in mean survival probability (figure 3) which presumably reflects among-year variation in environmental quality (e.g. prey abundance and weather conditions) [37,44].

The observed survival differences between current migrants with preceding resident versus migrant phenotypes do not stem from mortality during migration, because our current analyses compare survival after arrival at migrant sites. They could partly reflect carry-over effects of energy expended during migration, but such effects may be small since shag migration is relatively short distance, and we found no evidence of lower juvenile survival following similar movements back to residence. The survival differences are also unlikely to arise because late migrants move to lower-quality sites, since observations of juveniles, alongside analyses of adults, suggest that destinations do not vary markedly with migration timing [37]. They could potentially reflect within-cohort age effects, if younger juveniles (i.e. fledged later within a year) migrate later and are also less likely to survive (e.g. due to poorer condition and/or competitive abilities). However, post hoc analyses showed that survival differences between consistent and plastic migrants remained quantitatively similar after accounting for age (electronic supplementary material, A7). Rather, a more plausible mechanism arises because, unlike switches back to residence, recent migration by naive juveniles places them in unfamiliar locations, with no knowledge of local foraging or roosting sites. Resulting energetic challenges could reduce survival probabilities of newly arrived migrants, potentially exacerbated by competition with earlier migrants and/or local residents. These hypotheses could, in the future, be tested by collecting higher temporal and spatial resolution data on behaviour and space use of co-existing migrants that arrived at different times (e.g. using targeted tracking technologies [45,58]). This could reveal exact timeframes over which ecological, physiological, behavioural and survival impacts of recent migration might act.

Irrespective of the underlying mechanisms, the observed episodes of survival selection against early-life plasticity could impact a population's subsequent spatio-seasonal distribution and environmental responsiveness, if they translate into substantial selection against plasticity through longer periods and across environments. However, our results highlight that such translation is not inevitable. Rather, survival differences among longer-term canalized and plastic phenotypic sequences (spanning the autumn and winter following fledging) varied greatly among cohorts. There was thus overall fluctuating selection on phenotypic sequences, likely caused by spatio-temporal environmental variation between resident and migrant sites [37,44]. Hence, the overall survival probability of phenotypic sequences that included plastic switches from resident to migrant during autumn–winter was only slightly lower than for canalized migration after fledging. The evident short-term survival costs of plasticity are therefore attenuated when considering survival over slightly longer time periods of phenotypic expression across environments. These overall outcomes also imply that there are no consistent intrinsic differences in survival among individuals that migrated or returned at different times.

These results provide a valuable illustration that observations of costs of plasticity do not necessarily mean that plasticity is maladaptive overall, because phenotypic switching may result in phenotypes that increase subsequent fitness. Accordingly, even if expressing phenotypic plasticity induces instantaneous fitness costs, plastic strategies can be favoured by selection across environments [2,8,59]. Yet, how such principles typically play out in practice has rarely been evaluated, because the dynamics and cumulative impacts of selection on plasticity are rarely quantified (figure 1), particularly for labile traits expressed in nature [3,12–14]. Our study therefore provides a notable example of the emergence and attenuation of selection on plasticity in spatially and temporally varying environments.

Yet, fully predicting the ultimate population dynamic and evolutionary impacts of plasticity in seasonal migration versus residence will require substantial future data and analytical developments. First, it will entail quantifying forms of selection on phenotypic switches through sub-adult years and into adulthood, thereby revealing how dynamic early-life, and ultimately life-long, selection on expressed plasticity can shape overall capacity for adaptive phenotypic variation [37,41]. Moreover, quantitative predictions of evolutionary dynamics will require quantifying how selection on expressed phenotypes and phenotypic plasticity affects evolution of underlying 'liabilities' to migrate [35,60,61]. This is because the dichotomous phenotypic trait of migration versus residence is appropriately conceptualized as a quantitative genetic threshold trait, where expression of the alternative phenotypes is determined by latent liability values that fall above versus below a fixed threshold [60,62]. Combinations of genetic and environmental effects on liabilities then cause expression of phenotypic plasticity [41,52], and selection against such plasticity could in turn generate complex forms of selection on the underlying liabilities. Ultimately, there could be selection against additive genetic values that generate liabilities close to the threshold, where environmental effects are most likely to result in phenotypic switches (theoretical predictions in [61,63]). In juvenile shags, previous analyses demonstrated non-zero, and season-specific, additive genetic variances and heritabilities in liability to migrate [52], implying some potential for evolutionary responses to selection on phenotypic plasticity. The future ambition of comprehensively understanding such outcomes is enabled by our current conceptual framework, models and results, which rationalize the dynamics of selection on phenotypic plasticity in a labile dichotomous trait. We thereby reveal that consistent short episodes of strong directional selection against expressed phenotypic plasticity can translate into fluctuating net selection over longer periods in natural environments.

Ethics. Ringing was licensed by the British Trust for Ornithology (permits A400 and A4607). Work on IoM was annually licensed by NatureScot.

Data accessibility. Data and code to reproduce the analyses and figures are publicly available in Dryad [64] and Zenodo [65].

Supplementary material is available online [66].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. R.F.: conceptualization, data curation, formal analysis, methodology, software, validation, visualization, writing—original draft, writing—review and editing; P.A.: formal analysis, methodology, software, validation, writing—review and editing; C.R.U.: data curation, methodology, writing—review and editing; S.J.B.: data curation, investigation, writing—review and editing; C.G.: data curation, investigation; M.P.H.: investigation; J.H.H.: data curation, investigation; T.I.M.: data curation, investigation; M.A.N.: data curation, investigation; R.L.S.: investigation; E.A.T.: data curation, investigation; S.W.: investigation, writing—review and editing; F.D.: funding acquisition, investigation, project administration, supervision, writing—review and editing; J.M.R.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was funded by Research Council of Norway (grants 223257 and 313570), UK Natural Environment Research Council (awards NE/M005186/1, NE/R000859/1 and UKCEH National Capability for the UK Challenges programme NE/Y006208/1), European Research Council (Advanced Grant EcoEvoMove 101140637), NTNU and University of Aberdeen. Views and opinions expressed are those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Council Executive Agency. Neither the European Union nor the granting authority can be held responsible for them.

Acknowledgements. We thank everyone who contributed to long-term field data collection, particularly: Raymond Duncan, Sarah Fenn, Hannah Grist, Carl Mitchell, Calum Scott, Jenny Sturgeon, Moray Souter, John Anderson and Harry Bell for winter resightings; Ruth Dunn, Ella Benninghaus, Sam Langois, Sophie Bennett and Marine Quintin for long-term ringing; NatureScot for allowing work on the Isle of May National Nature Reserve; Isle of May Bird Observatory Trust for supporting long-term ringing; Thomas Haaland for helpful comments on the manuscript.

References

1. Pigliucci M. 2005 Evolution of phenotypic plasticity: where are we going now? *Trends Ecol. Evol.* **20**, 481–486. (doi:10.1016/j.tree.2005.06.001)
2. Ghalambor CK, McKAY JK, Carroll SP, Reznick DN. 2007 Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* **21**, 394–407. (doi:10.1111/j.1365-2435.2007.01283.x)
3. Chevin LM, Lande R, Mace GM. 2010 Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**, e1000357. (doi:10.1371/journal.pbio.1000357)
4. Kelly M. 2019 Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. *Phil. Trans. R. Soc. B* **374**, 20180176. (doi:10.1098/rstb.2018.0176)
5. Nussey DH, Postma E, Gienapp P, Visser ME. 2005 Selection on heritable phenotypic plasticity in a wild bird population. *Science* **310**, 304–306. (doi:10.1126/science.1117004)
6. Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC. 2008 Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**, 800–803. (doi:10.1126/science.1157174)
7. Merilä J, Hendry AP. 2014 Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol. Appl.* **7**, 1–14. (doi:10.1111/eva.12137)
8. Dewitt TJ, Sih A, Wilson DS. 1998 Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* **13**, 77–81. (doi:10.1016/s0169-5347(97)01274-3)
9. Pelletier F, Réale D, Garant D, Coltman DW, Festa-Bianchet M. 2007 Selection on heritable seasonal phenotypic plasticity of body mass. *Evolution* **61**, 1969–1979. (doi:10.1111/j.1558-5646.2007.00160.x)
10. Van Buskirk J, Steiner UK. 2009 The fitness costs of developmental canalization and plasticity. *J. Evol. Biol.* **22**, 852–860. (doi:10.1111/j.1420-9101.2009.01685.x)
11. Svensson EI, Gomez-Llano M, Waller JT. 2020 Selection on phenotypic plasticity favors thermal canalization. *Proc. Natl Acad. Sci. USA* **117**, 29767–29774. (doi:10.1073/pnas.2012454117)

12. Grenier S, Barre P, Litrico I. 2016 Phenotypic plasticity and selection: nonexclusive mechanisms of adaptation. *Scientifica (Cairo)* **2016**, 7021701. (doi:10.1155/2016/7021701)
13. Arnold PA, Nicotra AB, Kruuk LEB. 2019 Sparse evidence for selection on phenotypic plasticity in response to temperature. *Phil. Trans. R. Soc. B* **374**, 20180185. (doi:10.1098/rstb.2018.0185)
14. Fox RJ, Donelson JM, Schunter C, Ravasi T, Gaitán-Espitia JD. 2019 Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Phil. Trans. R. Soc. B* **374**, 20180174. (doi:10.1098/rstb.2018.0174)
15. Dupont L, Thierry M, Zinger L, Legrand D, Jacob S. 2024 Beyond reaction norms: the temporal dynamics of phenotypic plasticity. *Trends Ecol. Evol*. **39**, 41–51. (doi:10.1016/j.tree.2023.08.014)
16. Padilla DK, Adolph SC. 1996 Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol. Ecol*. **10**, 105–117. (doi:10.1007/bf01237730)
17. Gabriel W. 2005 How stress selects for reversible phenotypic plasticity. *J. Evol. Biol*. **18**, 873–883. (doi:10.1111/j.1420-9101.2005.00959.x)
18. Quinn JL, Cresswell W. 2005 Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour* **142**, 1377–1402. (doi:10.1163/156853905774539391)
19. Brommer JE. 2013 Phenotypic plasticity of labile traits in the wild. *Curr. Zool*. **59**, 485–505. (doi:10.1093/czoolo/59.4.485)
20. Caldwell AJ, While GM, Wapstra E. 2017 Plasticity of thermoregulatory behaviour in response to the thermal environment by widespread and alpine reptile species. *Anim. Behav*. **132**, 217–227. (doi:10.1016/j.anbehav.2017.07.025)
21. Reid JM, Travis JMJ, Daunt F, Burthe SJ, Wanless S, Dytham C. 2018 Population and evolutionary dynamics in spatially structured seasonally varying environments. *Biol. Rev*. **93**, 1578–1603. (doi:10.1111/brv.12409)
22. Reid JM, Acker P. 2022 Conceptualizing the evolutionary quantitative genetics of phenological life-history events: breeding time as a plastic threshold trait. *Evol. Lett*. **6**, 220–233. (doi:10.1002/evl3.278)
23. Piersma T, Drent J. 2003 Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol*. **18**, 228–233. (doi:10.1016/s0169-5347(03)00036-3)
24. Stager M, Velotta JP, Cheviron ZA, Senner NR. 2024 Assessing the evidence for treating developmental plasticity and phenotypic flexibility as different phenomena. *Funct. Ecol*. **39**, 2949–2961. (doi:10.1111/1365-2435.14590)
25. Callahan HS, Maughan H, Steiner UK. 2008 Phenotypic plasticity, costs of phenotypes, and costs of plasticity. *Ann. NY Acad. Sci*. **1133**, 44–66. (doi:10.1196/annals.1438.008)
26. Auld JR, Agrawal AA, Relyea RA. 2010 Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proc. R. Soc. B* **277**, 2009. (doi:10.1098/rspb.2009.1355)
27. Murren CJ *et al*. 2015 Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity* **115**, 293–301. (doi:10.1038/hdy.2015.8)
28. Hendry AP. 2016 Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *J. Hered*. **107**, 25–41. (doi:10.1093/jhered/esv060)
29. Iler AM, CaraDonna PJ, Forrest JRK, Post E. 2021 Demographic consequences of phenological shifts in response to climate change. *Annu. Rev. Ecol. Evol. Syst*. **52**, 221–245. (doi:10.1146/annurev-ecolsys-011921-032939)
30. Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA. 2011 The ecology and evolution of partial migration. *Oikos* **120**, 1764–1775. (doi:10.1111/j.1600-0706.2011.20131.x)
31. Berg JE, Hebblewhite M, St. Clair CC, Merrill EH. 2019 Prevalence and mechanisms of partial migration in ungulates. *Front. Ecol. Evol.* **7**, 325. (doi:10.3389/fevo.2019.00325)
32. Hegemann A, Marra PP, Tieleman BI. 2015 Causes and consequences of partial migration in a passerine bird. *Am. Nat*. **186**, 531–546. (doi:10.1086/682667)
33. Grayson KL, Wilbur HM. 2009 Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology* **90**, 306–312. (doi:10.1890/08-0935.1)
34. Brodersen J, Nilsson PA, Hansson LA, Skov C, Brönmark C. 2008 Condition-dependent individual decision-making determines cyprinid partial migratioN. *Ecology* **89**, 1195–1200. (doi:10.1890/07-1318.1)
35. Dodson JJ, Aubin-Horth N, Thériault V, Páez DJ. 2013 The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biol. Rev. Camb. Philos. Soc*. **88**, 602–625. (doi:10.1111/brv.12019)
36. Acker P *et al*. 2021 Episodes of opposing survival and reproductive selection cause strong fluctuating selection on seasonal migration versus residence. *Proc. R. Soc. B* **288**, 20210404. (doi:10.1098/rspb.2021.0404)
37. Acker P *et al*. 2021 Strong survival selection on seasonal migration versus residence induced by extreme climatic events. *J. Anim. Ecol*. **90**, 796–808. (doi:10.1111/1365-2656.13410)
38. Buchan C, Gilroy JJ, Catry I, Franco AMA. 2020 Fitness consequences of different migratory strategies in partially migratory populations: a multi-taxa meta-analysis. *J. Anim. Ecol*. **89**, 678–690. (doi:10.1111/1365-2656.13155)
39. Grayson KL, Bailey LL, Wilbur HM. 2011 Life history benefits of residency in a partially migrating pond-breeding amphibian. *Ecology* **92**, 1236–1246. (doi:10.1890/11-0133.1)
40. Reid JM, Souter M, Fenn SR, Acker P, Payo-Payo A, Burthe SJ, Wanless S, Daunt F. 2020 Among-individual and within-individual variation in seasonal migration covaries with subsequent reproductive success in a partially migratory bird. *Proc. R. Soc. B* **287**, 20200928. (doi:10.1098/rspb.2020.0928)
41. Acker P *et al*. 2023 Hierarchical variation in phenotypic flexibility across timescales and associated survival selection shape the dynamics of partial seasonal migration. *Am. Nat*. **201**, 269–286. (doi:10.1086/722484)
42. Aikens EO, Nourani E, Fiedler W, Wikelski M, Flack A. 2024 Learning shapes the development of migratory behavior. *Proc. Natl. Acad. Sci. USA* **121**, e2306389121. (doi:10.1073/pnas.2306389121)
43. Chan Y, Kormann UG, Witczak S, Scherler P, Grüebler MU. 2024 Ontogeny of migration destination, route and timing in a partially migratory bird. *J. Anim. Ecol*. **93**, 1316–1327. (doi:10.1111/1365-2656.14150)
44. Ugland CR *et al*. 2024 Early-life variation in migration is subject to strong fluctuating survival selection in a partially migratory bird. *J. Anim. Ecol* **93**, 1567–1581. (doi:10.1111/1365-2656.14172)
45. Rotics S *et al*. 2021 Early-life behaviour predicts first-year survival in a long-distance avian migrant. *Proc. R. Soc. B* **288**, 20202670. (doi:10.1098/rspb.2020.2670)
46. Pulido F, Widmer M. 2005 Are long-distance migrants constrained in their evolutionary response to environmental change?: Causes of variation in the timing of autumn migration in a blackcap (*S. atricapilla*) and two garden warbler (*Sylvia borin*) populations. *Ann. NY Acad. Sci*. **1046**, 228–241. (doi:10.1196/annals.1343.020)
47. Both C, Bouwhuis S, Lessells CM, Visser ME. 2006 Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83. (doi:10.1038/nature04539)
48. Eggeman SL, Hebblewhite M, Bohm H, Whittington J, Merrill EH. 2016 Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *J. Anim. Ecol*. **85**, 785–797. (doi:10.1111/1365-2656.12495)
49. Xu W *et al*. 2021 The plasticity of ungulate migration in a changing world. *Ecology* **102**, 3293. (doi:10.1002/ecy.3293)
50. Grist H, Daunt F, Wanless S, Nelson EJ, Harris MP, Newell M, Burthe S, Reid JM. 2014 Site fidelity and individual variation in winter location in partially migratory european shags. *PLoS One* **9**, e98562. (doi:10.1371/journal.pone.0098562)
51. Barlow EJ, Daunt F, Wanless S, Reid JM. 2013 Estimating dispersal distributions at multiple scales: within-colony and among-colony dispersal rates, distances and directions in European shags *Phalacrocorax aristotelis*. *Ibis* **155**, 762–778. (doi:10.1111/ibi.12060)

52. Fortuna R *et al*. 2024 Season-specific genetic variation underlies early-life migration in a partially migratory bird. *Proc. R. Soc. B* **291**, 20241660. (doi:10.1098/rspb.2024.1660)
53. Rouan L, Choquet R, Pradel R. 2009 A general framework for modeling memory in capture–recapture data. *JABES* **14**, 338–355. (doi:10.1198/jabes.2009.06108)
54. Carpenter B *et al*. 2017 Stan: a probabilistic programming language. *J. Stat. Softw.* **76**, 1. (doi:10.18637/jss.v076.i01)
55. Stan Development Team. 2022 RStan: the R interface to Stan. R package version 2.26.13. See https://mc-stan.org.
56. R Core Team. 2022 R: a language and environment for statistical computing. R Foundation for Statistical Computing.
57. Gelman A. 2006 Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Anal.* **1**, 515–534. (doi:10.1214/06-BA117A)
58. Yanco SW, Rutz C, Abrahms B, Cooper NW, Marra PP, Mueller T, Weeks BC, Wikelski M, Oliver RY. 2025 Tracking individual animals can reveal the mechanisms of species loss. *Trends Ecol. Evol*. **40**, 47–56. (doi:10.1016/j.tree.2024.09.008)
59. Sultan SE, Spencer HG. 2002 Metapopulation structure favors plasticity over local adaptation. *Am. Nat*. **160**, 271–283. (doi:10.1086/341015)
60. Pulido F. 2011 Evolutionary genetics of partial migration: the threshold model of migration revis(it)ed. *Oikos* **120**, 1776–1783. (doi:10.1111/j.1600-0706.2011.19844.x)
61. Acker P *et al*. 2023 Additive genetic and environmental variation interact to shape the dynamics of seasonal migration in a wild bird population. *Evolution* **77**, 2128–2143. (doi:10.1093/evolut/qpad111)
62. Roff DA. 1996 The evolution of threshold traits in animals. *Q. Rev. Biol*. **71**, 3–35. (doi:10.1086/419266)
63. Reid JM, Acker P. 2022 Properties of phenotypic plasticity in discrete threshold traits. *Evolution* **76**, 190–206. (doi:10.1111/evo.14408)
64. Fortuna R, Acker P, Ugland C *et al*. 2025 Data from: temporal dynamics of selection on early-life phenotypic plasticity in seasonal migration versus residence. Dryad Digital Repository. (doi:10.5061/dryad.sj3tx96h8)
65. Fortuna R *et al*. 2025 Temporal dynamics of selection on early-life phenotypic plasticity in seasonal migration versus residence. Zenodo. (doi:10.5281/zenodo.16093912)
66. Fortuna R *et al*. 2026 Supplementary material from: Temporal dynamics of selection on early-life phenotypic plasticity in seasonal migration versus residence. Figshare. (doi:10.6084/m9.figshare.c.8230368)