RESEARCH ARTICLE

Carry-over effects of seasonal migration on reproductive success through breeding site retention in a partially migratory bird

Jennifer Morinay[1] | Francis Daunt[2] | Tim I. Morley[3] | Sarah R. Fenn[3] | Sarah J. Burthe[2] | Jane M. Reid[1,3]

[1]Centre for Biodiversity Dynamics, Institutt for Biologi, NTNU, Norwegian University of Science and Technology, Trondheim, Norway

[2]UK Centre for Ecology & Hydrology, Penicuik, UK

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

Correspondence
Jennifer Morinay
Email: jennifer.morinay@gmail.com

Abstract

1. Understanding the maintenance and dynamics of phenotypic polymorphisms requires unpicking key ecological mechanisms shaping the fitness costs and benefits of expressing alternative phenotypes, generating selection. Seasonal migration versus year-round residence expressed in partially migratory populations represents one common polymorphism that can experience strong selection through differential reproductive success. Yet, key hypothesised pathways that could generate such selection remain to be empirically tested.

2. One hypothesis is that migratory tactics affect subsequent reproductive success through carry-over effects on breeding site retention and resulting breeding dispersal. By remaining in breeding areas all year round, residents could retain their preferred breeding site between years, and consequently have higher reproductive success. Conversely, migrants that escape harsh non-breeding season conditions could return in better condition, with high resource holding potential, and outcompete residents to retain their site. Such effects could further depend on migration timing and vary between years. Yet, such pathways have not been quantified, precluding empirical parameterisation of partial migration theory.

3. We used 4 years of breeding and non-breeding season data from partially migratory European shags (*Gulosus aristotelis*) to test whether the three most frequent migratory tactics in this population (full resident, early migrant departing soon after breeding, and late migrant departing in late autumn) differed in their breeding site retention; whether site retention predicted reproductive success; and hence whether effects of migratory tactic on reproductive success were explicable through site retention.

4. Overall, residents were much more likely to retain their breeding site between years than both early and late migrants, and site retention was associated with increased reproductive success. Yet, these effects varied somewhat among years: late migrants were always least likely to retain their site but had variable relative

reproductive success. Path analyses revealed that effects of migratory tactic on reproductive success were only partly attributable to breeding site retention.

5. These results indicate that multiple mechanisms underlie reproductive selection on migratory tactics, potentially contributing to maintaining behavioural polymorphisms. Yet, the clear associations between migratory tactics and local breeding dispersal reveal that these movements can be strongly interlinked across seasons, shaping overall spatioseasonal dynamics in partially migratory systems.

1 | INTRODUCTION

Natural biological variation commonly encompasses discrete morphs and behaviours, which are flexibly expressed within or among individuals (Dingemanse & Wolf, 2013; Ehlinger & Wilson, 1988; Reid & Acker, 2022). Broad ambitions are to understand how such phenotypic polymorphisms can be maintained and reshaped by environmental changes, potentially flipping populations between alternative phenotypic states (Fusco & Minelli, 2010; Sahashi & Morita, 2018; Taborsky et al., 2008; Wennersten & Forsman, 2012). Such ambitions require quantifying relative magnitudes and temporal dynamics of fitness costs and benefits of expressing alternative phenotypes, thereby requiring empirical efforts to identify key underlying ecological mechanisms (Galeotti et al., 2003; Germain et al., 2017).

One prime example of an ecologically important dichotomous trait is seasonal migration versus year-round residence in partially migratory systems. Here, some individuals within a focal breeding population remain resident at the breeding area all year, while others migrate seasonally before returning to breed. Such movement polymorphisms are commonplace, occurring in fish, birds, mammals, amphibians and reptiles (Chapman et al., 2011; Reid et al., 2018). Expression of seasonal migration versus residence can experience strong selection manifested as differential survival and/or subsequent reproductive success, and such selection can vary among years and/or locations (Acker, Daunt, et al., 2021; Buchan et al., 2020; Eggeman et al., 2016; Sanz-Aguilar et al., 2012). Identifying mechanisms by which such fitness costs and benefits can arise and be modulated is necessary to understand the basis of selection on migratory tactics and resulting spatioseasonal population dynamics (Reid et al., 2018).

Numerous potential fitness costs and benefits of seasonal migration versus residence have been proposed (Balstad et al., 2021; Buchan et al., 2020; Lundberg, 1988; Sabal et al., 2021; Shaw & Couzin, 2013). Not least, in species utilizing distinct breeding sites or territories as key resources for reproductive success, arriving first could enable acquiring high-quality sites. This advantage could promote full residence or partial rather than full migration (Chapman et al., 2011; Kokko, 1999; Sirot & Touzalin, 2014). Here, seasonal

migrants could lose their preferred breeding sites and exhibit breeding dispersal (on small or larger spatial scales; Greenwood, 1982; Pärt & Gustafsson, 1989). Residents might consequently achieve higher reproductive success on average (Figure 1; Kokko, 1999; Kokko et al., 2006).

Yet, such prior residence effects could be overturned if residents and migrants differ in competitive ability and resulting 'resource holding potential' (Kokko, 2011; Lundblad & Conway, 2020). Specifically, individuals may migrate to access better non-breeding season environmental conditions (Boyle, 2008; Jahn et al., 2010). If residents endure sub-optimal non-breeding season conditions on breeding grounds, they may be outcompeted for breeding sites by returning migrants. Migrants may hence retain their preferred site despite their non-breeding season absence and any costs of movements (Jahn et al., 2010; but see Senar & Pascual, 2015).

Theoretically, effects of both prior residence and resource holding potential on site retention or acquisition, and on resulting reproductive success, could contribute to maintaining migratory polymorphism (Figure 1; Kokko, 2011). Specifically, populations can shift from full year-round residence given strong prior residence effects to full migration given strong migrant resource holding potential, with any degree of partial migration when both effects act (Kokko, 2011). Consequently, partial migration theory has invoked two opposing, yet non-mutually exclusive, assumptions regarding breeding dispersal of seasonal migrants versus residents.

Moreover, there could be multiple complexities to the proposition that seasonal migration versus residence hinder or facilitate breeding site retention and thereby shape relative reproductive outcomes (through prior residence and/or resource holding potential). For instance, differences in reproductive success between seasonal migrants and residents arising through site retention could be reinforced, negated, or even reversed by other carry-over effects of migratory tactic (Figure 1; e.g. differences in condition or foraging efficiency). Further, phenotypic variation within partially migratory systems is often more complex than simply migration versus residence. In particular, individuals commonly vary in migration timing, for example departing soon after breeding ('early' or pre-emptive migrants),
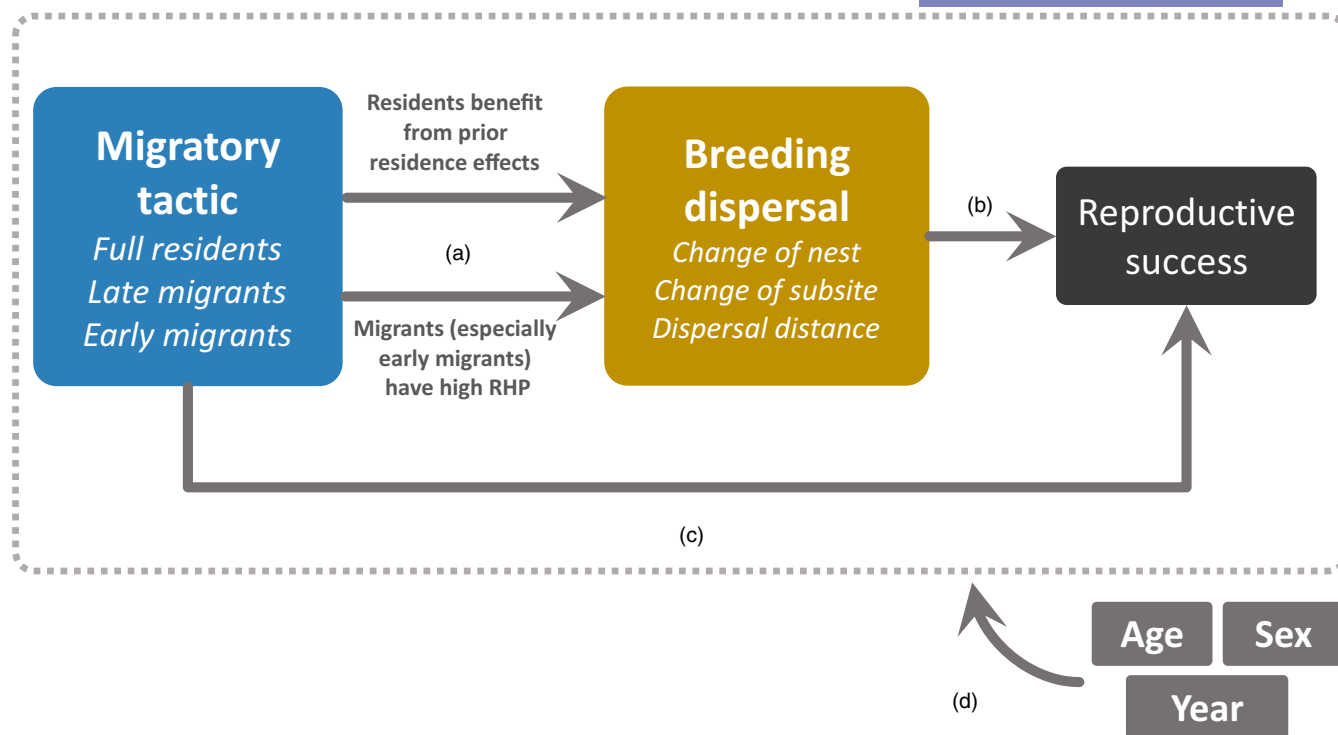
FIGURE 1 Postulated direct effects of (a) migratory tactic on breeding dispersal and (b) breeding dispersal on reproductive success, generating a mechanistic pathway by which migratory tactic affects reproductive outcomes by modulating dispersal versus (c) through any other ecological mechanism. (d) All such links could depend on individual age and sex and vary among years. Focal migratory tactics and dispersal metrics are shown in italics. RHP, resource holding potential.

or weeks or even months later ('late' or responsive migrants; Figure 1; Franklin et al., 2022; Reid et al., 2020). This affects how long they experience local environmental conditions. Such phenological variation could induce complex joint outcomes of prior residence and resource holding potential. Residents may benefit from stronger prior residence effects than all migrants. Meanwhile, early migrants may benefit from greater resource holding potential than late migrants, and even more than residents, by spending more time away. Conversely, late migrants may be less likely to retain their breeding site than residents or early migrants if late departure reduces the benefits gained from favourable environments elsewhere while also reducing prior residence effects.

Such outcomes could also depend on individual states such as age or sex (Figure 1). For example, individuals' abilities to progressively acquire and retain better sites could increase with age. Moreover, young individuals may be more likely to migrate if they are unable to compete successfully for scarcer non-breeding season resources (Chapman et al., 2011; Gauthreaux, 1982). Further, the benefits of breeding site retention, and the costs/benefits of migrating, could differ between sexes (e.g. Grist et al., 2017; Terraube et al., 2015). For instance, with sexual size dimorphism, the smaller sex could be less able to endure harsh non-breeding season environmental conditions, and hence be more prone to migrate. Finally, all postulated relationships between migration, breeding site retention and reproductive success could vary among

years, for example depending on non-breeding season conditions in the breeding area relative to migrants' destinations (Acker, Daunt, et al., 2021; Rushing et al., 2015). However, no empirical studies have yet quantified full associations between migratory tactics and breeding site retention, or quantified to what degree such effects translate into detectable differences in reproductive success, or examined how such effects vary among ages, sexes, or years (Figure 1; Lundblad & Conway, 2020). Consequently, there is little empirical basis on which mechanistic models considering the dynamics of partial migration as functions of breeding site retention can be formulated or validated.

Accordingly, we used 4 years of breeding and non-breeding season data from a partially migratory European shag (*Gulosus aristotelis*, hereafter 'shag') population to test for (i) effects of migratory tactic on breeding site retention (Figure 1a), (ii) effects of site retention on reproductive success (Figure 1b), and (iii) overall effects of migratory tactic on subsequent reproductive success (Figure 1c). We examined the degree to which such effects varied with individual age and sex and among four study years (Figure 1d). We then used path analyses to dissect whether effects of migratory tactic on subsequent reproductive success in each year were primarily mediated through breeding site retention versus other factors. We thereby quantify dynamic associations between two key ecological processes, seasonal migration and breeding site retention, and reveal how pathways to reproductive success through local breeding dispersal vary with migratory tactic.

2 | MATERIALS AND METHODS

2.1 | Field data collection

Testing whether individuals expressing different migratory tactics have different probabilities of retaining their breeding site, and hence different mean reproductive success (Figure 1), requires recording individuals' sequences of breeding site, migratory tactic, subsequent breeding site and resulting reproductive success. During 2017–2021, we collected these data in a partially migratory shag population breeding at Bullers of Buchan, Aberdeenshire, Scotland (hereafter 'Bullers', 57°26′ N, 1°48′ W, Figure S1). Here, individuals express three migratory tactics: early migrant, late migrant or year-round resident (Reid et al., 2020).

At Bullers, shags typically breed once per year (during April–August) from age 3 years and nest openly on cliff sites that are readily observable (only ~5% of ~600 recently occupied sites along the ~11 km cliff area are unobservable, e.g. in sea caves). Each year during 2009–2020, the subset of sites that are human-accessible (~5%–10%) was visited during chick-rearing (June–July) to mark chicks with individually colour-coded field-readable rings (total: 1024). Additionally, 76 breeding adults were caught and colour-ringed at diverse sites. Ringing was licenced by British Trust for Ornithology (A4389 to JMR), and no further permits or ethical approvals were required. Due to frequent short-distance natal and breeding dispersal within the Bullers area, ringed individuals could subsequently breed at any nest site across the whole area, not just at the sites that were accessible for ringing. During 2017–2021, all visible nests were observed every 5–10 days through April–September to identify colour-ringed adults and record reproductive success (range 0–4 fledglings) following standard protocols (Walsh et al., 1995). Overall, 194 ringed adults were observed throughout the area during the breeding seasons 2017–2021 (including 7 immigrants from other colonies; resighting probability close to 1, Reid et al., 2020). Of these, 138 individuals bred locally in ≥2 consecutive years, allowing evaluation of breeding dispersal. The others were either non-breeders in all years they were observed (5), or were observed breeding with certainty only once (36), or only in non-consecutive years (15).

Shags are size dimorphic (males 15%–20% bigger than females). Yet, sex attributions are difficult when seeing only one partner, and most confidently achieved from sexually dimorphic calls heard during ringing or subsequent monitoring. We assigned sexes to 58% of 194 adults (49 females, 63 males), either directly or inferred from partner sex. Adult ages were known for individuals ringed as chicks (63% of 194 adults, mean age at breeding observation 6 years, range 2–14), and unknown otherwise.

2.2 | Breeding site retention and dispersal distances

All occupied nest sites (i.e. at least partial nest built) during 2017–2021 were accurately mapped and numbered to allow consistent site identification within and across years. This is facilitated because nests are positioned on discrete rock ledges, and hence on fixed positions on the cliffs. We extracted three measures of breeding dispersal spanning three biologically relevant spatial scales (Figure 1). First, we quantified whether an individual that bred in two consecutive breeding seasons retained its exact same nest site (binary variable 'nest site retention'). Second, we quantified whether an individual retained the same local environment (and thus was exposed to the same local conditions, and partly the same neighbours) by remaining in the same subsite (defined as an assemblage of nest sites located in the same cliff area within a radius of 100 m, Figure S2; binary variable 'subsite retention'). Sample sizes differed across these two metrics because, for four breeding events, individuals certainly changed nest site, but subsite was not explicitly recorded. Third, to further examine variation in breeding dispersal distance and hence investigate whether some migratory phenotypes might be more prone to stay very close to previous sites versus disperse far, we quantified the approximate distance between the nest sites that dispersing individuals used in consecutive years (Supporting Information SI.1). Since distance estimates were relatively coarse, we defined categories of <50, 100, 150, 200, 250, 400 and ≥400 m, treated as an ordinal variable.

Individuals repeatedly observed loafing during the breeding season but never seen attending an active nest site were excluded from the analyses of between-year breeding dispersal (8% of all breeding season records of ringed individuals; Supporting Information SI.1).

2.3 | Non-breeding season data

To assign individuals' migratory tactics, we undertook intensive non-breeding season resighting surveys to record the presence of local ringed adults within the breeding area. Such resightings are facilitated because shags return to shore every day to dry their wettable plumage. Ringed individuals can consequently be directly observed all year, at day roosts used between foraging bouts and at night roosts. Accordingly, local roost sites were visited on ≥1 day within each sequential 10-day period from 1 September to 18 February, in all four winters from 2017–2018 to 2020–2021 (following Reid et al., 2020). Present shags were scanned with a telescope, and ringed individuals identified.

To estimate the probability that each focal adult undertook a specific migratory tactic within each winter, we fitted capture-mark-recapture mixture models to individual encounter histories built from local resighting data for each non-breeding season and the two adjacent breeding seasons (Supporting Information SI.2, detailed methods in Reid et al., 2020). Briefly, these models estimate the probabilities that individuals belong to latent mixture classes. Our models identified three classes, which were not predefined but are biologically interpretable as 'resident' (i.e. present in the local area throughout the non-breeding season), 'early migrant' (i.e. departed from the local area by mid-September) and 'late migrant' (i.e. departed later in autumn, typically during

October–November, Reid et al., 2020). Migrant classes identified by the models were thus separated based on departure timing, not return timing (typically during February–March). Class assignment probabilities for most individuals were high (≥0.95 for 86%, 83%, 73% and 81% of individuals in winters 2017–2018 to 2020–2021 respectively; Figure S3). For subsequent analyses of relationships with site retention and reproductive success, individuals were assigned to their most probable migratory tactic. Results remained quantitatively similar when analyses were iterated with 10,000 random draws from individuals' simplexes of tactic probabilities (Figure S4).

2.4 | Statistical analyses

We fitted three sets of generalized linear mixed effects models (GLMMs) to interrogate the postulated pathways linking migratory tactic to reproductive success (Figure 1). First, we tested whether an individuals' migratory tactic during an intervening non-breeding season (three-level fixed effect: resident, late migrant, early migrant) predicted its nest or subsite retention from one breeding season to the next (binomial response variables, Figure 1a). Then, we extracted observations of individuals that changed nest site between years and fitted an ordinal mixed model for inter-nest distance to test whether migratory tactic predicted the probability of falling into the different distance categories.

Second, we tested whether nest or subsite retention between two consecutive years predicted an individual's reproductive success in the second year (number of fledglings; generalized Poisson response variable, thereby accommodating underdispersed count data; considering Poisson or Normal distributions gave qualitatively similar results; Figure 1b). We did not consider dispersal distance as initial results showed that most breeding dispersal events occurred at small spatial scales (71% <100 m).

Third, we tested whether an individual's migratory tactic predicted its subsequent reproductive success (Figure 1c).

All models included fixed year effects (four levels) and the two-way interaction with either migratory tactic or site retention metric, to test whether tactic and retention effects varied among study years. We modelled age as a two-level fixed effect defined as young versus older breeders (≤4 vs. ≥5 years, following Reid et al., 2020) to estimate age-specific site retention or reproductive success, and its two-way interaction with either migratory tactic or site retention. Here, individuals ringed as adults were accurately included in the 'older' class from 2 years after ringing and excluded from analyses in their two first years after ringing (assuming minimum age at first breeding of 3 years, as known for 99.5% of known-age individuals). All models also included random individual effects to account for any non-independence of observations on individuals that appeared multiple times in the datasets. For 23% of focal breeding events, both pair members were colour-ringed, generating duplicated data points in the reproductive success data. For models of reproductive success as the response variable, we fitted random effects of nest

ID per year when modelling migratory tactic as a fixed factor. To aid convergence for the model including site retention as a fixed factor, we randomly removed data from one pair member. However, since there were relatively few pairs where both adults were ringed, we could not explicitly examine effects of pairwise migratory tactic or mate retention, on site retention or reproductive success (see Section 4). For all analyses, we additionally fitted secondary models to the restricted data subset comprising known-sex individuals, with a fixed effect of sex and its two-way interactions with age and either migratory tactic or site retention (but no higher-order interactions).

2.5 | Path analysis

We used path analyses to explicitly test whether effects of migratory tactic on reproductive success were fully explained by the postulated pathway through nest or subsite retention or were exacerbated or obscured by other carry-over effects collectively comprising an alternative path (Figure 1). Since the preceding analyses indicated some year-specific effects, we performed separate path analyses for each year, controlling for age effects. We did not consider sex effects as these would have severely restricted sample sizes, and there were no evident interacting effects of sex in the preceding models. To attribute effect sizes for each path, we fitted three GLMMs estimating effects of age on migratory tactic (ordinal distribution, with a scaling effect of age to respect the model's assumption for 2017–2018 [proportional odds]); effects of age and migratory tactic on site retention (binomial distribution); and finally, effects of age, migratory tactic, and site retention between years y and $y+1$ on reproductive success in year $y+1$ (generalized Poisson distribution). Effect sizes reported in path diagrams were obtained from model summaries and are the effect of reported categories compared to the reference. In these analyses, effects of migratory tactic on reproductive success are entirely explained by the mechanism of site retention if there are effects of (a) migratory tactic on site retention and (b) of site retention on reproductive success, (c) without any parallel effect of migratory tactic on reproductive success (i.e. arrows for Figure 1a,b but not Figure 1c). Conversely, parallel effects of migratory tactic on reproductive success (Figure 1c) imply a substantive alternative mechanistic pathway.

2.6 | Model fit and selection

Analyses were performed in R v.4.1.2 (R Development Core Team, 2021). Models with generalized Poisson distributions were fitted with '*glmmTMB*' (*glmmTMB* package, Brooks et al., 2017). Other GLMMs were fitted with '*glmer*' (*lme4* and *lmerTest* packages; Bates et al., 2015; Kuznetsova et al., 2017). We used logit link for binomial distributions and log link for generalized Poisson distributions. We used the '*emmeans*' function to perform posthoc pairwise comparisons, back-transform model estimates onto observed scales and obtain marginal means and associated 95% confidence intervals

(*emmeans* package, Lenth, 2019). Models' fit and assumptions were checked using simulated residual plots and uniformity, outliers, dispersion and zero-inflation tests (*DHARMa* package; Hartig, 2022). Receiver Operating Characteristic (ROC) curves were plotted and area under the curve estimated for binomial models (functions '*roc*' and '*auc*'; *pROC* package; Robin et al., 2011). Ordinal mixed models were fitted with the '*clmm*' function from the *ordinal* package (Christensen, 2019) using the *ggpredict* function to obtain probabilities (i.e. model estimates on the observed scale for each category; *ggeffects* package, Lüdecke, 2018). Ordinal models' assumptions were checked based on non-mixed versions of the models (functions '*nominal_test*' and '*scale_test*'; Christensen, 2019). Statistical significance of variables was based on *p*-values ($\alpha = 0.05$). We removed not statistically significant interactions, with no other variable selection.

3 | RESULTS

3.1 | Effects of migratory tactic on site retention

Overall, 198 (54%) of 369 observations of two consecutive breeding attempts by ringed individuals resulted in nest site retention. At a slightly larger spatial scale, 278 (76%) of 365 events resulted in subsite retention. There was consequently substantial opportunity for variation in site retention in relation to migratory tactic (Figure 2, with tactic- and year-specific sample sizes).

Across all 4 years combined, year-round residents were 2.3 and 2.0 times more likely to retain their nest site between years than late migrants and early migrants respectively (*p*-values = 10^{-4} and 0.01 respectively; probabilities for residents = 0.61 ± 0.08 SE, late migrants = 0.31 ± 0.08 SE and early migrants = 0.26 ± 0.06 SE; Figure 2a, $N = 341$, Table S2). Probabilities for early and late migrants did not differ (*p*-value = 0.80). These patterns were similar for subsite retention between years ($N = 337$); probabilities were much higher for residents (0.87 ± 0.05 SE) than late migrants (0.58 ± 0.08 SE, *p*-value = 8×10^{-4}) and early migrants (0.61 ± 0.08 SE, *p*-value = 0.01), but did not differ between the two migrant tactics (*p*-value = 0.96; Figure 2b, Table S2). There was no strong evidence that these effects of migratory tactic on nest or subsite retention varied among years (year-by-tactic interaction, *p*-values 0.31 and 0.57 for nest and subsite retention respectively, Table S2). Accordingly, probabilities were consistently high and low for residents and late migrants, respectively (Figure 2a,b). However, relative retention probabilities were slightly more variable for early migrants and tended towards those for late migrants in 2018–2019 and 2019–2020, but residents in 2017–2018 and 2020–2021 (Figure 2a,b).

Probabilities of nest and subsite retention were higher for older than young breeders (nest site: probabilities of 0.56 ± 0.05 vs. 0.24 ± 0.09, *p*-value = 0.01; subsite: probabilities of 0.84 ± 0.03 vs. 0.54 ± 0.11, *p*-value = 0.01). However, there was no evidence that effects of migratory tactic on nest or subsite retention varied with age (age-by-tactic interaction *p*-values = 0.81 and 0.48 respectively, Table S2).

Analyses restricted to known-sex adults showed that males were twice as likely to retain their nest and subsite as females (nest site: probabilities of 0.57 ± 0.09 SE vs. 0.27 ± 0.08 SE, *p*-value = 6×10^{-4}, $N = 248$; subsite: 0.80 ± 0.07 SE vs. 0.58 ± 0.10 SE, *p*-value = 0.01, $N = 246$). However, there was little evidence that effects of migratory tactic on nest or subsite retention differed between sexes (sex-by-tactic interaction, *p*-values = 0.98 and 0.41 for nest and subsite retention respectively, Table S3).

Across individuals that changed nest sites between years, the probabilities of moving different distances slightly differed between migratory tactics (estimate for early migrants versus residents: 1.22 ± 0.59 SE, *p*-value = 0.04, $N = 155$ events). The probability to move <50 m was high for all three tactics but tended to be higher for residents than early or late migrants (Figure 2c). Conversely, early migrants tended to have higher probabilities to move longer distances than year-round residents, while late migrants were intermediate (Figure 2c). There were no effects of age or sex on the probabilities of dispersing different distances (*p*-value = 0.60, $N = 155$ and *p*-value = 0.94, $N = 116$ respectively).

3.2 | Effects of site retention on reproductive success

Across all 4 years combined, reproductive success in a focal breeding season was substantially higher in individuals that retained their nest or subsite from the previous breeding season than individuals that changed site, with estimated mean increases of 0.41 and 0.29 fledglings for individuals retaining their nest or subsite respectively (*p*-values = 0.002 and 0.04 respectively; Figure 3). However, the effects of nest site retention on breeding success varied among years (retention-by-year interaction *p*-value = 0.02, Table S4). This interaction reflects slightly different effects in 2018 versus other years, with low reproductive success for individuals that changed nest, contrasting with smaller or no differences between groups in subsequent years (Figure 3). There were no strong effects of age (*p*-values = 0.70 and 0.44) or sex (*p*-values = 0.38 and 0.43; for the models including nest and subsite retention respectively) on individual reproductive success across the current dataset. There was also no evidence that effects of nest and subsite retention varied with age (*p*-values = 0.68 and 0.30) or sex (*p*-values = 0.75 and 0.22; for the models including nest and subsite retention respectively; Tables S4-S5).

3.3 | Effects of migratory tactic on reproductive success

Across all 4 years combined, reproductive success did not differ between the three migratory tactics (*p*-value = 0.32; Figure 4, Table S6). However, the effect of migratory tactic on subsequent breeding success tended to vary among years (tactic-by-year interaction *p*-value = 0.08, Table S6). This marginal trend primarily reflects that

FIGURE 2 Predicted probabilities of (a) nest site and (b) subsite retention between consecutive breeding seasons in relation to migratory tactic, across all four years combined and separately, and (c) predicted probabilities to disperse a certain distance for individuals changing nest site in relation to migratory tactic. In (c), dispersal distances were divided into categories (grey and white areas) across all four years combined; for each migratory tactic (here 34 residents, 60 late migrants and 54 early migrants), the sum of the probabilities over all distance categories equals one. Points denote marginal mean estimates (a, b) and predicted probabilities (c). Whiskers indicate 95% confidence intervals. Numbers are sample sizes.

Migratory tactic: ○ Resident ● Late migrant ● Early migrant
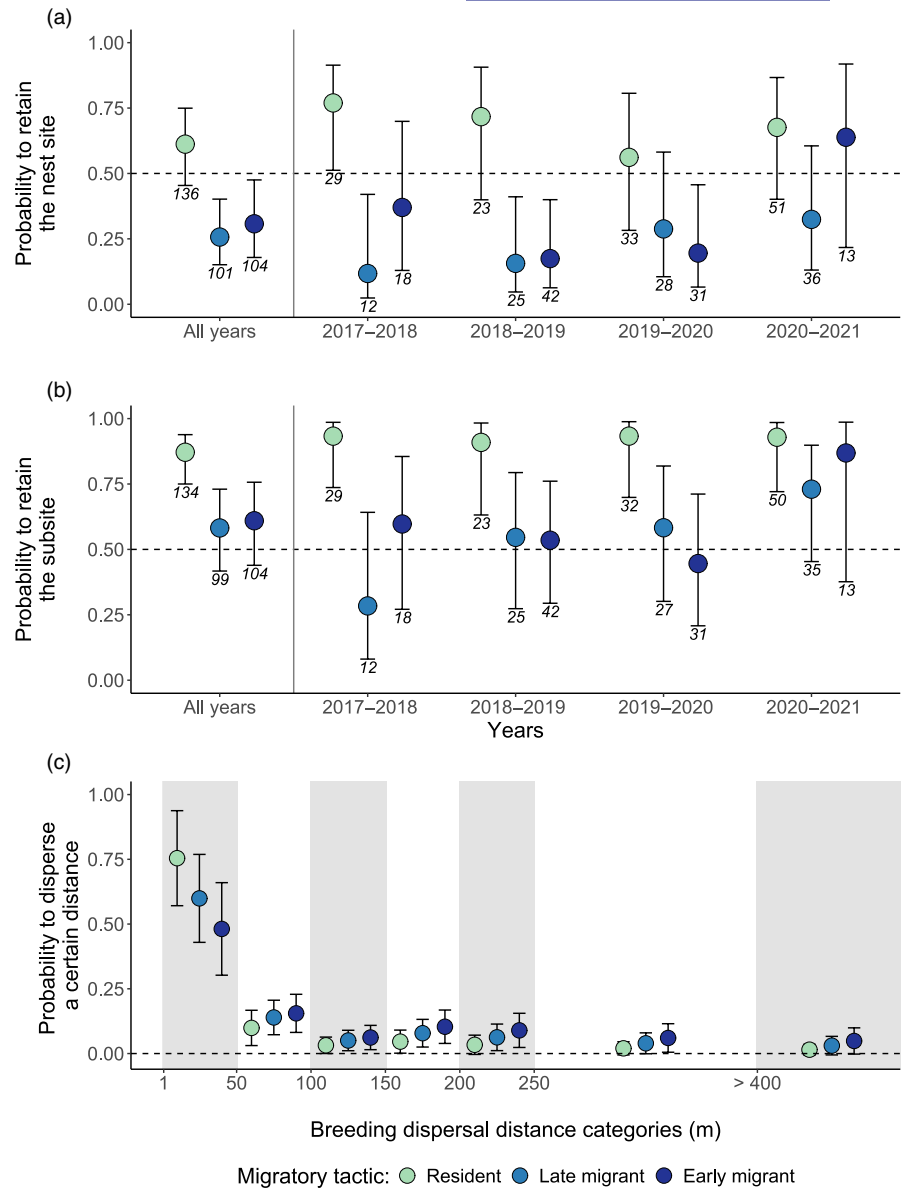
reproductive success of residents exceeded that of early migrants by 0.69 fledglings on average in 2017–2018. In contrast, late migrants tended to have higher reproductive success than residents or early migrants in 2018–2019 (0.44 and 0.30 fledglings more on average respectively; Figure 4). There was no evidence that effects of migratory tactic on reproductive success varied with age (*p*-value = 0.11) or sex (*p*-value = 0.98).

3.4 | Path analysis

The preceding results show that migratory tactic can predict nest and subsite retention, while nest and subsite retentions can predict reproductive success, leaving open the postulated pathway by which migratory tactic could affect reproductive success (Figure 1). Yet, migratory tactic did not strongly predict reproductive success, implying that some alternative pathway could act, and estimated

effects varied slightly among years. Accordingly, we undertook year-specific path analyses to tease apart compound relationships between tactic and success.

These analyses revealed that, in all years, migratory tactic affected either nest or subsite retention. Late migrants were always less likely to retain either their nest or subsite than residents (solid horizontal blue arrows between "M" and "SR" in Figure 5, *p*-values < 0.05), as were early migrants in 2018–2019 (nest site retention: *p*-value = 0.005), and 2019–2020 (subsite retention: *p*-value = 0.02; dashed horizontal blue arrows between "M" and "SR" in Figure 5; Table S7). In 2017–2018, there was evidence of strong effects of migratory tactic on reproductive success acting through nest or subsite retention, and through the alternative pathway encompassing other mechanisms (Figure 5a; Table S7). Here, late migrants were less likely to retain their nest or subsite than residents, those retaining their site had higher reproductive success, and, independently of site retention, early migrants had lower
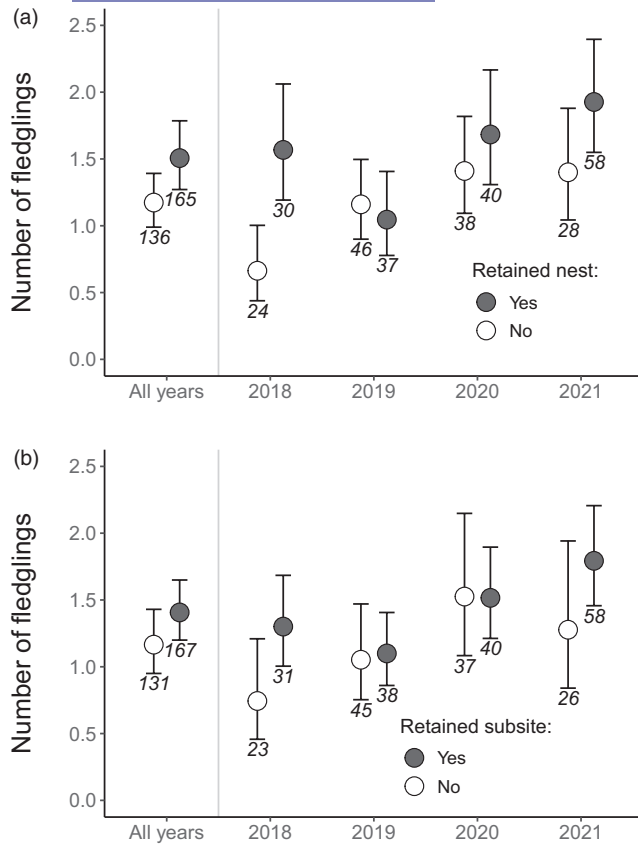
(a)

(b)

FIGURE 3 Predicted reproductive success of breeders that did (filled symbols) and did not (open symbols) retain their (a) nest or (b) subsite from the previous year. Points denote back-transformed predictions from models without ('all years') and with retention-by-year interactions (individual year estimates). Whiskers denote associated 95% confidence intervals. Numbers are sample size.

FIGURE 4 Predicted reproductive success in relation to migratory tactic expressed during the preceding non-breeding season across all 4 years combined and separately. Points denote back-transformed predictions from models without ('all years') and with tactic-by-year interactions (individual year estimates). Whiskers denote associated 95% confidence intervals. Numbers are sample size.

reproductive success than residents (p-values = 0.07 and 0.03 for the models with nest and subsite retention respectively). There was also a positive effect of nest site retention on reproductive success in 2020–2021 (p-value = 0.05). Here, any weak effects of migratory tactic on reproductive success were substantially attributable to nest site retention, with no strong evidence of any alternative path (p-values = 0.37 and 0.63 for late and early migrants versus residents respectively; Figure 5d; Table S7). In contrast, in the 2 years spanning 2018–2020, nest and subsite retention did not strongly affect reproductive success after controlling for migratory tactic and age (p-values > 0.31). Old breeders were more likely to retain their subsite in 2019–2020 (p-values = 0.04), with no discernible effects of age on migratory tactic or reproductive success in other years (Figure 5; Table S7).

4 | DISCUSSION

Understanding the dynamics and maintenance of behavioural polymorphisms requires identifying key ecological pathways generating costs and benefits of alternative phenotypic expression (Buchan
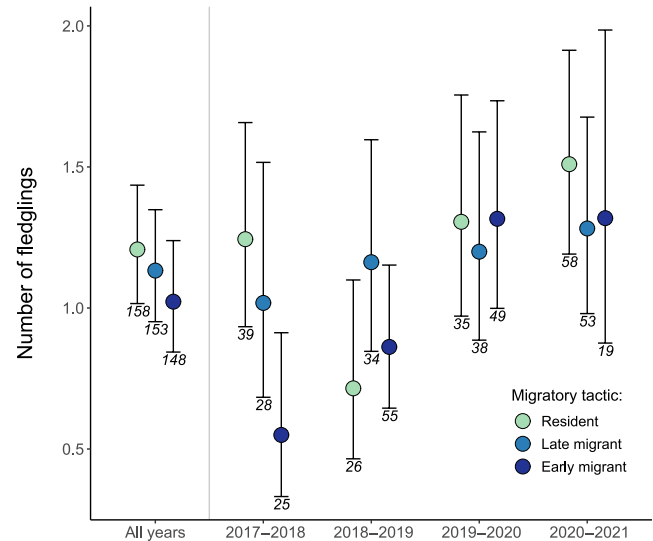
et al., 2020; Fusco & Minelli, 2010). Our analyses of 4 years of breeding and non-breeding season data from partially migratory European shags provided partial support for postulated carry-over effects of alternative seasonal migration tactics on reproductive success, acting through breeding site retention versus change (i.e. through small-scale breeding dispersal). Yet, while relationships between migratory tactic and site retention, and between site retention and reproductive success, were sometimes strikingly strong, effects did not necessarily translate into strong effects of migratory tactic on reproductive success. Our results also indicate that ecological mechanisms causing selection on migratory tactics may vary among years, potentially contributing to maintaining behavioural polymorphisms. Nevertheless, the strong observed associations between migratory tactics and breeding site retention showed that forms of breeding and non-breeding season movement are interlinked, potentially shaping cross-season dynamics in partially migratory systems.

4.1 | Inter-linked seasonal migration and breeding dispersal

Observed phenotypic associations between migratory tactics and breeding site retention were strong and spanned multiple within-colony spatial scales. Specifically, individuals that remained resident through the non-breeding season were more likely to retain their exact same nest site and breeding subsite than early migrants that were away throughout the non-breeding season, and furthermore moved shorter distances when they did change site. Yet, individuals that migrated late, and hence spent part of the

FIGURE 5 Path diagrams showing links between age, migratory tactic (M), site retention (SR), and reproductive success (RS) for the four study years spanning 2017–2021 (a–d). Arrows denote postulated effects of one variable on the next variable, with estimated path coefficients. When two coefficients are provided, the top one represents nest site retention, and the bottom one in brackets represents subsite retention. Solid and dashed blue arrows respectively denote contrasts of late migrants and early migrants from residents. Reference categories are residents, young, and site change. Bold asterisk coefficients differed significantly from the reference (*p*-value < 0.05), while solely bold coefficients were marginally significant (0.05 < *p*-value < 0.1).
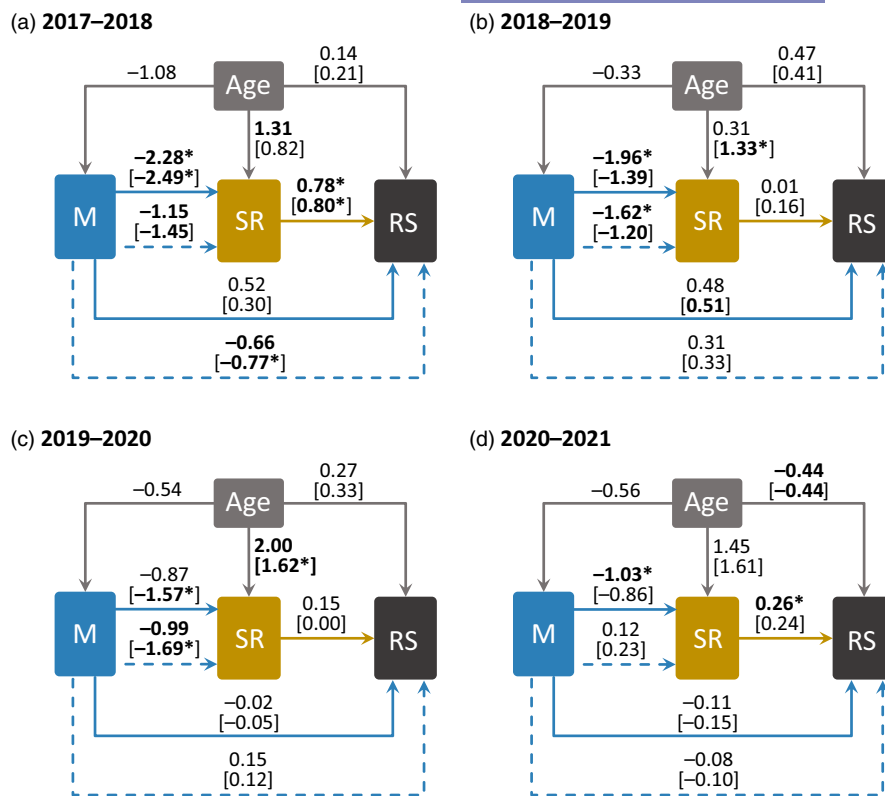
non-breeding season in their breeding area and part away, were even more likely to change site between years. These overall phenotypic associations are broadly consistent with patterns that are expected given combinations of prior residence and resource holding potential, as postulated to shape reproductive outcomes (Kokko, 1999, 2011; Lundblad & Conway, 2020). Residents may benefit from strong prior residence effects compared to all migrants, while early migrants may benefit from increased resource holding potential compared to late migrants by spending a greater time away. This interpretation implies that prior residence effects exceed resource holding potential, which in turn scales with time away.

While no other empirical studies have directly quantified effects of different migratory tactics on breeding dispersal, wider results are consistent with prior residence effects, especially where competition for breeding sites is high. Higher quality breeding sites were occupied earlier and more often during the non-breeding season than poorer sites within a common guillemot (*Uria aalge*) colony (Bennett et al., 2022). Residents initiated breeding earlier than migrants in American kestrels (*Falco sparverius*, Anderson et al., 2016) and in another population of European shags (Grist et al., 2017). Prime access to breeding sites was also suggested to benefit residents by increasing male reproductive probability and female breeding success in Lanyu scops owls (*Otus elegans botelensis*, Bai et al., 2012). In some fully migratory species, individuals migrating earlier have characteristics that imply higher resource holding potential than individuals migrating later (e.g. better body condition, Heim et al., 2016). Future studies should aim to couple information on migratory tactic, dispersal, and

underlying proximate behaviours (e.g. pair formation, reproductive phenology, nest acquisition) and physiologies to fully dissect the basis of cross-season carry-over effects of movements.

Rather than necessarily strictly reflecting prior residence and/or resource holding potential, observed phenotypic associations between seasonal migration and breeding dispersal could represent independent manifestations of a common basis (e.g. a behavioural syndrome with strong physiological or genetic components), generating intrinsic links between different forms of movement. Two previous empirical studies, both on birds, directly examined links between forms of obligate seasonal migration and natal dispersal. Individual American redstarts (*Setophaga ruticilla*) that spent the non-breeding season in wet mangrove versus drier scrub habitats subsequently recruited south and north of their natal area respectively, likely reflecting carry-over effects of non-breeding habitat quality acting through individual condition (Studds et al., 2008). Meanwhile, in song sparrows (*Melospiza melodia*), large-scale natal dispersers tended to migrate further (Kelly et al., 2016). More indirectly, American kestrels hatched at higher latitudes, which should be prone to migrate, showed longer dispersal distances than those hatched at lower latitudes (McCaslin et al., 2020), while migratory populations showed weaker genetic structure than resident populations, further implying greater dispersal (Miller et al., 2012). These few studies accord with our findings that key aspects of seasonal migration and breeding dispersal are phenotypically linked in shags. Hence, rather than viewing seasonal migration as an isolated process that primarily impacts the dynamics of single focal populations, while dispersal additionally shapes meta-population dynamics (Semlitsch, 2008), both

forms of movement could jointly shape dynamics across temporal and spatial scales.

Although seasonal migration and dispersal can be clearly linked, they are also partially decoupled. Even though migratory tactic strongly affected nest site retention in shags, the two processes differ in cross-year repeatability. Migratory tactic is highly repeatable across years (estimated repeatabilities ≥0.6; Acker et al., 2023; Grist et al., 2014; Reid et al., 2020, as also observed in other species, Franklin et al., 2022), while nest site is quite plastic (estimated repeatability: 0.22 ± 0.06 SD [0.06; 0.30], $N = 369$ observations of 142 individuals). Any overall movement syndrome could therefore be uncoupled by additional ecological effects on breeding dispersal. In our system, mate retention between years was often concomitant with nest site retention ($N = 15$ of 19 observations of colour-ringed pairs that bred together two consecutive years), and mate change was often concomitant with nest change for females, but not for males ($N = 10$ and 6 nest changes for females and males respectively, of 12 observations of mate change, through mate loss or divorce). Our measure of site retention could thus act as a proxy for multiple potential components of carry-over effects on reproduction, which may in turn depend on previous reproductive success (Robert et al., 2014). Indeed, previous studies on other systems found that individuals with increased reproductive effort and success delayed their autumn migration (Briedis et al., 2018; Fayet et al., 2016). In contrast, analyses of our data for 2017–2019 showed no effect of reproductive success on subsequent migratory tactic in our system. First, individuals very rarely switched from early migrant to resident or late migrant despite considerable variation in reproductive success among the early migrants. Second, residents that remained residents or became migrants had similar reproductive success (Reid et al., 2020). Longitudinal analyses of further years of data on ringed individuals and pairs in our population or others, may reveal subtle full year-round carry-over effects, or pair effects (e.g. migrant females paired to resident males could have higher reproductive success, benefiting from the combination of male prior residence and good female non-breeding environmental conditions).

4.2 | Pathways to reproductive success and partial migration

Phenotypic associations among migratory tactics, site retention and reproductive success were complex and varied somewhat among study years. In 2017–2018, migratory tactic strongly affected site retention, which in turn affected reproductive success. This pathway substantially explains the relatively low reproductive success of late migrants compared to residents, but additional negative effects were responsible for the very low reproductive success of early migrants, independently of site retention (Figure 5a). The effect of site retention on reproductive success implies that even very small-scale breeding dispersal (here commonly <50 m) can have major reproductive consequences. Such

short-distance breeding dispersal is common in colonial and territorial species (e.g. smallmouth bass *Micropterus dolomieu*, Ridgway et al., 1991; Scopoli's shearwater *Calonectris diomedea*, Thibault & Thibault, 1994; another population of European shags, Barlow et al., 2013), and can greatly alter immediate physical and social environments and hence site 'quality' (e.g. here in terms of susceptibility to waves, predators, or parasites and access to social information).

Yet, the postulated pathway from migratory tactic to reproductive success via site retention did not always hold. For example, late migrants in 2018–2019 had highest subsequent reproductive success (Figure 4) yet lowest site retention (Figures 2 and 5c), while nest site retention did not predict reproductive success (Figures 3 and 5c). Among-year variation in reproductive selection on seasonal migration versus residence has also recently been demonstrated in another shag population, with weakened selection against migration following harsher local winters (Acker, Burthe, et al., 2021). Future ambitions, which require multiple years of full-annual-cycle monitoring of wild partially migratory populations, should be to formally connect such variation to prevailing environmental conditions and to population dynamics, encompassing density-dependent restrictions on breeding site availability, and resulting spatio-temporal dynamics of the migration-dispersal syndrome.

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.ffbg79d2t (Morinay et al., 2024).

ORCID
Jennifer Morinay https://orcid.org/0000-0002-7905-9691
Francis Daunt https://orcid.org/0000-0003-4638-3388
Sarah R. Fenn https://orcid.org/0000-0003-0393-3597

Sarah J. Burthe https://orcid.org/0000-0001-8871-3432

Jane M. Reid https://orcid.org/0000-0002-5007-7343

REFERENCES

Acker, P., Burthe, S. J., Newell, M. A., Grist, H., Gunn, C., Harris, M. P., Payo-Payo, A., Swann, R., Wanless, S., Daunt, F., & Reid, J. M. (2021). Episodes of opposing survival and reproductive selection cause strong fluctuating selection on seasonal migration versus residence. *Proceedings of the Royal Society B: Biological Sciences*, *288*, 20210404. https://doi.org/10.1098/rspb.2021.0404

Acker, P., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., Grist, H., Sturgeon, J., Swann, R. L., Gunn, C., Payo-Payo, A., & Reid, J. M. (2021). Strong survival selection on seasonal migration versus residence induced by extreme climatic events. *Journal of Animal Ecology*, *90*(4), 796–808. https://doi.org/10.1111/1365-2656.13410

Acker, P., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., Gunn, C., Swann, R., Payo-Payo, A., & Reid, J. M. (2023). Hierarchical variation in phenotypic flexibility across timescales and associated survival selection shape the dynamics of partial seasonal migration. *The American Naturalist*, *201*(2), 269–286. https://doi.org/10.1086/722484

Anderson, A. M., Novak, S. J., Smith, J. F., Steenhof, K., & Heath, J. A. (2016). Nesting phenology, mate choice, and genetic divergence within a partially migratory population of American Kestrels. *Auk*, *133*(1), 99–109. https://doi.org/10.1642/AUK-15-129.1

Bai, M. L., Severinghaus, L. L., & Philippart, M. T. (2012). Mechanisms underlying small-scale partial migration of a subtropical owl. *Behavioral Ecology*, *23*(1), 153–159. https://doi.org/10.1093/beheco/arr168

Balstad, L. J., Binning, S. A., Craft, M. E., Zuk, M., & Shaw, A. K. (2021). Parasite intensity and the evolution of migratory behavior. *Ecology*, *102*(2), 1–10. https://doi.org/10.1002/ecy.3229

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

Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bennett, S., Harris, M. P., Wanless, S., Green, J. A., Newell, M. A., Searle, K. R., & Daunt, F. (2022). Earlier and more frequent occupation of breeding sites during the non-breeding season increases breeding success in a colonial seabird. *Ecology and Evolution*, *12*(9), 1–24. https://doi.org/10.1002/ece3.9213

Boyle, W. A. (2008). Partial migration in birds: Tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology*, *77*(6), 1122–1128. https://doi.org/10.1111/j.1365-2656.2008.01451.x

Briedis, M., Krist, M., Král, M., Voigt, C. C., & Adamík, P. (2018). Linking events throughout the annual cycle in a migratory bird—Non-breeding period buffers accumulation of carry-over effects. *Behavioral Ecology and Sociobiology*, *72*(6), 93. https://doi.org/10.1007/s00265-018-2509-3

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Maechler, M., & Bolker, B. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Buchan, C., Gilroy, J. J., Catry, I., & Franco, A. M. A. (2020). Fitness consequences of different migratory strategies in partially migratory populations: A multi-taxa meta-analysis. *Journal of Animal Ecology*, *89*(3), 678–690. https://doi.org/10.1111/1365-2656.13155

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

Christensen, R. H. B. (2019). *ordinal—Regression models for ordinal data*. R package version 2019.12-10. https://cran.r-project.org/package=ordinal

Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Animal Behaviour*, *85*(5), 1031–1039. https://doi.org/10.1016/j.anbehav.2012.12.032

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

Ehlinger, T. J., & Wilson, D. S. (1988). Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences of the United States of America*, *85*(6), 1878–1882. https://doi.org/10.1073/pnas.85.6.1878

Fayet, A. L., Freeman, R., Shoji, A., Kirk, H. L., Padget, O., Perrins, C. M., & Guilford, T. (2016). Carry-over effects on the annual cycle of a migratory seabird: An experimental study. *Journal of Animal Ecology*, *85*(6), 1516–1527. https://doi.org/10.1111/1365-2656.12580

Franklin, K. A., Nicoll, M. A. C., Butler, S. J., Norris, K., Ratcliffe, N., Nakagawa, S., & Gill, J. A. (2022). Individual repeatability of avian migration phenology: A systematic review and meta-analysis. *Journal of Animal Ecology*, *91*, 1416–1430. https://doi.org/10.1111/1365-2656.13697

Fusco, G., & Minelli, A. (2010). Phenotypic plasticity in development and evolution: Facts and concepts. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *365*(1540), 547–556. https://doi.org/10.1098/rstb.2009.0267

Galeotti, P., Rubolini, D., Dunn, P. O., & Fasola, M. (2003). Colour polymorphism in birds: Causes and functions. *Journal of Evolutionary Biology*, *16*(4), 635–646. https://doi.org/10.1046/j.1420-9101.2003.00569.x

Gauthreaux, S. A. J. (1982). The ecology and evolution of avian migration systems. In D. S. Farner & J. R. King (Eds.), *Avian biology* (pp. 93–168). Academic Press.

Germain, M., Pärt, T., Gustafsson, L., & Doligez, B. (2017). Natal dispersers pay a lifetime cost to increased reproductive effort in a wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20162445. https://doi.org/10.1098/rspb.2016.2445

Greenwood, P. J. (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, *13*, 1–21. https://www.jstor.org/stable/2097060

Grist, H., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., & Reid, J. M. (2017). Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. *Journal of Animal Ecology*, *86*(5), 1010–1021. https://doi.org/10.1111/1365-2656.12691

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

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multilevel/mixed) regression models*. R package version 0.4.5. https://cran.r-project.org/package=DHARMa

Heim, K. C., Wipfli, M. S., Whitman, M. S., & Seitz, A. C. (2016). Body size and condition influence migration timing of juvenile Arctic grayling. *Ecology of Freshwater Fish*, *25*(1), 156–166. https://doi.org/10.1111/eff.12199

Jahn, A. E., Levey, D. J., Hostetler, J. A., & Mamani, A. M. (2010). Determinants of partial bird migration in the amazon basin. *Journal of Animal Ecology*, *79*(5), 983–992. https://doi.org/10.1111/j.1365-2656.2010.01713.x

Kelly, T. R., MacGillivray, H. L., Sarquis-Adamson, Y., Watson, M. J., Hobson, K. A., & MacDougall-Shackleton, E. A. (2016). Seasonal migration distance varies with natal dispersal and predicts parasitic infection in song sparrows. *Behavioral Ecology and Sociobiology*, *70*(11), 1857–1866. https://doi.org/10.1007/s00265-016-2191-2

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*(5), 940–950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

Kokko, H. (2011). Directions in modelling partial migration: How adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos*, *120*(12), 1826–1837. https://doi.org/10.1111/j.1600-0706.2011.19438.x

Kokko, H., López-Sepulcre, A., & Morrell, L. J. (2006). From hawks and doves to self-consistent games of territorial behavior. *The American Naturalist*, *167*(6), 901–912. https://doi.org/10.1086/504604

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Lenth, R. (2019). *emmeans: Estimated marginal means, aka least-squares means*. R package version 1.4.3.01. https://cran.r-project.org/package=emmeans%0A

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

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

Lundblad, C. G., & Conway, C. J. (2020). Testing four hypotheses to explain partial migration: Balancing reproductive benefits with limits to fasting endurance. *Behavioral Ecology and Sociobiology*, *74*(2), 26. https://doi.org/10.1007/s00265-019-2796-3

McCaslin, H. M., Caughlin, T. T., & Heath, J. A. (2020). Long-distance natal dispersal is relatively frequent and correlated with environmental factors in a widespread raptor. *Journal of Animal Ecology*, *89*(9), 2077–2088. https://doi.org/10.1111/1365-2656.13272

Miller, M. P., Mullins, T. D., Parrish, J. W., Walters, J. R., & Haig, S. M. (2012). Variation in migratory behavior influences regional genetic diversity and structure among American Kestrel populations (*Falco sparverius*) in North America. *Journal of Heredity*, *103*(4), 503–514. https://doi.org/10.1093/jhered/ess024

Morinay, J., Daunt, F., Morley, T. I., Fenn, S. R., Burthe, S. J., & Reid, J. M. (2024). Data from: Carry-over effects of seasonal migration on reproductive success through breeding site retention in a partially migratory bird. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.ffbg79d2t

Pärt, T., & Gustafsson, L. (1989). Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): Possible causes and reproductive consequences. *Journal of Animal Ecology*, *58*(1), 305–320. https://www.jstor.org/stable/5002

R Development Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reid, J. M., & Acker, P. (2022). Properties of phenotypic plasticity in discrete threshold traits. *Evolution*, *76*(2), 190–206. https://doi.org/10.1111/evo.14408

Reid, J. M., Souter, M., Fenn, S. R., Acker, P., Payo-Payo, A., Burthe, S. J., Wanless, S., & Daunt, F. (2020). Among-individual and within-individual variation in seasonal migration covaries with subsequent reproductive success in a partially migratory bird: Plastic migration & reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20200928. https://doi.org/10.1098/rspb.2020.0928rspb20200928

Reid, J. M., Travis, J. M. J., Daunt, F., Burthe, S. J., Wanless, S., & Dytham, C. (2018). Population and evolutionary dynamics in spatially structured seasonally varying environments. *Biological Reviews*, *93*(3), 1578–1603. https://doi.org/10.1111/brv.12409

Ridgway, M. S., MacLean, J. A., & MacLeod, J. C. (1991). Nest-site fidelity in a centrarchid fish, the smallmouth bass (*Micropterus dolomieui*). *Canadian Journal of Zoology*, *69*(12), 3103–3105. https://doi.org/10.1139/z91-436

Robert, A., Paiva, V. H., Bolton, M., Jiguet, F., & Bried, J. (2014). Nest fidelity is driven by multi-scale information in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 1–7. https://doi.org/10.1098/rspb.2014.1692

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., & Müller, M. (2011). pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, *12*, 77. https://doi.org/10.1186/1471-2105-12-77

Rushing, C. S., Dudash, M. R., Studds, C. E., & Marra, P. P. (2015). Annual variation in long-distance dispersal driven by breeding and non-breeding season climatic conditions in a migratory bird. *Ecography*, *38*(10), 1006–1014. https://doi.org/10.1111/ecog.01196

Sabal, M. C., Boyce, M. S., Charpentier, C. L., Furey, N. B., Luhring, T. M., Martin, H. W., Melnychuk, M. C., Srygley, R. B., Wagner, C. M., Wirsing, A. J., Ydenberg, R. C., & Palkovacs, E. P. (2021). Predation landscapes influence migratory prey ecology and evolution. *Trends in Ecology & Evolution*, *36*(8), 737–749. https://doi.org/10.1016/j.tree.2021.04.010

Sahashi, G., & Morita, K. (2018). Adoption of alternative migratory tactics: A view from the ultimate mechanism and threshold trait changes in a salmonid fish. *Oikos*, *127*(2), 239–251. https://doi.org/10.1111/oik.03715

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

Semlitsch, R. D. (2008). Differentiating migration and dispersal processes for pond-breeding amphibians. *Journal of Wildlife Management*, *72*(1), 260–267. https://doi.org/10.2193/2007-082

Senar, J. C., & Pascual, J. (2015). Prior residence effect in wintering male Eurasian siskins is not related to resource holding power. *Behavioral Ecology and Sociobiology*, *69*(7), 1113–1118. https://doi.org/10.1007/s00265-015-1923-z

Shaw, A. K., & Couzin, I. D. (2013). Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *The American Naturalist*, *181*(1), 114–124. https://doi.org/10.1086/668600

Sirot, E., & Touzalin, F. (2014). Temporal patterns of arrival from migration as a response to competition for breeding space. *Journal of Avian Biology*, *45*(1), 109–112. https://doi.org/10.1111/j.1600-048X.2013.00184.x

Studds, C. E., Kyser, T. K., & Marra, P. P. (2008). Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(8), 2929–2933. https://doi.org/10.1073/pnas.0710732105

Taborsky, M., Oliveira, R. F., & Brockmann, H. J. (2008). The evolution of alternative reproductive tactics: Concepts and questions. In R. F. Oliveira, M. Taborsky, & H. J. Brockmann (Eds.), *Alternative reproductive tactics: An integrative approach* (pp. 25–51). Cambridge University Press. https://doi.org/10.1017/CBO9780511542602.003

Terraube, J., Vasko, V., & Korpimäki, E. (2015). Mechanisms and reproductive consequences of breeding dispersal in a specialist predator under temporally varying food conditions. *Oikos*, *124*(6), 762–771. https://doi.org/10.1111/oik.01974

Thibault, J. C., & Thibault, J. C. (1994). Nest-site tenacity and mate fidelity in relation to breeding success in cory's shearwater *Calonectris*

diomedea. *Bird Study*, 41(1), 25–28. https://doi.org/10.1080/00063 659409477193

Walsh, P., Halley, D., Harris, M., del Nevo, A., Sim, I., & Tasker, M. (1995). *Seabird monitoring handbook for Britain and Ireland* (J. Group. (ed.); Vol. 1). NCC/RSPB/ITE/Seabird Group.

Wennersten, L., & Forsman, A. (2012). Population-level consequences of polymorphism, plasticity and randomized phenotype switching: A review of predictions. *Biological Reviews*, 87(3), 756–767. https://doi.org/10.1111/j.1469-185X.2012.00231.x

SUPPORTING INFORMATION

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

SI.1: Nest site and breeding data.

Figure S1: Location of the European shag colony at Bullers of Buchan, the subsites considered (blue circles) and examples of breeding dispersal events between subsites (yellow lines).

Figure S2: Examples of subsite definition and localisation (blue circles).

SI.2: Assignment of migratory tactic from non-breeding sightings.

Table S1: Numbers of positive non-breeding season survey days (i.e., the number of days with at least one local sighting of a local ringed adult), the total numbers of sightings of ringed individuals recorded over these days (i.e., total number of rings read), and the total numbers of ringed individuals resighted for each of the four focal non-breeding seasons (Sept–Feb 2017–2021).

Figure S3: Ternary plots visualizing individual's simplex of class propensities (in %).

SI.3: Results.

Table S2: Output of the GLMMs fitting either the nest site retention (left), subsite retention (middle) or dispersal distance (right), with (top) or without (bottom) non-significant interactions.

Table S3: Output of the GLMMs fitting either the nest site retention (left), subsite retention (middle) or dispersal distance (right) with sex as a covariate, with (top) or without (bottom) non-significant interactions.

Table S4: Output of the GLMMs fitting the individual's reproductive success, when considering nest site retention (left) or subsite retention (right), with (top) or without (bottom) non-significant interactions.

Table S5: Output of the GLMMs fitting the individual's reproductive success, when considering nest site retention (left) or subsite retention (right), with sex as a covariate and with (top) or without (bottom) non-significant interactions.

Table S6: Output of the GLMMs fitting the individual's reproductive success, when considering migratory tactic. We present the models excluding (left) and including (right) the sex effects, with (top) or without (bottom) non-significant interactions.

Table S7: Output of the LMMS and GLMMs fitted for the patch analysis. We present the models considering nest (left) and subsite (right) retention.

Figure S4: Comparison of models fitting the site retention when accounting (red values) or not (triangle) for the uncertainty in migratory tactic assignment.