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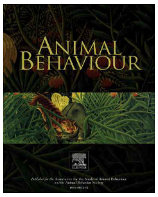

Effects of environmental conditions on mate fidelity in a socially monogamous seabird

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In iteroparous, socially monogamous species, individuals vary in the extent of mate fidelity across breeding attempts, often with important fitness consequences. Numerous studies have demonstrated intrinsic drivers of mate fidelity, notably previous breeding success and parental age. Environmental conditions may also influence mate fidelity, and the habitat-mediated hypothesis predicts that fidelity will be lower when environmental conditions are poor. However, limited testing of this hypothesis has been undertaken in longitudinal studies of single populations. Furthermore, studies have mainly focused on environmental conditions during the breeding season, yet conditions prior to breeding may be important for mate fidelity because this is a critical period for pair bond formation. We investigated the effects of prebreeding environmental conditions (onshore wind component and sea surface temperature) on mate fidelity over a 20-year period in the socially monogamous, iteroparous, long-lived marine bird, the European shag, *Gulosus aristotelis*. Average fidelity rate varied three- to four-fold between years. Mate fidelity was affected by prebreeding environmental conditions, being lower when onshore winds were more prevalent and sea surface temperature was higher. However, mate fidelity was more strongly affected by intrinsic factors, with higher rates when breeding success in the previous attempt and population density were higher, and among older females and middle-aged males. We found that mate fidelity affected timing of breeding, with faithful pairs laying earlier, and early laying pairs bred more successfully, but there was no independent effect of mate fidelity on breeding success. Our results support the habitat-mediated hypothesis whereby prebreeding environmental conditions affect individual pairing decisions. Given environmental conditions are predicted to change globally, further investigation of their impact on aspects of social behaviour in a range of species is warranted.

Social monogamy, in which a male and female form a pair bond to breed, is recorded in a wide range of taxa (Black, 1996; DeWoody et al., 2000). Among iteroparous species, mates may remain faithful between breeding attempts or divorce (Cézilly et al., 2000; Dubois & Cézilly, 2002). In birds, the group in which the majority of research on social monogamy has been conducted, there is considerable variation in mate fidelity rates; that is, the proportion of pairs that remain faithful between breeding attempts where both individuals are alive, from 100% in waved albatross, *Diomedia irrorate* (Harris, 1973), to 0% in greater flamingos, *Phoenicopterus roseus* (Johnson & Cézilly, 2008). Crucially, mate fidelity has important consequences on reproduction (reviewed in Black, 1996; Culina et al., 2015). Advantages of remaining together include better coordination of breeding activities, improved access to resources or energy savings associated with not having to find a new mate (Black, 1996; Chardine, 1987; Culina et al., 2020; McNamara & Forslund, 1996; Sánchez-Macouzet et al., 2014). Accordingly, breeding success is typically higher in faithful pairs (Black, 1996).

A key underpinning question is what factors determine variation in fidelity rates. Past work has shown that effects of environmental conditions on fitness varies among individuals, and accounting for this heterogeneity is crucial to population and evolutionary dynamics (Clutton-Brock, 1988; Nussey et al., 2007). Environmental conditions may also affect social interactions, with some evidence that fidelity rates are lower in populations in which

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environmental conditions are poor (the ‘habitat-mediated hypothesis’; Blondel et al., 2000; Desrochers & Magrath, 1996; Ens et al., 1996; Heg et al., 2003; Wyllie, 1996).

The habitat-mediated hypothesis has generally been tested in cross-sectional studies, whereby populations that vary in habitat or environmental quality are compared, and the focus has been on conditions experienced during the breeding season. However, quantifying temporal variation in mate fidelity in one population allows environmental drivers to be investigated under consistent ecological and life history structures (Bentlage et al., 2025; Sun et al., 2024; Ventura et al., 2021). Furthermore, we lack empirical tests of the effects of conditions in the prebreeding period, often a critical time for pair bond formation. Poor conditions prior to breeding could affect individuals differently, such that former mates come into breeding condition at different times, destabilising pair bonds and resulting in divorce (Gatt et al., 2021; Gunnarsson et al., 2004). The additional time required to form new pair bonds could result in delayed breeding of divorced pairs compared to faithful pairs, with potential consequences for productivity as many studies have shown a negative relationship between breeding timing and success (Verhulst & Nilsson, 2008).

A longitudinal study of black-browed albatross, *Thalassarche melanophris,* demonstrated that mate fidelity rates were typically high (>92%), but they were depressed when prebreeding conditions were poor (Ventura et al., 2021). A second longitudinal study of Seychelles warbler, *Acrocephalus sechellensis*, showed that annual fidelity rates varied from 84%–99% and were lower when preseason rainfall was low or high (Bentlage et al., 2025). Additional tests of the habitat-mediated hypothesis in species in which mate fidelity rates are lower and annual variation in fidelity rates is higher would be useful, because effects of environmental conditions on mate fidelity and consequences for demography could differ. Increased understanding of the links between environmental conditions and mate fidelity rate in socially monogamous species is timely because many populations are being adversely affected by climate change due to rising temperatures (Parmesan, 2006; Spooner et al., 2018) and extreme weather events (Parmesan et al., 2000; van de Pol et al., 2017).

In this study, we investigated the effects of environmental conditions prior to the breeding season on mate fidelity, as a test of the ‘habitat-mediated hypothesis’, and quantified the extent to which mate fidelity affects subsequent breeding timing and success, in a breeding population of European shags, *Gulosus aristotelis* (hereafter ‘shag’), on the Isle of May, southeast Scotland. The shag is long-lived and socially monogamous in each breeding event, and both members of the pair contribute to incubation and chick rearing (B. Snow, 1960). A previous short-term study of this population estimated a mate fidelity rate of 69% (Aebischer et al., 1995), a value which is comparatively low for a long-lived species (Black, 1996). A large number of individuals are marked with unique colour-rings, enabling their life histories to be recorded. Analyses using these data have shown that annual survival rates are strongly affected by environmental conditions during the winter, including extreme weather events (Acker, Burthe, et al., 2021; Acker, Daunt, et al., 2021; Acker et al., 2023; Aebischer, 1993; Frederiksen et al., 2008). Winter conditions also affect the foraging performance of surviving individuals, with carryover effects on subsequent breeding timing (Daunt et al., 2006; Lewis et al., 2015), which, in turn, has a strong effect on breeding success, with a marked decline in productivity apparent in later breeders (Keogan et al., 2021). Variation in individual responses to winter conditions including carryover effects on breeding performance thus make this is an excellent study population to test for links between prebreeding environmental conditions and mate fidelity, and consequences for subsequent breeding timing and success.

METHODS

Study Population and Data Collection

The shag population on the Isle of May National Nature Reserve, southeast Scotland (56°11′N, 02°33′W) has been the subject of a long-term population study since 1961 (Aebischer, 1986; Aebischer et al., 1995; Daunt et al., 1999, 2014; Harris et al., 1994; Howells et al., 2017). Colour-ringing of adults and chicks commenced in 1982 and 1997, respectively, and has continued annually to the present, with more than 12 000 chicks and adults colour-ringed in total. This study is focused on the period of 1997–2016. Colour-ringed breeders were sexed by vocalizations, behaviour and size (B. K. Snow, 1963). During each breeding season, intensive observations identified the sites where colour-ringed birds bred. Our measure of breeding timing was lay date of the first egg in the clutch, either recorded directly or backcalculated from hatching date or chick wing length (following Keogan et al., 2021). Direct recording of laying date was undertaken at a sample of study nests in 18 monitoring plots checked every seven days from before laying. For most nesting attempts, lay date was taken to be three days prior to the first date that incubation was recorded (Keogan et al., 2021). In some cases, the number of eggs in the nest could be counted during the laying period, and lay date could then be estimated with greater accuracy based on standard laying intervals of three days (Potts et al., 1980). The maximum error in lay date was therefore four days for a nest where laying occurred just after the previous check. Laying date was also estimated directly for nests outside monitoring plots from frequent, systematic checks. When laying dates were not directly recorded, they were backcalculated from hatch date using the mean incubation duration of 36 days (Potts et al., 1980) or from chick wing length at ringing (at approximately 20 days of age), using the relationship between wing length and age (F. H. J. Daunt, 2000). Previous work has shown that for broods for which hatch date was both recorded directly and backcalculated from wing length, the mean difference in estimated hatch date was 1.6 ± 2.4 SD days (283 broods; Grist et al., 2017). In this study, of the 1047 cases for which there were two measures of lay date, the correlation between estimates was 0.97. When more than one estimate of lay date was available for a breeding event, and in cases for which the estimates differed, we prioritized direct estimates of laying date, then laying date estimated from hatch date and finally laying date estimated from wing length. Given that natural variation in laying dates between nests is much greater than the uncertainty in estimates of individual lay dates, we are confident that this uncertainty in laying date estimation did not affect our results. Breeding success was recorded as the number of chicks fledged per nest (range 0–4). When a nesting attempt failed and a second clutch was laid, the timing and success of the second attempt was also recorded.

Mate Fidelity

Each female and male in each breeding event was given a mate fidelity score of 1 (that is, faithful individual that bred with the same mate as in the previous breeding event) or 0 (that is, divorced individual that paired with a different mate from the previous breeding event and the former mate was confirmed to be alive and therefore potentially available for pairing). We excluded breeding events in which the former mate was not confirmed alive, since the mate change could have arisen from the death of the former mate. The sampling unit for breeding timing and success was the breeding attempt, and since the fidelity score of females and males was the same in the majority of cases—in particular, they were identical in faithful pairs—we needed to focus our analysis on the fidelity score of one sex. We selected females since they are more likely to have stronger control over timing of laying. In 95.1% of cases, the two adjacent breeding attempts were from separate breeding seasons, the remainder arising when individuals undertook a second breeding attempt in the same year.

Environmental Variables

We considered environmental variables that are known to affect fitness in the study population. Sea surface temperatures (SSTs) in the foraging area used by shags during the prebreeding period (February and March), in the current and previous year, are linked to breeding timing and success in shags and other seabirds breeding on the Isle of May (Burthe et al., 2012, 2014; Frederiksen et al., 2007; Frederiksen, Wanless, et al., 2004; Howells, 2019). The effect is considered indirect, with temperature playing a critical role in somatic development in the lesser sandeel, *Ammodytes marinus*, and the extent of matching with its zooplankton prey (Régnier et al., 2019; 2024; van Deurs et al., 2009). Lesser sandeels aged at least one year old are the principal prey of shags during and outside the breeding season in this population (Howells et al., 2017, 2018), and the dietary proportion is negatively related to prebreeding SST in the previous year (Howells et al., 2017). Young of the year sandeels are also important in the diet of shags, and past studies have found negative links between temperature and recruitment (Arnott & Ruxton, 2002; Lindegren et al., 2018; note that other studies have not found such a relationship e.g. Eerkes-Medrano et al., 2017). In contrast, prebreeding temperatures in the current year may have a positive effect on breeding success (Howells, 2019), potentially by acting directly on shag energy balance, since daily energetic requirements are lower when temperatures are high (White et al., 2011). Prebreeding and lagged prebreeding SST may therefore affect the body condition of shags at this time with carryover effects on breeding performance (Daunt et al., 2006, 2014). Variation in individual responses to prebreeding environmental conditions is strongly evident in this population (Daunt et al., 2014) and could thus lead to heterogeneity in key life history measures including breeding condition and/or commencement of breeding activities, leading to asynchrony in condition or timing between former mates and thus, a greater probability of divorce. Following Frederiksen, Harris, et al. (2004), SST data were extracted for February and March in each year from http://www.bsh.de for an area surrounding the Isle of May that overlapped with foraging distribution in the breeding season (following Bogdanova et al., 2014; bounded by ca. 56°0′N to 56°4′N, and 2°7′W to 2°3′W). The monthly records were averaged to obtain a mean combined February/March SST (°C) for each year.

We also investigated the effect of prebreeding weather, specifically the strength of onshore winds, which influences foraging behaviour, survival and subsequent breeding performance in the study population at this time (Acker, Burthe, et al., 2021; Acker, Daunt, et al., 2021; Aebischer, 1986; Daunt et al., 2006; Frederiksen et al., 2008; Lewis et al., 2015). Following Frederiksen et al. (2008), the February onshore (easterly, 0–180 degrees) wind component (OC) was calculated for each day by multiplying the mean daily wind speed (in knots) by sine (mean daily wind direction) using data from the closest weather station to the breeding colony (Leuchars; 29 km from the Isle of May; 56°23′N, 2°52′W, http://catalogue.ceda.ac.uk/uuid/dbd451271eb04662beade68da43546e1) and then setting the resulting value to 0 if wind direction was westerly (180–360 degrees). Daily values were summed to give the monthly OC for February (February OC days of easterlies).

The Isle of May shag population is partially migratory, with a proportion of adults remaining resident throughout the year and the remainder migrating to destinations located from 500 km to the north to 150 km to the south of the colony outside the breeding season (Acker, Daunt, et al., 2021; Grist et al., 2014). Although the nonbreeding season location of most individuals in this study was unknown, previous work has shown that most migrant individuals return to colonies in January or February (Reid et al., 2020). As such, study individuals could have been distributed across this range during the prebreeding period. We therefore investigated the consistency in conditions experienced across the range. We found SST in February and March to be strongly correlated between waters off the Isle of May and Lossiemouth (57°42′N, 03°18′W, 386 km linear coastline distance to the north of the Isle of May: 0.92), Peterhead (57°30′N, 01°46′W, 247 km to the north: 0.90) and Boulmer (55°25′N, 01°35′W, 108 km to the south: 0.94). Similarly, there was a strong correlation in February OC across the nonbreeding season range (correlation coefficients between Leuchars weather station and those at Lossiemouth: 0.96; Peterhead: 0.87; Boulmer: 0.86). As such, we were confident that all individuals experienced similar sea temperatures and wind conditions in each prebreeding period.

Intrinsic Factors

We also considered intrinsic factors because numerous past studies have shown them to be important determinants of mate fidelity (Black, 1996). In particular, divorce is more likely following poor breeding performance the previous year (hereafter, ‘previous breeding success’) and is lower in middle-aged individuals (Black, 1996; Culina et al., 2015; Daunt et al., 1999; Dubois & Cézilly, 2002; Forslund & Pärt, 1995; Gousy-Leblanc et al., 2023; Sánchez-Macouzet et al., 2014).

Population density is also an important intrinsic population characteristic that may affect mate fidelity. At lower density following a winter of poor survival, effects of individual heterogeneity in prebreeding condition on fidelity rates may be exacerbated by a higher number of individuals whose mates have died, increasing the availability of potential mates and opportunities for divorce (Jeschke & Kokko, 2008; McNamara & Forslund, 1996). In contrast, at higher population densities following winters in which survival is above average, there may be elevated recruitment of inexperienced individuals seeking a mate for the first time, thereby providing more alternative mates that could trigger higher probability of divorce. The effects of population size on mate fidelity rates might therefore be, respectively, negative or positive depending on the relative importance of these two mechanisms.

As the previous breeding success of females and males among faithful pairs was identical, we only fitted one term that of female previous breeding success. We also considered linear and quadratic female and male age to account for the higher fidelity rates and breeding success in middle-aged individuals on average. Individuals were either of known age if ringed as chicks or assumed to be aged 3 at ringing (the modal age at first breeding) if ringed as adults (following Grist et al., 2014). Population size in each year was the number of breeding pairs estimated from a count of Apparently Occupied Nests undertaken each June (Outram & Steel, 2016).

Statistical Analysis

Our sample comprised 1839 breeding events from 763 females and 761 males. We did not include second breeding attempts in the analysis because mechanisms linking preseason environmental conditions to pairing decisions are unlikely to apply in the same way. We fitted three main sets of models to the following response variables: (1) mate fidelity, where the response was 1 (faithful) or 0 (divorced); (2) lay date (1 January = 1); and (3) breeding success (chicks fledged per laying female, with value of 0–4 inclusive). We fitted the three environmental variables (prebreeding SST; lagged prebreeding SST; February OC), quadratic female and male age, previous breeding success and current population size to models of mate fidelity. All predictor variables were standardized using *scale* in R. Year was included in models of mate fidelity as a continuous variable to account for the possibility of a spurious relationship between the response variable and fixed effects where both show correlated trends over time. The environmental time series were detrended prior in the analysis to avoid additional spurious relationships that may arise due to between-year correlations between predictor and response variables. We then modelled the effect of mate fidelity on lay date and the effect of mate fidelity and lay date on breeding success. All models of mate fidelity, lay date and breeding success included individual female identity (*bird*) and categorical year (*yearF*) as random effects to account for nonindependence of observations within individuals and years. Because random terms are structural, we included them in all models. The structure of the three models was as follows:

Model 1:

$$\text{mate fidelity} \sim \text{Binomial}(p, 1)$$

$$\begin{aligned}\log\left(\frac{p}{1-p}\right) = {} & \text{previous breeding success} + \text{female age} \\ & + \text{female age}^2 + \text{male age} + \text{male age}^2 \\ & + \text{population size} + \text{year} + \text{february oc} \\ & + \text{feb}\Big/\text{mar sst} + \text{lagged feb}\Big/\text{mar sst} + \textit{bird} \\ & + \textit{yearF}\end{aligned}$$

Model 2:

$$\text{lay date} \sim \text{Normal}\left(\mu, \sigma^2\right)$$

$$\mu = \text{mate fidelity} + \textit{bird} + \textit{yearF}$$

Model 3:

$$\text{breeding success} \sim \text{Binomial}(p, m)$$

$$\log\left(\frac{p}{1-p}\right) = \text{mate fidelity} + \text{lay date} + \textit{bird} + \textit{yearF}$$

where m is maximum brood size.

The relationship between mate fidelity (0 and 1) and explanatory variables was modelled in a generalized linear mixed model (GLMM) with a binomial error distribution with logit link (Zuur et al., 2009). The relationship between lay date and mate fidelity was modelled with a linear mixed model with a Gaussian error distribution (Zuur et al., 2009). Although date is a circular variable, the constrained range of lay dates relative to the full set of date values justified the choice of error distribution. Lay date values were standardized using *scale* in *R*, which subtracts the mean and divides by the SD (range −2.5 to 5). The effect of mate fidelity and lay date on breeding success was modelled in a GLMM with a binomial error distribution with logit link (Zuur et al., 2009), with four as the maximum number of fledged chicks. In using a binomial model, we were essentially treating the maximum brood size as representing the number of 'potential' chicks that exist for each nest and are then treating the fate of each of these potential chicks (e.g. whether they translate into a fledged chick) as a Bernoulli trial. The binomial probability is therefore quantifying the probability that each potential chick will translate into a fledged chick. The idea of a potential chick is a conceptual one: the number of eggs actually laid will often be lower than this number. This model is designed to capture the assumption that there is a biological constraint on the maximum number of fledged chicks per nest, in contrast to alternative count models, such as the Poisson or negative binomial, which would not impose any upper limit on the number of fledged chicks.

For the models on mate fidelity, model selection was performed on the 576 possible model combinations of the fixed effects (model 1) using Akaike Information Criterion (AIC). We considered all possible model combinations because the evidence for the effects of environmental variables, intrinsic variables and population density on mate fidelity are from other populations (e.g. Black, 1996; Blondel et al., 2000; Culina et al., 2015; Dubois & Cézilly, 2002; Jeschke & Kokko, 2008; Ventura et al., 2021) or, in the case of parental age, from incomplete evidence on the extent of the effect across all age classes (Aebischer et al., 1995 compared first time and older breeders only). Models within two AIC of the model with lowest AIC (ΔAIC <2) were, in general, considered to have equivalent support to the model with lowest AIC (Burnham & Anderson, 2002). When applying this rule, however, we did not regard models as having equivalent support if they were more complicated than the model with lower AIC value and the model with lower AIC value was nested within them. To model lay date, we compared the AIC of a model with mate fidelity (model 2) and a null model to determine the importance of mate fidelity on lay date. For breeding success, we compared the AIC models of mate fidelity, lay date and fidelity + lay date (model 3) with a null model to determine the importance of mate fidelity on breeding success.

Correlations between all predictor variables in the models on mate fidelity were checked (Table S1) to ensure that none were >0.7, at which problems are considered to arise when fitting two variables to the same model (Dormann et al., 2013). We also calculated variance inflation factors (R package *car*) to assess multicollinearity of predictor variables (Table S2). All our values were well below 5 (maximum 1.866; thresholds of 5 or 10 are commonly used; Marcoulides & Raykov, 2019). As such, we were confident that we could fit all variables to the same model without compromising the robustness of the results.

In all cases, model selection was performed using the *lme4* and *MuMIn* packages in *R* version 3.5.1 (RStudio version 1.1.456). Diagnostic plots to assess distributional assumptions were checked when appropriate (e.g. to assess the assumption of normality in the linear mixed models). In plots, confidence intervals were calculated via a semiparametric bootstrap procedure using the 'bootMer' function from the 'lme4' package. The number of bootstrap samples was set to 100, the maximum that was practically feasible given the computational time required for bootstrapping. The lines of best fit use predicted values derived by varying, in turn, each of the explanatory variables included in the top model, with all other explanatory variables held at their mean value.

Ethical Note

All breeding data were collected under an annual National Nature Reserve research licence issued by NatureScot (no. MON/RP/169 and its predecessors). All ringing was undertaken under a British Trust for Ornithology permit (no. S4607, colour-ringing endorsement project no. 5952). Birds were captured by standard BTO catching techniques for seabirds, using a crook on the end of a long pole (adults and chicks) or by hand (chicks). Handling time was typically <5 minutes, and birds returned to normal behaviour immediately or within a few minutes after release.

RESULTS

Variation in Mate Fidelity, Population Size, Timing of Breeding and Breeding Success

Of 1839 breeding events from 763 females and 761 males, mate fidelity rate in females and males was 45.4% and 45.3% respectively. Mate fidelity rate varied between years (range 20%–72% in females; 18%–75% in males; Fig. S1). Annual variation was also apparent in breeding population size (range 259–968 pairs; Fig. S1); timing of breeding (range in median lay date: 2 April to 18 May; Fig. S1) and breeding success (range in average chicks fledged per nest: 1.17–2.50; Fig. S1).

Mate Fidelity

The standardized, and therefore comparable, effect sizes of each explanatory variable of all models within two ΔAIC of the top model are presented in Table 1 (full list of models in Table S3). There was evidence for a negative effect of February OC on mate fidelity, which was present in 8 of the top 10 models (range across models excluding those that were more complicated than the model with lower AIC value and the model with lower AIC value was nested within them: −0.203 to −0.118; Table 1, Fig. 1). We found more limited support for an effect of SST, present in 5 of the 10 models (range −0.145 to −0.139; Table 1, Fig. 1). There was little evidence for an effect of lagged SST on mate fidelity (present in 1 of 10 models; Table 1).

Intrinsic effects generally had stronger effects on mate fidelity, present in a high proportion of supported models and most with higher effect sizes. Specifically, previous breeding success and population size were both positively related to mate fidelity, with a greater likelihood of faithfulness if previous breeding success was high and at larger population sizes (both variables present in all 10 models; previous breeding success: range 0.239–0.253; population size: range 0.427–0.464; Table 1, Fig. 1). There was evidence of a positive effect of female age on mate fidelity (present in 9 of 10 models; range 0.113–0.114; Table 1; Fig. 1) and a quadratic effect of male age such that mate fidelity was higher among middle-aged individuals (present in all 10 models; linear effect size: range 0.364–0.387; quadratic effect size: range −0.135 to −0.128; Table 1, Fig. 1). However, there was only limited support for an effect of quadratic female age (present in 2 of 10 models; Table 1) or year (present in 3 of 10 models; Table 1).

Breeding Timing and Success

The model of lay date containing mate fidelity had stronger support than the null model (ΔAIC = 13.84). The effect of mate fidelity on lay date was negative, such that faithful pairs laid earlier in the season on average (Table 2, Fig. 2). The models of breeding success containing lay date had strong support (Table 3). There was no support for an effect of mate fidelity on breeding success, as the model containing mate fidelity and laying date had a higher AIC than the model just containing lay date (Table 3; ΔAIC = 1.70).

DISCUSSION

In this study, we investigated the environmental determinants of mate fidelity in European shags and found support for the habitat-mediated hypothesis. Mate fidelity was affected by environmental conditions in the prebreeding period, such that when

Table 1
Output from the top models (1–10) ranked by AIC on mate fidelity in relation to female and male age, previous breeding success, population size, February onshore wind component, SST, lagged SST and year in European shags

Top models	1		2		3		4		5		6		7		8		9		10	
Fixed effects	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Female prev bs	0.24	0.06	0.25	0.06	0.24	0.06	0.24	0.06	0.25	0.06	0.24	0.06	0.25	0.06	0.25	0.06	0.25	0.06	0.24	0.06
Female age	0.11	0.06	0.11	0.06	0.11	0.06	0.11	0.06	0.11	0.06	0.14	0.07			0.11	0.06	0.11	0.06	0.15	0.07
Female age^2											−0.03	0.05							−0.03	0.05
Male age	0.36	0.07	0.37	0.07	0.37	0.07	0.36	0.07	0.37	0.07	0.36	0.07	0.39	0.06	0.37	0.07	0.37	0.07	0.36	0.07
Male age^2	−0.13	0.05	−0.13	0.05	−0.13	0.05	−0.13	0.05	−0.13	0.05	−0.12	0.05	−0.14	0.05	−0.13	0.05	−0.13	0.05	−0.13	0.05
Pop size	0.45	0.07	0.43	0.07	0.43	0.08	0.43	0.07	0.42	0.08	0.45	0.07	0.46	0.07	0.39	0.09	0.40	0.09	0.44	0.07
Feb OC	−0.20	0.09	−0.12	0.08			−0.22	0.09	−0.19	0.09	−0.20	0.09	−0.20	0.09			−0.11	0.08	−0.12	0.08
Feb Mar SST	−0.14	0.09					−0.15	0.09	−0.14	0.09	−0.14	0.09	−0.14	0.09						
Feb Mar SST-1							−0.06	0.08												
Year									−0.05	0.08					−0.08	0.09	−0.06	0.08		
Random effects	Var	SD	Var	SD	Var	SD	Var	SD	Var	SD	Var	SD	Var	SD	Var	SD	Var	SD	Var	SD
Individual	0.46	0.68	0.46	0.68	0.47	0.68	0.46	0.68	0.46	0.68	0.46	0.68	0.46	0.68	0.47	0.68	0.46	0.68	0.46	0.68
Year	0.03	0.16	0.04	0.20	0.05	0.23	0.02	0.14	0.03	0.16	0.03	0.16	0.03	0.18	0.06	0.24	0.04	0.20	0.04	0.20
AIC	2382.6		2383.0		2383.2		2384.0		2384.1		2384.2		2384.2		2384.4		2384.4		2384.5	
ΔAIC	0.00		0.40		0.60		1.40		1.50		1.60		1.60		1.80		1.80		1.90	

Estimates (Est), SE, variance components (Var), SD, Akaike information criterion (AIC) and ΔAIC from the models on mate fidelity in relation to previous breeding success (prev bs), female and male linear and quadratic age, population (pop) size, February onshore wind component (OC), February/March sea surface temperature (SST), lagged February/March sea surface temperature and study year for European shags breeding on the Isle of May from 1997–2016. Only models ($N = 10$) within 2 ΔAIC of the model with the lowest AIC (model 1) are shown. Models are ordered by increasing AIC (see Table S3 for full set of models).

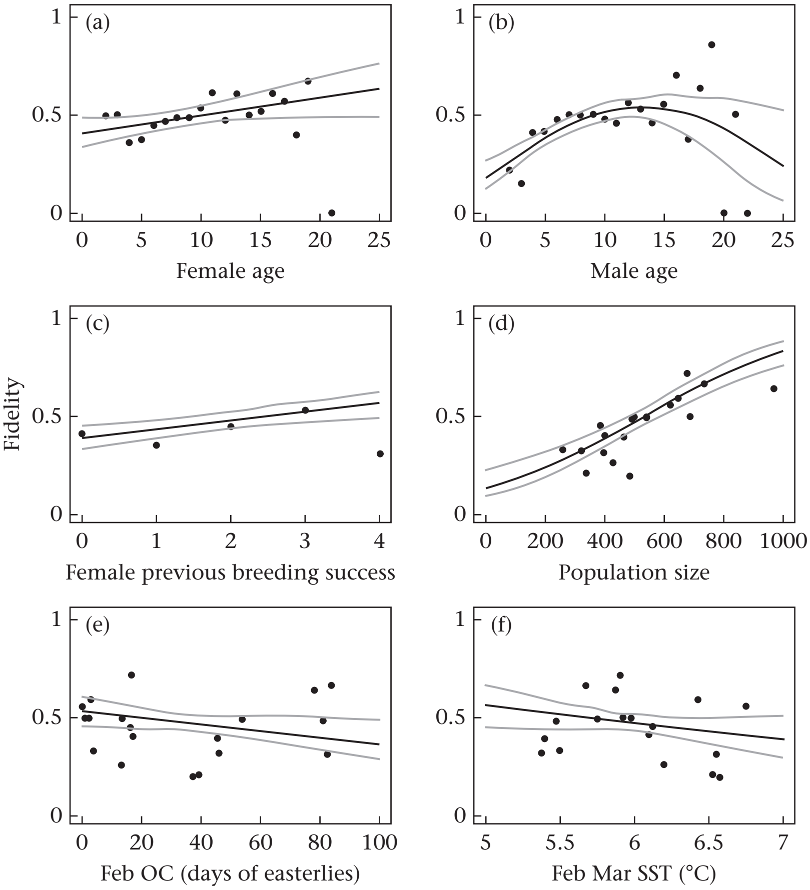

Figure 1. The relationship between mate fidelity and (a) female age (years), (b) male age (years), (c) previous breeding success (chicks fledged per laying female), (d) population size (number of breeding pairs), (e) February onshore wind component (OC, days of easterlies) and (f) February/March sea surface temperature (SST, °C) for European shags breeding on the Isle of May from 1997–2016. Lines of best fit shown as thick line and confidence intervals as thin lines; mate fidelity rates (that is, the proportion of pairs that remain faithful between breeding attempts when both individuals are alive) for each value of x are shown as points.

Table 2
Output from the model on timing of breeding (lay date) in relation to mate fidelity in European shags

Fixed effects	Estimate	SE
(Intercept)	0.599	0.202
Mate fidelity	−0.068	0.017
Random effects	Variance component	SD
Variance of individual effects	0.188	0.434
Variance of year effects	0.749	0.866
Residual variance	0.355	0.596

Estimates, SE, variance components and SD from the model on timing of breeding (lay date) in relation to mate fidelity in European shags breeding on the Isle of May from 1997–2016. The intercept corresponds to the centred value for females.

conditions were less favourable (increased onshore wind and higher SST), mate fidelity was lower. However, intrinsic factors had a stronger effect on mate fidelity, notably previous breeding success, parental age and population size.

The link between environmental conditions and mate fidelity has to date largely been considered in the context of habitat quality in the breeding season (habitat-mediated hypothesis: Blondel et al., 2000; Desrochers & Magrath, 1996; Ens et al., 1996; Heg et al., 2003; Wyllie, 1996). To our knowledge, only two studies have tested the effects of prebreeding conditions on mate fidelity rates (Bentlage et al., 2025; Ventura et al., 2021). They demonstrated the importance of environmental conditions prior to the

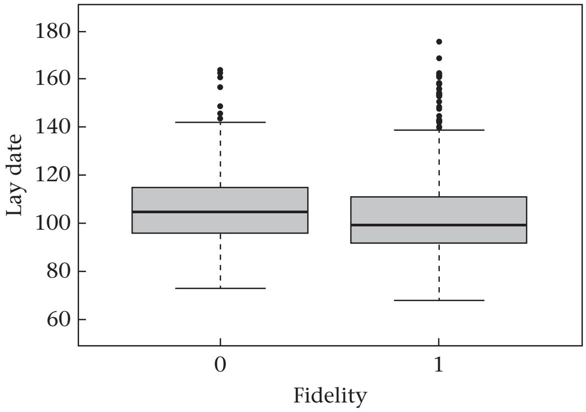

Figure 2. The relationship between lay date (1 January = 1) and mate fidelity (0 = divorced; 1 = faithful) for European shags breeding on the Isle of May from 1997–2016.

breeding season on mate fidelity in the black-browed albatross and Seychelles warbler, respectively. Both followed the rationale that mating decisions may be dependent on decisions made at various times prior to breeding but took different approaches to the time window of environmental conditions considered. Ventura et al. (2021) considered a fixed 12-month period prior to the breeding season. In contrast, Bentlage et al. (2025) undertook a

Table 3
Output from the models on breeding success in relation to mate fidelity and lay date in European shags

Models	Lay date		Fidelity + lay		Fidelity × lay		Null		Fidelity	
Fixed effects	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Fidelity			−0.015	0.025	−0.014	0.025			0.021	0.024
Lay date	**−0.294**	**0.031**	−0.297	0.031	−0.303	0.032				
Fidelity × lay date					0.032	0.025				
Random effects	Var	SD	Var	SD	Var	SD	Var	SD	Var	SD
Individual	**0.000**	**0.000**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Year	**0.055**	**0.235**	0.054	0.233	0.055	0.235	0.091	0.302	0.092	0.303
AIC	**4678.7**		4680.4		4680.7		4770.9		4772.2	
ΔAIC	**0.00**		1.63		1.93		92.21		93.49	

Estimates (Est), SE, variance components (Var), SD, Akaike information criterion (AIC) and ΔAIC from all models on breeding success in relation to mate fidelity and lay date in European shags breeding on the Isle of May from 1997–2016, ordered by AIC. Values for the best or 'top' model (the model with the lowest AIC) are shown in bold.

climate window analysis of all possible combinations of months before and during the breeding season to identify the window that had the largest effect on probability of divorce. Here, we focused on a time window in the prebreeding period that previous studies had shown was important in determining foraging effort and subsequent breeding timing and success in the study population, and is thus a critical window driving variation in condition and fitness (Daunt et al., 2006, 2014; Frederiksen et al., 2007; Lewis et al., 2015).

In contrast to the high fidelity rates in black-browed albatrosses and Seychelles warblers reported in Ventura et al. (2021) and Bentlage et al. (2025), respectively, shags in our population exhibited a much lower mate fidelity rate (45%), with marked interannual variation. The late winter condition that had the strongest effect on annual variation in fidelity rates was wind, such that mate fidelity was lower when onshore wind conditions were more challenging. This finding aligns with previous work showing that wind conditions have an important effect on key aspects of this population's ecology and life history, affecting foraging performance (Daunt et al., 2006), breeding propensity (Aebischer, 1986) and survival probability (Acker, Daunt, et al., 2021; Frederiksen et al., 2008). We also found some evidence that mate fidelity rates were lower following warm late winter SST in the current year, which may result from temperature-related effects on prey abundance or quality (Arnott & Ruxton, 2002; Lindegren et al., 2018). In socially monogamous species exhibiting biparental care, individuals typically form pair bonds over an extended period prior to the onset of breeding (egg laying in birds; Black, 1996; Clutton-Brock, 1988, 1991). At this time, individuals will interact socially and undertake mate choice. It is therefore critical that individuals attain good condition to pair up and then breed at the optimal time. Individual variation is predicted to be most marked when environmental conditions are poor, and this may lead to mismatches in terms of condition and timing (Gatt et al., 2021; Gunnarsson et al., 2004). Although we had no individual data on prebreeding body condition or scheduling, we know that shags commence key social interactions such as pair formation and nest site defence several weeks prior to laying (B. K. Snow, 1963), and therefore, the effects of environmental conditions on individual state at this time likely play a role in determining mate fidelity.

We found that mate fidelity was affected by intrinsic processes, and these effects were mostly stronger than the impact of prebreeding environmental conditions. Predictions that mate fidelity would be lower following low breeding success in the previous year align with findings in numerous studies (Cézilly et al., 2000; Dubois & Cézilly, 2002; Gousy-Leblanc et al., 2023; Sánchez-Macouzet et al., 2014). Thus, individuals appear to be adopting a win-stay, lose-switch strategy whereby they remain with mates when they have been successful. Mate fidelity rates increased with increasing age of both sexes and then declined in males, findings that align with a considerable body of past research that has shown an increase with parental age or a quadratic relationship with senescent effects in old age (reviewed in Black, 1996; Culina et al., 2015). We also found that mate fidelity increased at higher population size. An earlier study in this population recorded an average fidelity rate of 69% in two years (1982 and 1983), which is somewhat higher than the average rate that we recorded, but when the population size was also higher at 1425 and 1567 breeding pairs, respectively (Aebischer et al., 1995). Those population sizes are outside the range recorded in our study years, so it is challenging to formally compare with our results, but they are in keeping with the relationship we found (Fig. 1d). This positive relationship with population size may be linked to over-winter environmental conditions, which determines the survival rate—and hence breeding population density—but also the intrinsic state of surviving individuals, which could determine their likelihood of mate fidelity. Effects could also be driven by population structure, whereby at low density the population comprises a higher proportion of widowed individuals that are available for mating, providing more opportunities for divorce (Jeschke & Kokko, 2008; McNamara & Forslund, 1996).

Mate fidelity was related to timing of breeding, such that divorced pairs bred later on average than faithful pairs, as previously recorded in this population (Aebischer et al., 1995). Although we could not test this directly with our data, it is possible that it takes time to establish a new pair bond, which delays the onset of laying. This could arise if divorce is not a mutual arrangement but largely determined by one individual, who pairs with a new mate, resulting in the former mate needing to find a new partner (Jeschke et al., 2007). In such cases, the individual that instigated the divorce may breed earlier, potentially at the same average time as faithful pairs, and the divorced mate may breed later on average because it requires time to find a new partner. This would lead to later average breeding among divorced pairs. As shown previously, there is a strong negative relationship between timing of breeding and success in this population (Keogan et al., 2021). However, we found no effect of mate fidelity on breeding success despite the link to timing of breeding. One possibility is that the effect of fidelity on timing of breeding was not sufficiently large to result in a detectable effect of mate fidelity on breeding success, despite the effect of lay date on breeding success. However, these results should be treated with caution, as we were unable to account for environmental or intrinsic factors that may drive lay date and breeding success because they had important effects on mate fidelity and could not therefore be fitted alongside fidelity to the subsequent models on lay date and breeding success.

The effects of prebreeding environmental conditions on mate fidelity have hitherto been underappreciated in iteroparous, socially monogamous species. Our study, coupled with findings in Ventura et al. (2021) and Bentlage et al. (2025) in two species with radically different mate fidelity rates from shags suggests that these effects warrant further investigation in a broader range of species, given that the climate is predicted to become warmer and more extreme over many parts of the world in the coming decades (Intergovernmental Panel on Climate Change, 2021).

Author Contributions

Sue Lewis: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Adam Butler:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Sarah Wanless:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition. **Mark A. Newell:** Resources, Methodology, Investigation, Data curation. **Michael P. Harris:** Resources, Project administration, Methodology, Investigation, Funding acquisition. **Sarah J. Burthe:** Resources, Methodology, Investigation, Data curation. **Carrie M. Gunn:** Resources, Methodology, Investigation, Data curation. **Richard J. Howells:** Writing – review & editing, Methodology, Investigation. **Francis Daunt:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation.

Data Availability

The data are available in the Supplementary material.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123356.

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. Biological Sciences, 288*(1951), Article 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. L., 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. *American Naturalist, 201*(2), 269–286. https://doi.org/10.1086/722484

Aebischer, N. J. (1986). Retrospective investigation of an ecological disaster in the shag, *Phalacrocorax aristotelis*: A general method based on long-term marking. *Journal of Animal Ecology, 55*(2), 613–629. https://doi.org/10.2307/4743

Aebischer, N. J. (1993). Immediate and delayed effects of a gale in late spring on the breeding of the shag Phalacrocorax aristotelis. *Ibis, 135*(3), 225–232. https://doi.org/10.1111/j.1474-919X.1993.tb02838.x

Aebischer, N. J., Potts, G. R., & Coulson, J. C. (1995). Site and mate fidelity of shags *Phalacrocorax aristotelis* at 2 British colonies. *Ibis, 137*(1), 19–28. https://doi.org/10.1111/j.1474-919X.1995.tb03215.x

Arnott, S. A., & Ruxton, G. D. (2002). Sandeel recruitment in the north sea: Demographic, climatic and trophic effects. *Marine Ecology Progress Series, 238*, 199–210. https://doi.org/10.3354/meps238199

Bentlage, A. A., Speelman, F. J. D., Komdeur, J., Burke, T., Richardson, D. S., & Dugdale, H. L. (2025). Rainfall is associated with divorce in the socially monogamous Seychelles warbler. *Journal of Animal Ecology, 94*(1), 85–98. https://doi.org/10.1111/1365-2656.14216

Black, J. M. (1996). *Partnerships in birds: the study of monogamy*. Oxford University Press. https://doi.org/10.1093/oso/9780198548614.001.0001

Blondel, J., Perret, P., & Galan, M. J. (2000). High divorce rates in Corsican blue tits: How to choose a better option in a harsh environment. *Oikos, 89*(3), 451–460. https://doi.org/10.1034/j.1600-0706.2000.890304.x

Bogdanova, M. I., Wanless, S., Harris, M. P., Lindström, J., Butler, A., Newell, M. A., Sato, K., Watanuki, Y., Parsons, M., & Daunt, F. (2014). Among-year and within-population variation in foraging distribution of European shags *Phalacrocorax aristotelis* over two decades: Implications for marine spatial planning. *Biological Conservation, 140*, 292–299. https://doi.org/10.1016/j.biocon.2013.12.025

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd ed.). Springer.

Burthe, S., Daunt, F., Butler, A., Elston, D. A., Frederiksen, M., Johns, D., Newell, M., Thackeray, S. J., & Wanless, S. (2012). Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Marine Ecology Progress Series, 454*, 119–133. https://doi.org/10.3354/meps09520

Burthe, S. J., Wanless, S., Newell, M. A., Butler, A., & Daunt, F. (2014). Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts. *Marine Ecology Progress Series, 507*, 277–295. https://doi.org/10.3354/meps10849

Cézilly, F., Préault, M., Dubois, F., Faivre, B., & Patris, B. (2000). Pair-bonding in birds and the active role of females: A critical review of the empirical evidence. *Behavioural Processes, 51*(1–3), 83–92. https://doi.org/10.1016/s0376-6357(00)00120-0

Chardine, J. W. (1987). The influence of pair-status on the breeding behaviour of the Kittiwake *Rissa tridactyla* before egg-laying. *Ibis, 129*(s2), 515–526. https://doi.org/10.1111/j.1474-919X.1987.tb08239.x

Clutton-Brock, T. H. (1988). *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton University Press.

Culina, A., Firth, J. A., & Hinde, C. A. (2020). Familiarity breeds success: Pairs that meet earlier experience increased breeding performance in a wild bird population. *Proceedings. Biological Sciences, 287*(1941), Article 20201554. https://doi.org/10.1098/rspb.2020.1554

Culina, A., Radersma, R., & Sheldon, B. C. (2015). Trading up: The fitness consequences of divorce in monogamous birds. *Biological Reviews of the Cambridge Philosophical Society, 90*(4), 1015–1034. https://doi.org/10.1111/brv.12143

Daunt, F. H. J. (2000). *The effects of parental age on reproductive performance in the shag Phalacrocorax aristotelis*. University of Glasgow.

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

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

Daunt, F., Wanless, S., Harris, M. P., & Monaghan, P. (1999). Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings. Biological Sciences, 266*(1427), 1489–1493. https://doi.org/10.1098/rspb.1999.0805

Desrochers, A., & Magrath, R. D. (1996). Divorce in the European blackbird: Seeking greener pastures? In J. M. Black (Ed.), *Partnerships in birds: the study of monogamy* (pp. 249–267). Oxford University Press.

DeWoody, J. A., Fletcher, D. E., Wilkins, S. D., Nelson, W. S., & Avise, J. C. (2000). Genetic monogamy and biparental care in an externally fertilizing fish, the largemouth bass (*Micropterus salmoides*). *Proceedings. Biological Sciences, 267*(1460), 2431–2437. https://doi.org/10.1098/rspb.2000.1302

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dubois, F., & Cézilly, F. (2002). Breeding success and mate retention in birds: A meta-analysis. *Behavioral Ecology and Sociobiology, 52*(5), 357–364. https://doi.org/10.1007/s00265-002-0521-z

Eerkes-Medrano, D., Fryer, R. J., Cook, K. B., & Wright, P. J. (2017). Are simple environmental indicators of food web dynamics reliable: Exploring the kittiwake–temperature relationship. *Ecological Indicators, 75*, 36–47. https://doi.org/10.1016/j.ecolind.2016.12.019

Ens, B. J., Choudhury, S., & Black, J. M. (1996). Mate fidelity and divorce in monogamous birds. In J. M. Black (Ed.), *Partnerships in birds: the study of monogamy* (pp. 344–402). Oxford University Press.

Forslund, P., & Pärt, T. (1995). Age and reproduction in birds - hypotheses and tests. *Trends in Ecology & Evolution, 10*(9), 374–378. https://doi.org/10.1016/S0169-5347(00)89141-7

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

Frederiksen, M., Harris, M. P., Daunt, F., Rothery, P., & Wanless, S. (2004). Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology, 10*(7), 1214–1221. https://doi.org/10.1111/j.1529-8817.2003.00794.x

Frederiksen, M., Mavor, R. A., & Wanless, S. (2007). Seabirds as environmental indicators: The advantages of combining data sets. *Marine Ecology Progress Series, 352*, 205–211. https://doi.org/10.3354/meps07071

Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P., & Wilson, L. J. (2004). The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology, 41*(6), 1129–1139. https://doi.org/10.1111/j.0021-8901.2004.00966.x

Gatt, M. C., Versteegh, M., Bauch, C., Tieleman, B. I., Granadeiro, J. P., & Catry, P. (2021). Costs of reproduction and migration are paid in later return to the colony, not in physical condition, in a long-lived seabird. *Oecologia, 195*(2), 287–297. https://doi.org/10.1007/s00442-020-04775-w

Gousy-Leblanc, M., Merkling, T., Whelan, S., Gaston, A. J., Friesen, V. L., & Elliott, K. H. (2023). Go your own way? Reasons for divorce in a monogamous seabird. *Animal Behaviour, 204*, 13–24. https://doi.org/10.1016/j.anbehav.2023.07.007

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), Article e98562. https://doi.org/10.1371/journal.pone.0098562

Gunnarsson, T. G., Gill, J. A., Sigurbjörnsson, T., & Sutherland, W. J. (2004). Pair bonds: Arrival synchrony in migratory birds. *Nature, 431*(7009), 646. https://doi.org/10.1038/431646a

Harris, M. P. (1973). The biology of the waved albatross *Diomedia irrorata* of the Hood Island. *Galapagos. Ibis, 115*(4), 483–510. https://doi.org/10.1111/j.1474-919X.1973.tb01988.x

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

Heg, D., Bruinzeel, L. W., & Ens, B. J. (2003). Fitness consequences of divorce in the oystercatcher, Haematopus ostralegus. *Animal Behaviour, 66*, 175–184. https://doi.org/10.1006/anbe.2003.2188

Howells, R. J. (2019). *European shag diet and demography at a North Sea colony over half a century of environmental change* ([Doctoral dissertation, University of Liverpool]).

Howells, R. J., Burthe, S. J., Green, J. A., Harris, M. P., Newell, M. A., Butler, A., Johns, D. G., Carnell, E. J., Wanless, S., & Daunt, F. (2017). From days to decades: Short- and long-term variation in environmental conditions affect offspring diet composition of a marine top predator. *Marine Ecology Progress Series, 583*, 227–242. https://doi.org/10.3354/meps12343

Howells, R. J., Burthe, S. J., Green, J. A., Harris, M. P., Newell, M. A., Butler, A., Wanless, S., & Daunt, F. (2018). Pronounced long-term trends in year-round diet composition of the European shag *Phalacrocorax aristotelis*. *Marine Biology, 165*(12), 188. https://doi.org/10.1007/s00227-018-3433-9

Intergovernmental Panel on Climate Change (IPCC). (2021). Summary for policymakers. In *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3–32). Cambridge University Press. https://doi.org/10.1017/9781009157896.001.

Jeschke, J. M., & Kokko, H. (2008). Mortality and other determinants of bird divorce rate. *Behavioral Ecology and Sociobiology, 63*(1), 1–9. https://doi.org/10.1007/s00265-008-0646-9

Jeschke, J. M., Wanless, S., Harris, M. P., & Kokko, H. (2007). How partnerships end in guillemots *Uria aalge*: Chance events, adaptive change, or forced divorce? *Behavioral Ecology, 18*(2), 460–466. https://doi.org/10.1093/beheco/arl109

Johnson, A., & Cézilly, F. (2008). *The greater flamingo*. T. & A.D. Poyser.

Keogan, K., Lewis, S., Howells, R. J., Newell, M. A., Harris, M. P., Burthe, S., Phillips, R. A., Wanless, S., Phillimore, A. B., & Daunt, F. (2021). No evidence for fitness signatures consistent with increasing trophic mismatch over 30 years in a population of European shag *Phalacrocorax aristotelis*. *Journal of Animal Ecology, 90*(2), 432–446. https://doi.org/10.1111/1365-2656.13376

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

Lindegren, M., Van Deurs, M., MacKenzie, B. R., Worsoe Clausen, L., Christensen, A., & Rindorf, A. (2018). Productivity and recovery of forage fish under climate change and fishing: North Sea sandeel as a case study. *Fisheries Oceanography, 27*(3), 212–221. https://doi.org/10.1111/fog.12246

Marcoulides, K. M., & Raykov, T. (2019). Evaluation of variance inflation factors in regression models using latent variable modeling methods. *Educational and Psychological Measurement, 79*(5), 874–882. https://doi.org/10.1177/0013164418817803

McNamara, J. M., & Forslund, P. (1996). Divorce rates in birds: Predictions from an optimization model. *American Naturalist, 147*(4), 609–640. https://doi.org/10.1086/285869

Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology, 20*(3), 831–844. https://doi.org/10.1111/j.1420-9101.2007.01300.x

Outram, B., & Steel, D. (2016). *Isle of may national nature Reserve annual report 2016. Scottish natural heritage (now NatureScot) report*.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics, 37*, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C., Root, T. L., & Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society, 81*(3), 443–450. https://doi.org/10.1175/1520-0477(2000)081%3C0443:IOEWAC%3E2.3.CO;2

Potts, G. R., Coulson, J. C., & Deans, I. R. (1980). Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *Journal of Animal Ecology, 49*(2), 465–484. https://doi.org/10.2307/4258

Régnier, T., Gibb, F. M., & Wright, P. J. (2019). Understanding temperature effects on recruitment in the context of trophic mismatch. *Scientific Reports, 9*(1), Article 15179. https://doi.org/10.1038/s41598-019-51296-5

Régnier, T., Wright, P. J., Harris, M. P., Gibb, F. M., Newell, M., Eerkes-Medrano, D., Daunt, F., & Wanless, S. (2024). Effect of timing and abundance of lesser sandeel on the breeding success of a North Sea seabird community. *Marine Ecology Progress Series, 727*, 1–17. https://doi.org/10.3354/meps14520

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. *Proceedings. Biological Sciences, 287*(1931), Article 20200928. https://doi.org/10.1098/rspb.2020.0928

Sánchez-Macouzet, O., Rodríguez, C., & Drummond, H. (2014). Better stay together: Pair bond duration increases individual fitness independent of age-related variation. *Proceedings. Biological Sciences, 281*(1786), Article 20132843. https://doi.org/10.1098/rspb.2013.2843

Snow, B. (1960). The breeding biology of the shag *Phalacrocorax aristotelis* on the island of Lundy, Bristol Channel. *Ibis, 102*(4), 554–575. https://doi.org/10.1111/j.1474-919X.1960.tb07132.x

Snow, B. K. (1963). The behaviour of the shag. *British Birds, 56*, 77–103.

Spooner, F. E. B., Pearson, R. G., & Freeman, R. (2018). Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology, 24*(10), 4521–4531. https://doi.org/10.1111/gcb.14361

Sun, R., Fay, R., Ventura, F., Şen, B., Barbraud, C., Delord, K., Krumhardt, K., & Jenouvrier, S. (2024). Climate change impacts pair-bond dynamics in a long-lived monogamous species. *Ecology Letters, 27*(12), Article e14555. https://doi.org/10.1111/ele.14555

van de Pol, M., Jenouvrier, S., Cornelissen, J. H. C., & Visser, M. E. (2017). Behavioural, ecological and evolutionary responses to extreme climatic events: Challenges and directions. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences, 372*(1723), Article 20160134. https://doi.org/10.1098/rstb.2016.0134

van Deurs, M., van Hal, R., Tomczak, M. T., Jónasdóttir, S. H., & Dolmer, P. (2009). Recruitment of lesser sandeel *Ammodytes marinus* in relation to density dependence and zooplankton composition. *Marine Ecology Progress Series, 381*, 249–258. https://doi.org/10.3354/meps07960

Ventura, F., Granadeiro, J. P., Lukacs, P. M., Kuepfer, A., & Catry, P. (2021). Environmental variability directly affects the prevalence of divorce in monogamous albatrosses. *Proceedings. Biological Sciences, 288*(1963), Article 20212112. https://doi.org/10.1098/rspb.2021.2112

Verhulst, S., & Nilsson, J.-k. (2008). The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences, 363*(1490), 399–410. https://doi.org/10.1098/rstb.2007.2146

White, C. R., Grémillet, D., Green, J. A., Martin, G. R., & Butler, P. J. (2011). Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in Great Cormorants. *Ecology, 92*(2), 475–486. https://doi.org/10.1890/09-1951.1

Wyllie, I. N. (1996). Monogamy in the sparrowhawk. In J. M. Black (Ed.), *Partnerships in birds: the study of monogamy* (pp. 249–267). Oxford University Press. https://doi.org/10.1093/oso/9780198548614.003.0014.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer.