Vital rates of intermittent nonbreeders and returning breeders strongly influence population dynamics of *Somateria mollissima* (Common Eider)

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ABSTRACT

Risks and costs associated with reproduction may induce iteroparous species to employ intermittent breeding, whereby individuals forgo attempting reproduction in some breeding periods following recruitment to the breeding population. We explore this behaviour through population-level analyses of *Somateria mollissima* (Common Eider), quantifying the survival cost of breeding and hence one benefit of skipping. Nonbreeding in a given year may be a short-term response to expected low fitness returns, avoiding either breeding-induced mortality or low offspring value. Alternatively, or additionally, intermittent breeding may be a long-term strategy maximising lifetime fitness, with breeding trajectories that include nonbreeding years resulting in more recruited offspring over the whole life course than those with the same number of consecutive breeding attempts. Reanalysis of 3 studies reporting annual mortality schedules for *S. mollissima* allowed estimation of the proportion of mortality incurred during the peak breeding season (~50%), and hence the difference in survival rates between breeders and nonbreeders. These were incorporated into a life cycle and associated matrix population model with a “refreshed breeder” stage to which individuals transition for the time-step following nonbreeding. We show that the transition to this stage strongly influences population growth rate – being more than twice as important as reproduction by continued breeders—mostly driven by the possibility of differential survival after skipping breeding. Our results emphasize the benefits of long-term individual-based studies that can identify refreshed breeders to further our understanding of intermittent breeding. Specifically, accuracy of population projections could be improved by factoring in post-skipped breeding transitions, and management enhanced by interventions facilitating return to the breeding pool, such as nest shelter provision.

Keywords: breeding propensity, Common Eider, matrix population model, mortality, population dynamics, refreshed breeder, seaduck, vital rates

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LAY SUMMARY

- Animals that can breed multiple times across their lifespan may not attempt to breed at every possible opportunity.
- Skipping breeding may avoid expected costs for a given attempt, and/or form part of a proactive strategy to increase offspring production over the lifetime. Taking breaks can improve future prospects for annual survival and/or reproduction.
- We investigated the population-level effects of skipping breeding in a well-studied seaduck, *Somateria mollissima* (Common Eider).
- We estimated that half of all *S. mollissima* deaths each year occur during the peak breeding season, suggesting that breeders have lower annual survival than nonbreeders.
- Populations are expected to grow faster if those returning to breed show improved survival after skipping.
- Therefore, monitoring individuals to record such “refreshed breeders” in the wild could improve accuracy of population projections, and aid the conservation of species for which returning to breeding after a break can be facilitated through targeted interventions.

Les taux vitaux des individus se reproduisant par intermittence et des individus se reproduisant à chaque année influencent fortement la dynamique des populations de *Somateria mollissima*

RÉSUMÉ

Les risques et les coûts associés à la reproduction peuvent inciter les espèces itéropares à recourir à la reproduction intermittente, par laquelle les individus renoncent à tenter de se reproduire pendant certaines périodes de reproduction après leur recrutement dans la population reproductrice. Nous explorons ce comportement par des analyses populationnelles de *Somateria mollissima*, en quantifiant le coût de survie de la reproduction, soit l'un des avantages de sauter une saison de reproduction. Le fait de ne pas se reproduire au cours d'une année donnée peut être une réponse à court terme à un faible retour attendu au niveau de la condition physique, en évitant soit la mortalité induite par la reproduction, soit une faible valeur de la progéniture. De façon alternative ou additionnelle, la reproduction intermittente peut être une stratégie à long terme qui maximise la condition physique tout au long de la vie, avec des trajectoires de reproduction qui incluent des années sans reproduction menant à un plus grand nombre de descendants recrutés tout au long de la vie que chez ceux ayant le même nombre de tentatives de reproduction consécutives. La réanalyse de trois études rapportant des schémas de mortalité annuelle pour *S. mollissima* a permis d'estimer la proportion de mortalité encourue pendant la saison de reproduction maximale (~50 %), et donc la différence dans les taux de survie entre les individus reproducteurs et les individus non reproducteurs. Ces données ont été incorporées dans un cycle vital et un modèle matriciel de population associé, avec un stade de « reproducteur rafraîchi » par lequel les individus passent dans l'étape suivant la non-reproduction. Nous montrons que la transition vers ce stade influence fortement le taux de croissance de la population – étant plus de deux fois aussi élevé que pour la reproduction par les reproducteurs en continu – principalement en raison de la possibilité de survie différentielle après avoir sauté une saison de reproduction. Nos résultats mettent en évidence les avantages des études à long terme basées sur les individus qui permettent d'identifier les reproducteurs rafraîchis afin d'approfondir notre compréhension de la reproduction intermittente. Plus particulièrement, la précision des projections démographiques pourrait être améliorée en prenant en compte les transitions après une reproduction manquée, et la gestion pourrait être améliorée par des interventions facilitant le retour dans le bassin de reproducteurs, comme la fourniture d'abris pour les nids.

Mots-clés : propension à la reproduction, *Somateria mollissima*, modèle matriciel de population, mortalité, dynamique de population, reproducteur rafraîchi, canard de mer, taux vitaux

INTRODUCTION

Breeding is a costly endeavour for birds (e.g., table 1 in Lindén and Møller 1989), starting with egg production by females (e.g., table 1 in Meijer and Drent 1999). Then, with a few notable exceptions, such as obligate nest parasites (Payne 1998), avian reproductive strategies involve an immutable requirement for incubation, which may increase energy expenditure and/or exposure to predation (e.g., Magnhagen 1991, Drake et al. 2018). The young of most bird species also demand some level of post-hatching care (Silver et al. 1985), in some cases leading to missed opportunities for preferred foraging in the later stages of parental supervision (e.g., Inger et al. 2010)—even in species with nidifugous and precocial young (Drake et al. 2018).

Breeding propensity is an important aspect of reproduction that is sometimes overlooked, under the assumption that any individual that has recruited to the breeding population will continue to attempt breeding every year (Lee et al. 2017, Nicol-Harper et al. 2023). Yet observational studies often document intermittent breeding, whereby not all potential breeders initiate a breeding attempt per breeding season; this phenomenon has been observed widely in birds (Lee et al. 2017), especially seabirds (e.g., Cam et al. 1998, Cubaynes et al. 2011) and wildfowl (e.g., Reed et al. 2004, Martin et al. 2009).

Beyond unavoidable constraints such as loss of the partner, intermittent breeding could be driven by "choosing" to skip breeding as a short-term response to prohibitively high costs of reproduction (e.g., due to poor body condition, Erikstad et al. 1998) and/or low expected reproductive success (e.g., due to poor projected environmental conditions for offspring; Sergio et al. 2018). This may be considered an extension to the "energetic incubation constraint hypothesis" (Kilpi and Lindström 1997): more future resources can be freed up by skipping breeding entirely than by reducing clutch size (Öst et al. 2008). Alternatively, intermittent breeding may form part of a long-term strategy whereby "sabbatical" or "gap" years enhance lifetime reproductive output (Cruz-Flores et al. 2021, Wood et al. 2021a). Such breaks might allow for a "head start" to facilitate future breeding through increased body mass or earlier arrival on breeding grounds, and/or a longer lifespan may increase the likelihood of being able to capitalise on occasional years with "boom" conditions (e.g., Péron et al. 2012, McKnight et al. 2018). These hypotheses, which are not mutually exclusive, have been described as "constraint versus restraint" (e.g., Reed et al. 2015), and "physical/physiological constraint" versus "adaptive response to a life-history trade-off" (Shaw and Levin 2013).

Nonbreeding as a short-term response to reproductive costs will be influenced by the perceived mortality risks associated with breeding. These may be realized through reduced survival of breeders compared to nonbreeders, or of successful breeders compared to failed breeders; the former has been observed in *Poecile montanus* (Willow Tit; Ekman and Askenmo 1986) and female *Bulweria bulwerii* (Bulwer's Petrel; Cruz-Flores et al. 2021), and the latter in various wildfowl species (Hartke et al. 2006, Drake et al. 2018). Individuals attempting breeding may face high energetic demands and risky behaviors involved in courtship, mating, and nest searching, and females initiating egg production undergo body mass gains that can increase vulnerability to predation (Lee et al. 1996, Hartke et al. 2006). Incubation may be shared between parents, but in most bird species it is carried out disproportionately by the female, and hence for females is often "an important reproductive cost" (e.g., Wood Duck [*Aix sponsa*]; Hepp and Kennamer 1990, p. 756).

Somateria mollissima (Common Eider) has an extreme breeding ecology in which females may encounter temporary flightlessness due to egg weight (Guillemette and Ouellet

2005), and then lose up to half of their body mass during a month of near-constant uniparental incubation (Parker and Holm 1990). While intermittent breeding has been observed in a range of seaduck species (e.g., Bertram and Roberts 1934, Bond et al. 2008), it is particularly well-documented in *S. mollissima* (e.g., Coulson 1984, Legagneux et al. 2016, Jaatinen et al. 2022, Steenweg et al. 2022). Breeding propensity has been quantified in various *S. mollissima* populations (reviewed by Nicol-Harper et al. 2021). In some cases, these time series reveal very high levels of nonbreeding: on the northeast coast of England, an average of 22% of females skipped breeding each year, rising to over 65% in a peak nonbreeding year (Coulson 1984); and in the more extreme environment of the Canadian Arctic, more females tended to skip than breed each year (Jean-Gagnon et al. 2018).

Recent work also emphasizes the role of intermittent breeding in facilitating a response to perceived predation risk, which may otherwise be constrained by *S. mollissima* females' strong nest-site fidelity restricting the opportunities to select a location with fewer predators. Annual survival, breeding propensity and nesting success have increased with intensified control of non-native predators (*Neovison/Neogale vison* [American mink]; *Nyctereutes procyonoides*, [raccoon dog]) in the Baltic (Jaatinen et al. 2022). High predation risk may interact with body condition to influence breeding propensity, with poor-condition females more likely to skip breeding compared to those in better condition (Mohring et al. 2022, Öst et al. 2022). Lifetime reproductive output in this species may depend particularly on a long lifespan: on average, individuals survive 8–10 yr after reaching adulthood (Waltho and Coulson 2015), with observed "boom and bust" patterns in duckling survival (e.g., Milne 1963; table 14 in Milne 1974; table 7 in Swennen 1983) and recruitment (Coulson 1984).

One way to quantify the contribution of reproduction to mortality schedules (and hence survival rate, lifespan, etc.) is to consider the pattern of deaths across the year. Three studies have provided such data for *S. mollissima*: Milne (1963) [Table 38], Coulson (1984) [Table 8] and Swennen (2002) [Table 2]. At Forvie, Scotland, there was "a very definite peak period of mortality of adult females immediately after the breeding season in June and July", with no corresponding increases in other age/sex categories – including first-year individuals, some of which undertake winter migration (Milne 1963, p. 195). On Coquet Island, England, 59% of deaths occurred in June and July, immediately following incubation (Coulson 1984). And in the Dutch Wadden Sea, "natural mortality rates are low outside of the breeding period", with a pollution incident that triggered a sharp population decline seemingly affecting breeding females most strongly, at the end of the breeding period (Swennen 2002, p. 63).

Given that these mortality peaks are observed in breeding females only, we postulate that they represent a survival cost of reproduction in this species. *S. mollissima* males do not contribute to incubation or parental care (Waltho and Coulson 2015), and breeding females are subject to increased predation (e.g., Ramula et al. 2018, Mohring et al. 2021, Jaatinen et al. 2022), heightened susceptibility to disease (e.g., Korschgen et al. 1978, Descamps et al. 2009), and physiological repercussions from fasting (e.g., Korschgen 1977, Bårdsen et al. 2018). Coulson (1984) and Swennen (2002) both describe the peaks as coinciding with the mid- to late nesting period, which aligns with nesting often forming the riskiest portion of the avian breeding process (e.g., as in *Anas platyrhynchos* [Mallard]; Kirby and Cowardin 1986), especially for those nesting in open versus cavity nests (Hartke et al. 2006) and for "conspicuous colonial breeders" (Mohring et al. 2021, p. 1). These breeding costs may subject breeding and nonbreeding females to differential survival rates, the incorporation of which into demographic models could help to improve population projection.

In addition to accounting for the survival cost of breeding, it may also be important to consider additional potential benefits of nonbreeding. Specifically, do break years improve subsequent breeding propensity and/or success, in addition to facilitating avoidance of a survival cost? This question can be formulated in terms of vital rates of continued breeders versus ‘refreshed breeders’ returning to breeding after skipping one or more years. Specifically, the vital rates of refreshed breeders may be: (1) higher than those of continued breeders, as expected if intermittent breeding forms part of a long-term strategy offering greater lifetime fitness; (2) approximately equal to those of continued breeders, if intermittent breeding is a result of individuals skipping breeding in response to extrinsic stochasticity such as weather conditions or predation risk; or (3) lower than those of continued breeders, if repeat skippers represent individuals of consistently poor condition. Option (3) is more speculative, given the difficulties associated with defining and demonstrating individual heterogeneity in quality (Bergeron et al. 2011, Fay et al. 2022), but the main distinction is between higher vital rates in refreshed breeders representing an adaptive, long-term driver of intermittent breeding, compared to equivalent or lower vital rates in refreshed breeders representing nonbreeding as a short-term response to some constraint.

Hence, our aim was to build a population model of intermittent breeding, quantifying those features that are missed when assuming all recruited individuals breed at every opportunity. We first calculated the survival cost of breeding for *S. mollissima* females by analyzing the mortality schedule data described above, then used this information, along with previously estimated demographic parameters (Nicol-Harper et al. 2023), to develop a matrix population model including a refreshed breeder stage to which individuals transition after nonbreeding. Perturbation analysis revealed the potential population impacts of a survival benefit for refreshed breeders, highlighting the need for greater consideration of this distinct breeding state.

METHODS

Calculating the Proportion of Mortality Incurred During the Breeding Season

We accounted for the survival cost of breeding for *S. mollissima* females by estimating the proportion of mortality incurred during the breeding season. Table 1 summarizes the information on annual mortality schedules in *S. mollissima* as described above, and Supplementary Material S1 replicates the data as provided by Milne (1963) [their table 38], Coulson (1984) [their table 8] and Swennen (2002) [their table 2]. Across the peak 2 months for each timeseries, the breeding season accounts for approximately half of annual mortality: 43% in Milne (1963), 59% in Coulson (1984), and 58% in Swennen (2002). Taking the mean value of 53%, we obtain a baseline mortality rate across the remaining months as (100% – 53%) / 10 = 4.7% per month. Subtracting 2 months’ worth of this baseline from the breeding season mortality gives an estimate of the proportion of annual mortality incurred while breeding: 44%. In order to conduct a conservative analysis, in the absence of explicit evidence that all excess deaths are in fact a direct consequence of breeding costs, we halve this value in subsequent analyses and use 22%. Sensitivity analysis shows that our findings (as presented in the Results section) do not qualitatively change when varying this value between 0 (no excess deaths during breeding) and 50% (half of all deaths, above baseline mortality rates, occur during breeding); unsurprisingly, higher survival costs of breeding are associated with lower population growth (see Supplementary Material S2).

The survival cost of breeding can be contextualized by considering the proportional reduction in annual survival of breeders relative to nonbreeders:

$$((\text{survival}_{\text{nonbreeding}} - \text{survival}_{\text{breeding}})/\text{survival}_{\text{nonbreeding}}) \times 100 \qquad (1)$$

The impacts of this discrepancy across the life course can be quantified by extrapolating survival across cohorts of individuals which always breed or always skip breeding. For example, the number of years after which at least 95% of a given cohort are expected to have died is calculated (by taking the inverse of the exponential equation: $\text{survival}^{Y} = 0.05$) with:

$$Y = \log_{\text{survival}}(0.05) \qquad (2)$$

Modelling A Refreshed-Breeder Life Cycle

We designed a matrix population model (Caswell 2001) building on Nicol-Harper et al. (2023). The demographic parameters used both here (see Table 2) and in Nicol-Harper et al. (2023) were based on a meta-analysis of estimates from the database described in Nicol-Harper et al. (2021), and relate to the female portion of the life cycle only. Here we implement some important developments to the life-cycle model presented in Nicol-Harper et al. (2023). First, we incorporate a “first-time breeder” stage with distinct subsequent breeding propensity, implementing the approximately doubled likelihood of skipping following recruitment, as described by Coulson (2010, p. 7): “nonbreeding in the year following the first breeding by females was greater than the overall nonbreeding rate for all ducks (15.6%), [at] about 32%”.

Next, we incorporate the different survival rates for breeders and nonbreeders, based on the survival cost of breeding as determined above. Previously, while the breeder and nonbreeder stages were distinct, they were subject to the same survival rates in their transitions; now, we can parameterize separate survival rates for breeders and nonbreeders. We assume that observed adult survival rates relate to combined observations of breeders and nonbreeders, as is the case with capture-recapture analyses (e.g., as implemented in MARK; White and Burnham 1999). Our estimated 22% excess mortality for breeders means that, relative to the breeder value at 100%, the nonbreeder value is equivalent to 78%, and the observed midpoint to 89%. Hence, disaggregated values from the observed survival rate of 0.86 are calculated as: Survival: midpoint (89%) = 0.86; breeder (100%) = 0.843; nonbreeder (78%) = 0.877; and

Mortality: midpoint (89%) = 0.14; breeder (100%) = 0.157; nonbreeder (78%): = 0.123.

We apply these rates throughout the life cycle, except for transitions from one-year-old, for which second-year survival has been previously estimated. We do not attempt to disaggregate this rate as the mortality schedules informing our methodology are based on adults.

Finally, to consider what happens after skipping a breeding season, we add the refreshed breeder stage, to which individuals transition for the time-step following nonbreeding (Figure 1). At each timestep, given survival: nonbreeders can remain as nonbreeder or transition to refreshed breeder; refreshed breeders can transition to continued breeder or nonbreeder; and continued breeders can remain as continued breeder or transition to nonbreeder. Refreshed breeders, like first-time breeders and continued breeders, contribute to next year's one-year-olds through fertility rates, which combine clutch size, hatch success, fledging success and first-year survival, and are halved to account for an assumed equal sex ratio at hatching (see Nicol-Harper et al. 2023).

Relative to Nicol-Harper et al.'s (2023) life-cycle model and corresponding matrix (their figure 1), we retain a pre-breeding projection, and have made explicit the state dependency in projection order across vital rates (Figure 2). Specifically, individuals identified as breeders at the census (i.e., those coming from the first-time breeder, continued breeder, or refreshed breeder stages) produce fledglings shortly after the census in year *t*, and these fledglings then survive across the year (with this survival rate built into fertilities; Kendall et al. 2019) in order to enter the next census as a one-year-old. All individuals censused at the start of year *t* first survive (at the rate determined by the stage they are coming from), and then transition (based on the breeding propensity of the stage they are coming from) to the new state at which they are censused at the start of year *t* + 1. Refreshed breeder vital rates are adjusted through the inclusion of modifiers (Figure 1), which apply to: the transition "refreshed breeder → one-year-old" for fertility (f.r); the transitions "refreshed breeder → continued breeder" and "refreshed breeder → nonbreeder" for survival (s.r); and the transitions "nonbreeder → refreshed breeder" (becoming a refreshed breeder) and "nonbreeder → nonbreeder" (deferring becoming a refreshed breeder) for breeding propensity (bp.r). The breeding propensity adjustment does not apply to transitions from refreshed breeders, as by the end of the year they have lost their "refreshed" status, having bred and experienced the elevated mortality to which breeders are subject. In all cases, these multipliers (along with f.f for first-time breeder fertility) are initially set to 1 given the lack of information on true values, but their inclusion allows for the calculation of potential influence on asymptotic population growth rate through perturbation analysis (see below).

To quantify influences on population dynamics across components of the final model, we first calculated matrix-entry elasticities to asymptotic population growth (i.e., the proportional contributions to asymptotic population growth rate of transitions between life stages), using the *elas()* function in the *popdemo* R package (v1.3-0; Stott et al. 2018). Additionally, we used the *vitalsens()* function in the *popbio* R package (Stubben and Milligan 2007) to calculate lower-level elasticities to asymptotic population growth (which may also be referred to as parameter or component elasticities), representing the proportional contributions to asymptotic population growth rate of the underlying vital rates, which are often what is measured empirically. For example, the matrix entry for the transition from refreshed breeder to continued breeder is the product of: breeder survival; the survival modifier for refreshed breeders; and breeding propensity of continued breeders. In turn, breeder survival is a combination of: adult survival, as estimated in Nicol-Harper et al. (2023) from 15 independent studies; and the survival cost of breeding, as estimated in this study from three datasets. Therefore, where a single matrix-element elasticity represents the importance of the life-stage transition from nonbreeder to refreshed breeder, lower-level perturbation analysis disentangles the importance of the underlying contributors and provides an elasticity for each of these individually estimable parameters.

All analyses were conducted in R v.4.0.3 (R Core Team 2020), with figures using the package *RColorBrewer* (v1.1-2; Neuwirth 2014).

RESULTS

The parameterized refreshed-breeder life cycle, incorporating the 4% survival cost of breeding (from Equation 1), is shown in Figure 3. The associated matrix population model generates an asymptotic population growth rate of 0.99 (as for the original model in Nicol-Harper et al. 2023), indicating that the underlying vital rates suggest a population in slow (1% per year) decline. The incorporation of Coulson (2010)'s approximately doubled likelihood of skipping following recruitment means that individuals are more likely to skip (transition to nonbreeder, probability = 0.49) than to breed for a second consecutive year (transition to continued breeder, probability = 0.36) after their first breeding attempt. Established individuals are then approximately three times more likely to breed than skip in any given year (0.61/0.24 for continued or refreshed breeders and 0.63/0.25 for nonbreeders). If refreshed breeder modifiers were to be adjusted (i.e., increased above 1 where refreshment is adaptive or decreased below 1 where skipping and hence returning after a break is associated with individuals in poor condition), transitions shown in bold and underlined would change accordingly.

Matrix-element elasticities demonstrate that transitions in and out of the refreshed breeder stage can strongly influence population growth rate (Figure 4). While remaining as a continued breeder is unsurprisingly the most influential transition on population growth for this long-lived seaduck, the second most influential transition is from nonbreeder to refreshed breeder, emphasizing our call for more attention to be devoted to this difficult-to-measure transition. For example, increasing the rate of transition from nonbreeder to refreshed breeder by 10%, would have more than double the impact on population growth than increasing by 10% the number of one-year-olds produced each year by continued breeders (0.14 as compared to 0.06). Analogously, lower-level elasticities show that the refreshed breeder survival modifier, which contributes to the transitions from refreshed breeder, is the second most important vital rate after adult survival (Table 3), albeit closely followed by fertility and second-year survival. For example, increasing by 10% the factor by which refreshed breeder survival exceeds that of continued breeders, would have four times the impact on population growth than the equivalent boost to refreshed breeders' fertility relative to that of continued breeders (0.117 as compared to 0.026). The relative contribution of breeding propensity decreased when accounting for the proportion of annual mortality incurred while breeding (Supplementary Material S2, Figure S1).

DISCUSSION

Our findings reveal two reasons why considering the survival impacts of intermittent breeding will improve understanding of *S. mollissima* reproductive ecology and population dynamics. First, we quantified a 4% reduction in survival of breeders relative to nonbreeders. We then developed a life-cycle model including a refreshed breeder stage that we believe provides a novel opportunity to consider simultaneously the various intrinsic and extrinsic drivers of nonbreeding and subsequent re-entry to the breeding pool. This showed that population dynamics were strongly influenced by adult survival in the most part, followed by its refreshed breeder modifier, which was more influential than fertility and second-year survival. The refreshed breeder modifier encodes an additional survival benefit of skipping, over and above the increased survival of nonbreeders relative to breeders, realized in the following year. Given a lack of empirical estimates, this result is by default based on refreshed breeder vital rates being equal to continued breeder counterparts (i.e., what could be expected when individuals skip in response to extrinsic stochasticity). Hence while we cannot distinguish "restraint" (higher vital rates in refreshed breeders representing an adaptive, long-term driver of intermittent breeding) versus "constraint" (equivalent or lower vital rates in refreshed breeders representing nonbreeding as a short-term response to a limiting factor), we demonstrate how valuable it would be to collect the required data, particularly in relation to survival following nonbreeding.

While a 4% reduction in annual survival of breeders relative to nonbreeders may seem trivial, this is unlikely to be the case for a species with slow life history such as *S. mollissima* (Öst et al. 2008), for whom lifespan is a key predictor of lifetime reproductive output (Reed et al. 2015) and long-term population growth (see "Adult survival" in Table 3, and e.g., Coulson et al. 1984). For example, calculation of breeding costs in *Rissa tridactyla* (Black-legged Kittiwake) led Golet et al. (1998) to conclude that annual reproduction reduced life expectancy by 55% relative to never breeding. In our case, a newly recruited individual embarking on consecutive breeding attempts has a 95% likelihood of dying within 18 years, as compared to 23 years if it never bred (from equation 2). Moreover, projecting a version of our updated life cycle including the conservative estimate of 22% of the annual mortality of breeders being avoided by nonbreeders (without splitting out refreshed breeders), results in a 7% reduction in population size relative to projecting the equivalent life cycle without accounting for differential survival of nonbreeders relative to breeders, across three generations (i.e., 27 years, as per the IUCN Red List: BirdLife International 2018; see Acknowledgments for R code).

Lower-level perturbation analysis showed that, while the survival cost of breeding had a relatively smaller influence on asymptotic population growth rate than allowing for differential refreshed breeder survival, its incorporation did indirectly explain some of the previously identified influence of breeding propensity on asymptotic growth rate (see Nicol-Harper et al. 2023). Specifically, we found that breeding propensity became less influential when accounting for the survival cost of breeding (Supplementary Material S2, Figure S1); the distinct mortality regimes associated with breeding and nonbreeding states accounted for a large part of the impact of individuals breeding or not, as opposed to the qualitatively different immediate fecundity outputs (potentially positive for breeders versus zero for nonbreeders). Model projections and their applications (e.g., population viability analysis) could therefore be improved through parameterization of mortality schedules or distinct non/breeder survival rates.

It is perhaps surprising that, given the number of studies quantifying adult survival in *S. mollissima* (Nicol-Harper et al. 2021), there are, to the best of our knowledge, no estimates disaggregated across breeders and nonbreeders. Nonbreeder survival has been separately estimated in other bird species including *Aptenodytes patagonicus* (King Penguin; Le Bohec et al. 2007), *Procellaria westlandica* (Westland Petrel; Waugh et al. 2015), and *Haematopus ostralegus* (Eurasian Oystercatcher; van Irsel et al. 2021). These studies determined breeding status of individually marked birds based on colony attendance and/or egg-laying; as in *S. mollissima* studies that distinguish individual (female) breeders and nonbreeders, albeit without disaggregating survival. In some cases, *S. mollissima* are fitted with markers designed to be visible while birds are on the nest or at sea (nasal tags: Legagneux et al. 2016, Jean-Gagnon et al. 2018, Steenweg et al. 2022; wing flags: Jaatinen et al. 2022), to aid in such classification. While in many cases nonbreeding status is assigned based on absence from the colony (e.g., Jean-

Gagnon et al. 2018, Steenweg et al. 2022), Öst et al. (2018) state that Baltic-breeding *S. mollissima* are an ideal study system for breeding propensity since "nonbreeders are present and equally conspicuous as breeders at and around the breeding colonies" (p. 130). Hence, methods exist to classify (female) *S. mollissima* as breeders versus nonbreeders for a given year, with the associated datasets likely already holding the potential to assign disaggregated survival rates.

Quantification of separate breeder and nonbreeder rates would allow for separate perturbation analysis for these two groups; in contrast, our method means that we are jointly estimating these rates from baseline survival (for which we found the highest elasticity) and the proportion of mortality incurred during breeding (for which we found a low absolute elasticity). Given a lack of information on the combination of breeder and nonbreeder survival rates in reported estimates, we took a midpoint for simplicity; using a 20:80 split based on Coulson's (1984) approximation of 1 in 5 females skipping breeding gives higher absolute values of survival for both states but a slightly smaller proportional disparity between breeders and nonbreeders (3.6% instead of 3.9%), without qualitatively changing our results (see Supplementary Material S2). Comparing like for like (i.e., empirically estimated breeder survival and nonbreeder survival) could potentially reveal different patterns, and would also facilitate comparisons of other features of their distributions, such as variability. Theoretical work by Lee *et al*. (2017) found that failing to incorporate nonbreeders into population models can bias population growth rates where individuals "frequently re-enter the breeding population after periods of nonbreeding" (p. 75); overestimated population growth rates evidently risk underestimating threat levels and potentially jeopardizing conservation efforts. Lee et al. (2017) also suggested that for long-lived species with costly breeding, nonbreeder survival is likely to be more influential than breeding propensities; our elasticity results agree with this prediction (Table 3), but evaluating nonbreeder survival separately would allow more robust assessment of this hypothesis, along with improved projection of population dynamics.

Although we found a relatively small influence of modified refreshed breeder fertility, Yoccoz et al. (2002) proposed a cyclical sequence of female *S. mollissima* breeding states, with the observation that small clutches tended to follow large explained by an unobserved, nonbreeding year that precedes large clutches (i.e., large → small → nonbreeding → large, etc.). Such a pattern may support the idea that refreshed breeders are able to invest more in reproduction following a break, speaking to the "fundamental ecological question" of carryover effects on life history strategies (Sutherland et al. 2013). Quantification of any actual fertility benefit to refreshed breeders could tie in to Shaw and Levin's (2013) theoretical consideration of intermittent breeding, which suggests that the relevant evolutionarily stable strategy is: postponing breeding until the fecundity benefits of delaying one more year (i.e., the extent to which refreshed breeder fertility may exceed continued breeder fertility, or the magnitude of f.r) are less than the survival cost of breeding in the focal year (i.e., the extent to which nonbreeder survival exceeds breeder survival). Empirical estimation of refreshed breeder modifiers, as required to parameterize such calculations, would also allow exploration of potential covariance (whereas here they are applied independently).

In addition to facilitating validation of our models, identification of nonbreeders and refreshed breeders in the field or existing datasets could further our understanding of intermittent breeding, especially in relation to their survival rates. Life-history theory and the demographic buffering hypothesis (Sæther and Bakke 2000; Hilde et al. 2020) would support expectations of high and stable refreshed breeder survival, more so than nonbreeder survival, given their respective high and low elasticities. However, as noted above, separate estimation of survival for breeders and nonbreeders may alter the patterns emerging from perturbation analysis. Here it would also be useful to place crèche-attending “aunts” (apparently nonbreeding females providing care to amalgamated broods; see, e.g., Bustnes and Erikstad 1991) within the context of their life course: are they one-time failed breeders, or long-time nonbreeders?

Where it has been measured, breeding propensity in *S. mollissima* adult females is neither particularly high (Nicol-Harper et al. 2021, Table 2), nor stable (e.g., see time series in Coulson 1984, 2010), perhaps implying a greater scope for conservation interventions to increase this vital rate. An example of a management technique that can be employed towards increased breeding propensity is the provision of nesting shelters, as used by eiderdown farmers in Iceland (Jónsson et al. 2013) and found to increase breeding numbers at various sites in Canada (Cooch 1965, Tomlik 2019; see also Noel 2022). Such external optimization of breeding conditions, coupled with individual-based data collection, may also help to disentangle inter-individual differences in breeding trajectories (some individuals being inherently more likely to attempt breeding in any given year than others) from synchronous responses to environmental conditions (fewer breeders in a year with scarce food resources, for example).

It is worth noting that the mortality schedules used to estimate the survival cost of breeding are potentially subject to biases. There is little associated metadata describing observation effort: the data from Milne (1963) relate to all individuals found dead at Forvie by a single observer, while Coulson (1984) uses information from ringing to estimate that 24% of dead ducks were reported. Raw recovery patterns would be influenced by irregular observation effort. Additionally, recoveries necessarily occur later than mortality events, with significant delays potentially skewing resulting schedules—although non-remote eider colonies tend to be well-observed (e.g., Wood et al. 2021*b*). Furthermore, these populations are likely not completely closed, with migration in and out of the population potentially altering apparent survival rates if not constant throughout the year. Hence, our results could be strengthened through the collection of new mortality schedule datasets, subject to consistent observation effort, and ideally with a closed population (and/or informed by supplementary ringing and tagging information). In the meantime, our sensitivity analyses and use of a conservative estimate for the excess mortality occurring during breeding (Supplementary Material S2), suggest that our results would hold across a wide range of potential parameterizations.

To conclude, we quantified the survival cost of breeding and observed benefit of skipping breeding in *S. mollissima*, and highlighted the potential differential survival of refreshed breeders as an important vital rate to be empirically determined. Hence, we expect that, if intermittent breeding is part of a long-term adaptive strategy in *S. mollissima*, the main driver of an associated increase in population growth rate would be increased lifespan as a result of enhanced survival on return to the breeding pool, over and above the avoidance of excess mortality during the sabbatical year. More broadly, while it is clear that breeding propensity should not generally be assumed equal to 1, increasing precision in its estimation at the population level may be less useful than accurately parameterizing survival of nonbreeders and studying individual life courses. Empirical quantification of the mean and variability of refreshed breeder vital rates would offer the opportunity to consider intermittent breeding as a long-term strategy (higher refreshed breeder vital rates) versus skipping being employed by individuals in poor condition (lower refreshed breeder vital rates). Being able to identify nonbreeders and refreshed breeders in the field or in existing individual-based datasets therefore presents the opportunity to further our understanding of the drivers of intermittent breeding and its consequences for projecting population dynamics, and hence to offer more tailored population management towards improved conservation.

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Ethics statement

There are no ethical implications of this study.

Conflict of interest statement

The authors declare no conflicts of interest.

Author contributions

All authors conceived the research; ANH developed the methods, analysed the data and produced figures; all authors contributed to writing and editing the manuscript.

Data availability

Analyses reported in this article can be reproduced using the R code deposited at https://doi.org/10.6084/m9.figshare.20124260. Parameter values are taken from table 1 and figure 2 in Nicol-Harper et al. (2023).

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TABLE 1. Proportion of deaths occurring in each month across the year for *S. mollissima* adults across 3 studies. The peak 2 months in each provided time series are shown in bold. The data for Milne (1963) refer to adult females found dead (*n* = 67; 1955–1962); the data for Coulson (1984) refer to adults found dead, without disaggregation by sex (*n* = 131; period unclear but likely about 1960–1980); and the data for Swennen (2002) refer to female ring recoveries (provided as proportions; *n* = 892; 1963–1988). Values are shown to two decimal places.

	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Milne (1963)	0.03	0.09	0.07	0.07	0.09	**0.28**	**0.15**	0.03	0.01	0.03	0.07	0.06
Coulson (1984)	0.05	0.06	0.05	0.05	0.11	**0.44**	**0.15**	0.05	0.00	0.00	0.02	0.02
Swennen (2002)	0.03	0.04	0.03	0.06	**0.26**	**0.32**	0.10	0.04	0.04	0.04	0.01	0.03
Mean	0.04	0.06	0.05	0.06	0.15	0.35	0.13	0.04	0.02	0.02	0.03	0.04

TABLE 2. Demographic parameters used for analyses of *S. mollissima* females. Based on Table 1 in Nicol-Harper et al. (2023). Breeding following survival from pre-breeder at 4 years old, is certain, as 5 is the oldest observed age at recruitment. Fertility is the product of clutch size, hatching success, fledging success, and survival to 1 year old, halved to account for an assumed equal sex ratio; we do not consider the individual vital rates here, since simple multiplication means that each contributes equally to fertility.

	Type	**Value**
Second-year survival	Vital rate	0.87
Adult survival	Vital rate	0.86
Breeding propensity at 2-years-old	Vital rate	0.17
Breeding propensity at 3-years-old	Vital rate	0.58
Breeding propensity at 4-years-old	Vital rate	0.71
Breeding propensity at 5-years-old	Vital rate	1.00
Breeding propensity of established breeders	Vital rate	0.72
Fertility (including survival to 1-year-old)	Life-cycle transition	0.24

TABLE 3. Lower-level elasticities for *S. mollissima* vital rates contributing to our refreshed breeder life-cycle model, shown in descending order. This table highlights the potential role of differential refreshed breeder survival: if those individuals returning to breed following a break survive better than continued breeders, the impact on population dynamics would be second only to that of changes in baseline adult survival. Values are shown to three decimal places. Note that the last two entries are negative, as an *increasing* mortality proportion *decreases* breeder survival, and an *increasing* drop in breeding propensity post-first breeding *decreases* breeding propensity, both *decreasing* asymptotic population growth rate.

Vital rate	**Lower-level elasticity**
Adult survival	0.816
Survival modifier for refreshed breeders	0.117
Fertility (i.e., transitions to one-year-old from first-time, continued or refreshed breeders)	0.105
Second-year survival	0.105
Breeding propensity of continued breeders	0.084
Fertility modifier for refreshed breeders	0.026
Breeding propensity modifier for nonbreeders (to become refreshed breeders)	0.021
Fertility modifier for first-time breeders	0.020
Breeding propensity at 3-years-old	0.007
Breeding propensity at 2-years-old	0.003
Breeding propensity at 4-years-old	0.003
Mortality proportion incurred during breeding season (for nonbreeder survival)	–0.004
Breeding probability decrease following first breeding (relative to continued breeding; for breeding propensity after first breeding)	–0.008

FIGURE 1. Matrix population model representing a refreshed-breeder life cycle for *S. mollissima*. Each matrix entry a_{ij} represents the contribution of individuals in the j^{th} stage (column) of year t to the i^{th} stage (row) of year $t + 1$; blank entries represent impossible transitions. Modifiers relating to refreshed breeders are shown in bold. Abbreviations: 1yo = one-year-old; PB_x = x-year-old pre-breeder (e.g., PB_2 = 2-year-old pre-breeder); FTB = first-time breeder; CB = continued breeder; NB = nonbreeder; RB = refreshed breeder; s_{1h} = first-year survival from hatching; s_2 = second-year survival; s_b = annual survival of breeders; s_{nb} = annual survival of nonbreeders; BP_x = breeding (recruitment) propensity at age x; BP_{afb} = breeding propensity after first breeding; BP_{cb} = breeding propensity of continued breeders; CS = clutch size; HS = hatching success; f.f = fertility modifier for first-time breeders; f.r = fertility modifier for refreshed breeders; s.r = survival modifier for refreshed breeders; bp.r = breeding propensity modifier for nonbreeders (to become refreshed breeders). BP5 is equal to 1, as all individuals recruit by 5 years old.

FIGURE 2. Schematic illustrating state dependency in projection order across vital rates in our *S. mollissima* life-cycle model, which has a pre-breeding census. State at the census between year $t - 1$ and year t determines survival (dashed lines for breeders and dotted lines for nonbreeders), after which breeding propensity (as displayed against the connecting lines) determines state at the beginning of year $t + 1$. Breeders (whether first-time, continued, or refreshed) contribute offspring, which will be one-year-olds by the end of the year, given survival. Abbreviations (as for Figure 1): 1yo = one-year-old; PB= pre-breeder; FTB = first-time breeder; CB = continued breeder; NB = nonbreeder; RB = refreshed breeder; BP_{afb} = breeding propensity after first breeding; BP_{cb} = breeding propensity of continued breeders; f.f = fertility modifier for first-time breeders; f.r = fertility modifier for refreshed breeders; s.r = survival modifier for refreshed breeders; bp.r = breeding propensity modifier for nonbreeders (to become refreshed breeders).

FIGURE 3. Parameterized refreshed breeder life-cycle model for *S. mollissima*, as used in our analysis. Transitions including refreshed breeder vital-rate modifiers (here set to 1 that is equivalent to those of other breeders) are shown in bold and underlined. Arrows show life-stage transitions, with stage transition values displayed to two decimal places. Most values refer to probabilities; those leading to “1yo” represent fertility (i.e., surviving offspring per breeder). Abbreviations as for Figure 1.

FIGURE 4. Elasticity matrix for the matrix population model associated with the life-cycle model in Figure 3. Matrix-element elasticities shown to 2 decimal places where ≥ 0.05. Darker colours represent life-stage transitions with greater influence on population growth rate: the most important is ‘continued breeder → continued breeder’, followed by ‘nonbreeder → refreshed breeder’ – hence we call for more attention to be devoted to the return to breeding following a skipped breeding season. Abbreviations (most as for previous figures): 1yo = one-year-old; PBx = x-year-old pre-breeder (e.g., PB2 = 2-year-old pre-breeder); FTB = first-time breeder; CB = continued breeder; NB = nonbreeder; RB = refreshed breeder; Elast. = elasticity. (Presentation based on code developed by Steve Ellner and Dylan Childs, available at https://github.com/ipmbook/first-edition/blob/master/Rcode/utilities/MatrixImage.R.)

Figure 1

	1yo	**PB$_2$**	**PB$_3$**	**PB$_4$**	**FTB**	**CB**	**NB**	**RB**
1yo					CS × HS × 0.5 × s_{1h} × f.f	CS × HS × 0.5 × s_{1h}		CS × HS × 0.5 × s_{1h} × **f.r**
PB$_2$	s_2 × (1-BP_2)							
PB$_3$		s_{nb} × (1-BP_3)						
PB$_4$			s_{nb} × (1-BP_4)					
FTB	s_2 × BP_2	s_{nb} × BP_3	s_{nb} × BP_4	s_{nb} × BP_5				
CB					s_b × BP_{afb}	s_b × BP_{cb}		s_b × **s.r** × BP_{cb}
NB					s_b × (1-BP_{afb})	s_b × (1-BP_{cb})	s_{nb} × (1-(BP_{cb} × **bp.r**))	s_b × **s.r** × (1-BP_{cb})
RB							s_{nb} × BP_{cb} × **bp.r**	

Figure 2

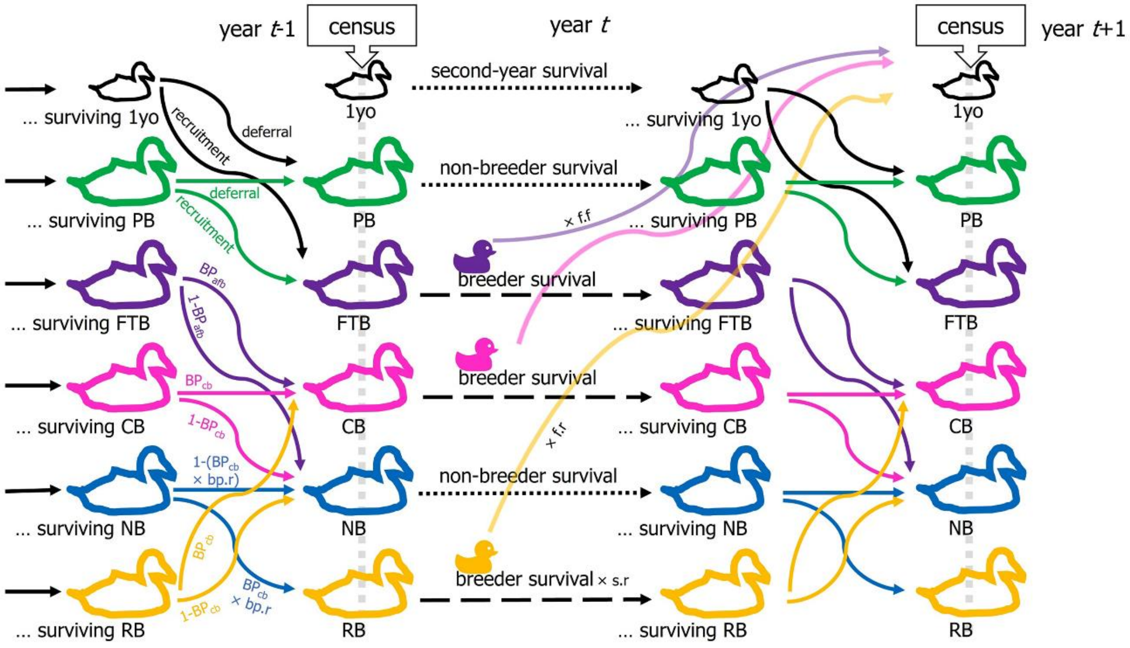

year t-1
census
year t
census
year t+1
second-year survival
non-breeder survival
breeder survival
breeder survival
non-breeder survival
breeder survival × s.r
× f.f
× f.r
... surviving 1yo
... surviving PB
... surviving FTB
... surviving CB
... surviving NB
... surviving RB
recruitment
deferral
deferral
recruitment
BP_{afb}
$1-BP_{afb}$
BP_{cb}
$1-BP_{cb}$
$1-(BP_{cb} \times bp.r)$
BP_{cb}
$1-BP_{cb}$
$BP_{cb} \times bp.r$
1yo
PB
FTB
CB
NB
RB
... surviving 1yo
... surviving PB
... surviving FTB
... surviving CB
... surviving NB
... surviving RB
1yo
PB
FTB
CB
NB
RB

Figure 3

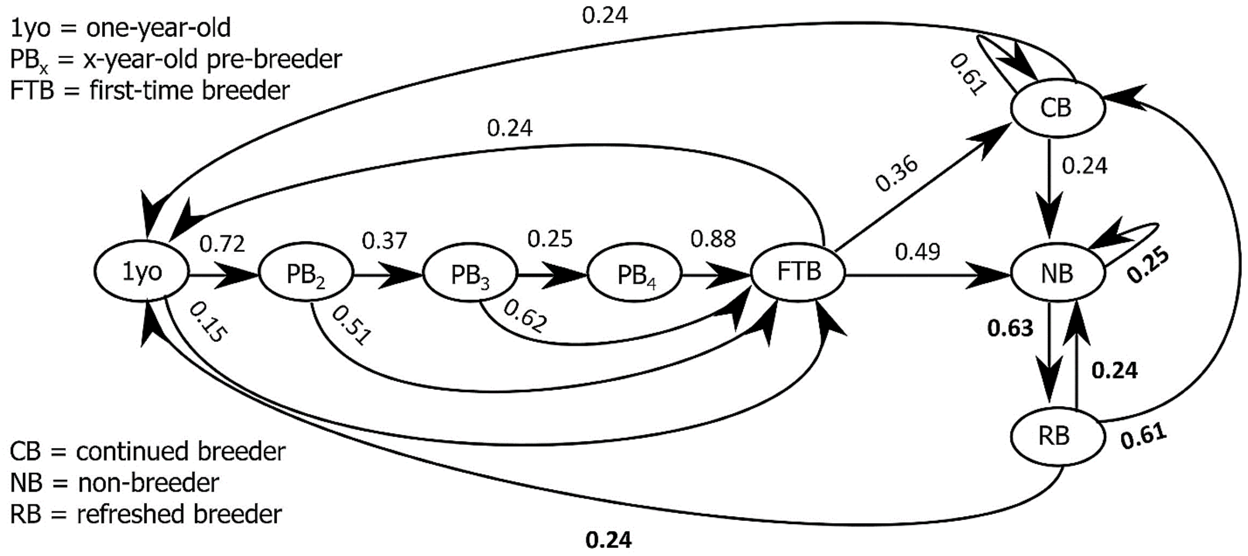
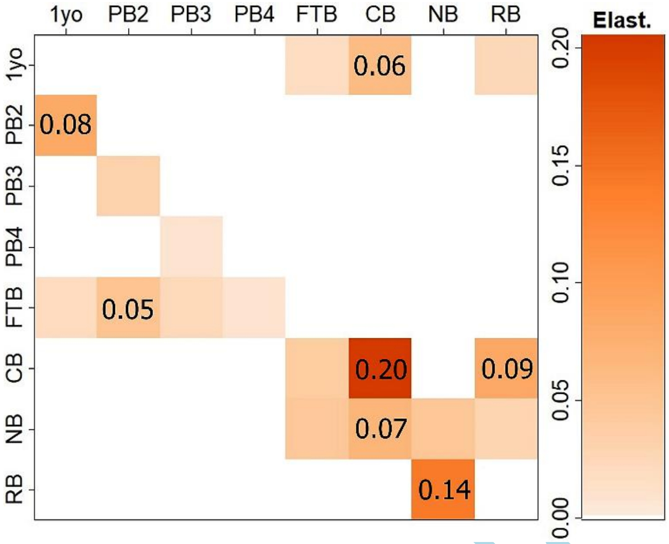

1yo = one-year-old
PB$_x$ = x-year-old pre-breeder
FTB = first-time breeder
CB = continued breeder
NB = non-breeder
RB = refreshed breeder
1yo
PB$_2$
PB$_3$
PB$_4$
FTB
CB
NB
RB
0.24
0.24
0.61
0.36
0.24
0.72
0.37
0.25
0.88
0.49
0.25
0.15
0.51
0.62
0.63
0.24
0.61
0.24

Figure 4


1yo
PB2
PB3
PB4
FTB
CB
NB
RB
1yo
PB2
PB3
PB4
FTB
CB
NB
RB
0.06
0.08
0.05
0.20
0.09
0.07
0.14
Elast.
0.20
0.15
0.10
0.05
0.00