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For Oecologia

To breed or not to breed: drivers of intermittent breeding in a seabird under increasing predation risk and male bias

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Abstract

Intermittent breeding may be adaptive for long-lived species subjected to large accessory reproductive costs, but it may also reflect reduced adaptation to the environment, reducing population growth. Nevertheless, environmental influences on breeding propensity, particularly that of predation risk, remain poorly understood and difficult to study because non-breeders are typically not identified. Female eiders *Somateria mollissima* from the Baltic Sea provide an excellent testbed, because nesting females have been exposed to intensifying predation and growing male bias that may increase female harassment. We based the study on long-term data (14 yrs) on females captured and marked at the nest, and females individually identified at sea irrespective of capture status. We hypothesized that breeding propensity decreases with increasing predation risk and male bias, and increases with breeder age. Consistent with our hypotheses, females nesting on islands with higher nest predation risk were more likely to skip breeding, and breeding probability increased with age. In contrast, the steep temporal decline in breeding propensity could not be reliably attributed to annual adult sex ratio or to the abundance of white-tailed sea eagles (*Haliaeetus albicilla*), the main predator on females, at the nearby Hanko Bird Observatory. Breeding probability showed significant consistent individual variation. Our results demonstrate that spatiotemporal variation in predation risk affects the decision to breed and high incidence of non-breeding was correlated with low fledging success. The increased frequency of intermittent breeding in this declining population should be explicitly considered in demographic models, and emphasis placed on understanding the preconditions for successful reproduction.

Keywords: breeding propensity, eider, environmental cues, non-breeders, reproductive strategies

Introduction

The evolution of intermittent breeding – non-breeding of sexually mature adults with prior breeding experience – is enigmatic because intermittent breeders face the risk of a dual fitness disadvantage: the loss of current reproduction and the risk of dying before the next chance at reproduction. However, long-lived species are expected to favour survival over current reproduction to maximize their future reproduction (Stearns 1992; Gaillard et al. 1998). Consequently, intermittent breeding may evolve in species with ‘slow’ life histories inhabiting temporally variable environments if breeding conditions fall below a certain threshold (Erikstad et al. 1998; Cubaynes et al. 2011; Shaw and Levin 2013, Jean-Gagnon et al. 2017). However, if environmental change exceeds a critical rate, this may lead to reduced adaptation to local conditions, and a concomitant increase in the incidence of intermittent breeding. As breeding propensity is a critical demographic parameter determining population growth (Nichols et al. 1994; Cam et al. 1998; Lee et al. 2017), such environment-induced changes in breeding behaviour may play an important role in population declines. Despite this importance, the impacts of environmental and ecological drivers on breeding propensity still remain understudied compared to the internal physiological and physical cues associated with the decision to breed (Bradley et al. 2000; Sergio and Hiraldo 2008). This is unfortunate, since we need to understand both external factors and intrinsic attributes underlying variation in breeding propensity (Hoy et al. 2016; Jean-Gagnon et al. 2017).

Life-history theory suggests that intermittent breeding should be particularly likely to evolve in long-lived species, in which reproduction entails an accessory cost in terms of survival, time or energy beyond the direct investment into gametes or fertilization (Shaw and Levin 2013). Environmental cues that enable individuals to anticipate food availability and to make facultative decisions about whether or not to breed are well-documented (reviewed in White

2008). The same is true for previous experience of breeding that positively affects future breeding prospects (Grieco et al. 2001; Brommer et al. 2004; Desprez et al. 2011; Warren et al. 2014). In contrast, demonstrating the indirect impact of predation risk on the decision to skip breeding has proven to be challenging under natural conditions, for both conceptual and practical reasons. First, the strategy of intermittent breeding requires substantial accessory costs of reproduction to evolve (Morbey and Shuter 2013) and also that reliable predictive cues about predation risk are available to breeders prior to the onset of breeding (Reed et al. 2015). Second, detection of non-breeders is difficult and sometimes even impossible because non-breeders are simply not present at the breeding grounds (Gimenez et al. 2008; Desprez et al. 2011). Sampling is often limited to a single occasion per breeding season only involving the actively breeding segment of the population, which provides only limited scope to differentiate the probability of being present from that of being detected given presence (Reed et al. 2004; Gimenez et al. 2008).

Eider ducks (*Somateria mollissima*) breeding in the Baltic Sea are long-lived animals (estimated life expectancy of 21 years; Coulson 1984) and provide an ideal testbed to address the role of external cues associated with the decision to forgo breeding. First, breeding philopatry is high (Öst et al. 2011) and non-breeders are present and equally conspicuous as breeders at and around the breeding colonies. Second, we had access to ancillary information about the breeding status of individually colour-ringed females outside the actual nest-capture occasions, owing to our long-term observational data (14 yrs) on all females encountered at sea during the brood-rearing season. Third, this population has recently experienced rapidly increased predation by a recovering population of an apex predator, the white-tailed sea eagle *Haliaeetus albicilla* (Jaatinen et al. 2011; Ekroos et al. 2012a; this study), concomitant with an increasing population-wide bias towards males (Lehikoinen et al. 2008). This allowed us to assess both the impact of spatial and temporal variation in predation risk and any effects of surplus unpaired males on breeding propensity, as these males may interfere with female preparations for breeding (Steele et al. 2007). Finally, we included female age estimates (based on ringing history; Jaatinen and Öst 2011) in our analysis: individual reproductive responses to changes in extrinsic conditions may depend on intrinsic attributes (Jean-Gagnon et al. 2017), foremost among which are age and breeding experience (Desprez et al. 2011; Warren et al. 2014). This is because individuals are expected to increasingly favour their current reproductive attempt with advancing age, to compensate for the decline in future breeding prospects (Stearns 1992). We tested the following hypotheses: (i) increasing predation pressure is associated with a higher incidence of intermittent breeding, (ii) an increasing male bias reduces breeding propensity, and (iii) breeding probability generally increases with age. Finally, we explored the connection between breeding propensity and population productivity, measured as fledging success.

Materials and methods

Study area and female capture and observation protocol

This study was conducted in Tvärminne (59°50′N, 23°15′E), western Gulf of Finland, in 2003–2016. The 31 study islands were either small and treeless with scattered stands of juniper (*Juniperus communis*; *N* = 16, referred to as open islands; mean area ± SD = 0.52 ± 0.40 ha) or larger and covered mainly by pine forest (*Pinus sylvestris*) (*N* = 15, referred to as forested islands; mean area ± SD = 5.54 ± 4.42 ha). Open islands have a higher predation pressure on incubating females (Ekroos et al. 2012a; this study), wherefore island type was included as a covariate in the statistical analysis. Female eiders were captured with hand nets predominantly during the end of incubation. On capture, the females were ringed with a standard metal ring, and uniquely colour-ringed on their leg(s) with plastic ring(s) for individual recognition at a distance (up to ca 600 m using a spotting scope under good light conditions). Females were also equipped with a temporary wing flag (lasting up to one month) with a unique combination to ease recognition while swimming at sea (recognition distance ca 800 m using a spotting scope). Because all females irrespective of capture status were colour-ringed and females showed no signs of aberrant behaviour apparently ignoring their markings, we consider it unlikely that our marking techniques would have affected female survival or decisions about whether or not to breed. The number of years since the bird was first ringed was used as an estimate of minimum age (Öst and Steele 2010; Jaatinen and Öst 2011). We acknowledge inevitable measurement error in this variable stemming from variation in the age at first breeding (typically 3 years, range 2–5 years; Hario and Rintala 2009). Nonetheless, this variable can still be considered a reasonably accurate indicator of minimum age. This is due to the facts that we trapped the majority of the successfully breeding females each year (Jaatinen and Öst 2011), and that females are very site-faithful to their previous breeding location (mean breeding dispersal distances are on the scale of tens of metres; Öst et al. 2011). Age-related reproductive senescence is unlikely to significantly affect breeding propensity in the current study. This is because most observed females were at their prime reproductive age, with very few individuals reaching the theoretical expected lifespan of about 21 years (Coulson 1984) or the age at which senescence effects on fecundity start to become apparent (> 17 years of age; Baillie and Milne 1982). Based on our capture success of all incubating females on the study islands, we also calculated the year-specific proportion of trapped females for each island (mean ± SD = 0.57 ± 0.25, N = 292), for use as a covariate (see ‘Statistical analysis’ below). This proportion excluded nests encountered as depredated at first encounter (see ‘Estimating predation risk’ below) since re-nesting, although highly unlikely, may still be possible after nest failure at an early stage.

During daily observations made by a team of two to five observers equipped with spotting scopes, we tried to locate all individually identifiable females in the entire study area, from the first appearance of a brood until the young were close to independence (~30 days after hatching) (observation period late-May until late-June) (Jaatinen and Öst 2013). At each sighting of an individually-marked female, we recorded her identity, whether she was attending a brood, the number of ducklings in the brood, and, if present, the number of other females in the brood. Each focal female was followed long enough to ensure correct assessment of her brood-rearing status. This assessment is straightforward in our study area, as non-tending females are not tolerated within broods and are promptly chased away by the tending female(s) (Öst et al. 2003). Based on all annual observations of a focal female, we grouped each individual into two distinct classes: solitary females never seen associated with young, and brood-tending females associated with young at least once during the brood-rearing season.

Spatial and temporal variation in predation risk

Predation risk was estimated using two indices that were specifically designed to separate the effects of spatial and temporal variation in predation risk on breeding propensity. The first index, the annual island-specific proportion of depredated nests (Jaatinen et al. 2014) was calculated as the number of depredated nests at first encounter divided by the total number of nesting attempts (including depredated nests at first encounter and nests in which the ducklings had already hatched) on each island in 2003–2016 (mean ± SD = 0.21 ± 0.22, N = 292). Clutches are depredated mainly by hooded crows (*Corvus corone cornix*), ravens (*Corvus corax*) and large gulls (*Larus* spp.), but they may also become depredated as a by-product of attacks on the nesting females (for predators on adults, see below). Only depredated nests found during our first visit to each part of the islands were considered (Öst et al. 2011) because additional visits may induce nest depredation and abandonment. The nest censuses on all study islands were done at a phenologically equivalent time in each year. For the statistical analysis, annual island-specific proportions of depredated nests were standardized within years (mean = 0, variance = 1) to obtain a time-detrended predation index only estimating spatial variation in predation risk among islands.

The second index measured the annual abundance of white-tailed sea eagles at Hanko Bird Observatory (HALIAS, 59°49′N, 22°54′E), situated ca 20 km west of the Tvärminne study area (Jaatinen et al. 2011). This index was calculated by dividing the total sum of daily numbers of resident white-tailed sea eagles observed during 1 April–15 June in 2003–2016 (corresponding to the breeding season of eiders) with the number of annual observation days during the same period (mean ± SD = 3.84 ± 1.84, N = 14 years). The eagle abundance index showed a steep increase over time (log-linear regression: 13.4% annual increase, $\mathrm{CI}_{95\%}$ = 9.4% to 17.5%, N = 14 years).

We also documented temporal trends in adult predation risk at Tvärminne. To this end, we recovered all incubating females killed at their nests during nest censuses in 1994–2016 (N = 493). The killer could be determined for 191 freshly killed carcasses according to the way the females had been killed and devoured (see Jaatinen et al. 2011).

Adult sex ratio

The overall adult sex ratio in the entire Gulf of Finland can be assessed by observing migrating birds at HALIAS located at the entrance of the Gulf, acting as a major migration funnel (Kilpi et al. 2003). HALIAS is manned year-round by professional observers using a standardized daily observation protocol and spring-migrating eiders pass close and in small flocks that allow accurate recording of the sex ratio in the group. Here, we determined the overall annual sex ratio in 2003–2016 during a 15-day period around peak migration (Lehikoinen et al. 2008). Because the timing of peak migration depends on the severity of the preceding winter (Lehikoinen et al. 2006), we selected the 15-day peak migration period separately for each year. This was done by selecting the first clear 5-day migration peak and adding, respectively subtracting, 5 days to/from that period (Lehikoinen et al. 2008). The data on the adult sex ratio was based on a total count of 177,525 spring-migrating eiders (annual mean ± SD = 12,680 ± 6267 birds, range 5351–24,443, $N = 14$ years), with an average (± SD) sex ratio of 60.9% (± 4.26%) males (range 53.3%–66.6%, $N = 14$ years).

Fledging success

Breeding success at Tvärminne was determined annually during large-scale brood counts at the turn of June and July (ca. 6 weeks after peak hatching), from fixed vantage points distributed evenly across the entire study area (Lehikoinen et al. 2006). The total number of ducklings and females (sum of brood-caring and solitary adult females) was recorded during these counts, and the ratio of ducklings per adult female was used as an annual index of duckling production.

Statistical analysis

Variation in predation pressure

First, we compared the predation risk on nests and adult breeding females between island types (open versus forested islands). This was done using a logistic regression on the island-specific proportion of depredated nests and killed females relative to the total number of nests on each island over the study period (2003-2016 and 1994-2016 for nest predation and adult predation, respectively; see “Spatial and temporal variation in predation risk”).

Temporal trends in white-tailed sea eagle abundance and observed cases of eagle- and mink-induced predation were investigated by using year as a predictor in log-linear and Poisson regressions (log link, quasi-Poisson errors), respectively. The average proportion and temporal trend in the proportion of eagle vs. mink predation was investigated using a logistic regression (logit link, quasi-binomial errors), with centralized year as the explanatory variable (at 50:50 the intercept is expected to be 0). To filter out confounding temporal trends and autocorrelation, correlation analyses between any two time-series were conducted on the first differences of both variables involved.

Breeding propensity

To determine the incidence of intermittent breeding, we used data from 2004–2016 on resighted colour-ringed females at sea and recaptured females on the nest. A female was considered to be a breeder if it was caught on the nest during the incubation stage and/or if it was observed and identified at sea associated with ducklings at least once. To reduce bias, we included only females known to be both marked and recruited into the breeding population in earlier breeding seasons. In other words, we excluded (1) all first-time breeders because females observed at sea in the year of their first capture had, by definition, been nesting in that season as evidenced by their earlier capture at the nest, (2) all records from 2003 when the colour-ringing scheme was initiated. After this selection, the data set included 1650 records of 698 females observed during the brood-rearing period (range = 1–10 annual resightings, i.e. all resightings of a female within a year were pooled) and associated with one of the breeding islands in 2004–2016.

We used a generalized linear mixed model with binomial errors and logit link to analyse the probability to breed. The explanatory variables in all analyses were standardized by subtracting the mean and dividing by the standard deviation to make effect sizes directly comparable. Our null model included the following fixed effects: island type (factor; open/forested), female minimum years of maternal experience (quantitative; hereafter ‘minimum age’), annual island-wise proportion of successfully trapped females (quantitative; ‘trapping success’), and the annual island-specific proportion of depredated nests (quantitative; ‘predation risk’, see above for variable descriptions). The factor variables female identity, island identity and year identity were included in the model as random effects on the intercept. The model was fitted using maximum likelihood, with Laplace approximation of the likelihood function, optimizer "bobyqa", and a maximum of 20,000 function evaluations.

The null model described above effectively assumes no temporal trend. To assess different hypotheses underlying a possible trend, we used AIC model selection to compare our null model and seven candidate models with temporal change. We evaluated all combinations of the following candidate explanatory variables: year (quantitative variable; annual trend), annual abundance of white-tailed sea eagles, and annual adult sex ratio – all being variables with clear temporal trends (ESM Table S1). We expect that any strong driver of intermittent breeding should provide a more parsimonious model compared to the year-only-model. We present the fixed effect coefficients (± SE) of the most parsimonious model and the statistical significance of the fixed effect coefficients are based on *z* tests.

To test the null hypothesis of no consistent individual variation in breeding propensity, we performed a Monte Carlo test with 10,000 repetitions, where we for each trial simulated a situation with no individual variation and refitted the model. Similar to parametric bootstrapping, we generated new data sets by drawing all random components from their assumed distributions, given the fitted model parameters; however, excluding the individual level random effect. The *P*-value is simply the proportion of larger-than-observed individual SD among the repetitions.

Female body condition

Finally, we indirectly assessed the influence of female body condition on breeding decisions. Body condition is an important confounding factor because a minimum threshold body mass is required to initiate reproduction (see “Discussion”), yet this variable is unquantifiable for the non-nesting females included in our study. However, we may draw indirect inferences about the body condition dynamics in non-nesting birds by analysing temporal trends in body condition of breeding birds. This is because the ‘reproductive suppression model’ (Wasser and Barash 1983) predicts that the condition threshold for initiating breeding may increase under unfavourable conditions, which typically delay the onset of breeding. To this end, we analysed the body condition at hatching and timing of breeding for nesting females at Tvärminne during 2003-2016. Body condition was estimated as size-corrected residual body mass at hatching; the detailed procedure for deriving these indices has been described elsewhere (Öst and Steele 2010). The estimated hatching date was calculated based on egg floatation at capture (Kilpi and Lindström 1997). For analysing both response variables, we used linear mixed models (LMMs) with Gaussian errors and based on restricted maximum likelihood estimation, and with female identity included as a random effect. All statistical analyses were performed using R 3.3.1 (R Core Team 2016).

Results

Variation in predation pressure and correlation between adult and egg predation

Out of the totally 1176 nests depredated at first encounter in 2003-2016, 799 were found on forested islands (nest depredation rate per nest 0.19, N = 4215 nests on 15 islands) and 377 on open islands (nest depredation rate per nest 0.224, N = 1682 nests on 16 islands). The probability of nest depredation was significantly lower on forested than on open islands (logistic regression: b = 0.21 ± 0.07 SE, z_{29} = 3.00, P = 0.003). Correspondingly, out of the 493 females found killed at their nests in 1994-2016, 325 were nesting on forested islands (predation rate per nest 0.081, N = 4025 nests on 15 islands) and 168 on open islands (predation per nest 0.134, N = 1256 nests on 27 islands). The probability of a female being killed was significantly lower on forested than on open islands (logistic regression: b = 0.56 ± 0.10 SE, z_{40} = 5.58, P < 0.001).

The two most important predators on adult females were the white-tailed sea eagle (44.5% of kills, N = 85) and the American mink (*Neovison vison*) (37.2% of kills, N = 71), while predation by the eagle owl (*Bubo bubo*) (11.5% of kills, N = 22), the raccoon dog (*Nyctereutes procyonoides*) (6.3% of kills, N = 12), and the goshawk (0.5% of kills, N = 1) was more uncommon or occasional. The absolute numbers of annual kills showed steep increases in the two main predators. Based on Poisson regression, the annual increase in white-tailed sea eagle-caused mortality was 14.2% ($CI_{95\%}$ = 8.2% to 20.5%) and the increase in predation by minks was 11.0% ($CI_{95\%}$ = 3.7% to 18.9%). In the less important predators, data were not sufficient for testing such trends. The relative proportion of eagle predation vs. mink predation did not differ significantly from 50:50 (logistic regression, intercept: 0.083 ± 0.233 SE, t_{17} = 0.36, P = 0.73) and there was no significant temporal trend in the proportion of eagle predation (logistic regression: 0.027 ± 0.037 SE, t_{17} = 0.73, P = 0.48). Annual predation risks on incubating females and nests were strongly positively correlated (based on first-differenced time-series: $r = 0.751$, $\mathrm{CI}_{95\%} = 0.462$ to 0.896, $N = 20$).

Breeding propensity and its connections to population productivity

We ran seven models with different additive combinations of the explanatory variables and compared these to the null model that included island type, minimum age, trapping success and predation risk as fixed effects (see “Statistical analysis”; ESM Table S1). The candidate models all fitted the data better than the null model with no additional predictors (ΔAIC = 15.29). The most parsimonious model was one including only year added to the null model, describing an unspecified annual trend (marginal $R^2 = 0.19$, conditional $R^2 = 0.31$). Neither addition of annual adult sex ratio (ΔAIC = 12.14) nor of the annual white-tailed sea eagle index (ΔAIC = 8.01) to the null model were supported. Similarly, adding simultaneous effects of year, eagles or adult sex ratio to the null model did not better models as judged by AIC (range of ΔAIC = 1.09–9.88). After ignoring models with uninformative parameters *sensu* Arnold (2010), only the most parsimonious model was considered further.

Investigation of the explanatory variables in the most parsimonious model revealed that after correcting for island-specific trapping success (b = 0.23 ± 0.08, $z = 2.96$, $P = 0.003$), breeding propensity did not differ depending on island type ($z = 0.80$, $P = 0.42$). Females associated with islands with higher predation risk were more likely to skip breeding (Fig. 1, predation risk, b = –0.43 ± 0.07, $z = –6.39$, $P < 0.001$). There was a strong annual trend where a female’s probability to breed decreased over the course of the study period (Fig. 1, annual trend, b = –0.85 ± 0.14, $z = –5.90$, $P < 0.001$). Older females were more likely to breed than younger ones (Fig. 2, $b = 0.22$ ± 0.07, $z = 3.01$, $P < 0.003$). The model intercept was 1.32 ± 0.19.

There was also evidence for consistent variation between individual females in their propensity to breed (random effect, female ID, V = 0.22) and our Monte Carlo test revealed that this individual variation was significant ($P = 0.032$; ESM Fig. S1). The individual random effect SD was estimated at 0.47, but its peaked sampling distribution (ESM Fig. S1), suggests that this quantitative result should be interpreted with caution (rather qualitatively; rejection of the null hypothesis). In addition, a female's breeding island explained her propensity to breed (breeding island, SD = 0.34), and annual variation in breeding propensity was high (factor year, SD = 0.43).

Fledgling production showed large annual variation during the study period, ranging between 0.13 and 1.82 fledged young per adult female (mean ± SD = 0.82 ± 0.50, $N = 13$ years). The annual proportion of presumed non-breeding females and fledgling production showed a negative correlation (Fig. 3; based on first-differenced time-series: $r = –0.620$, $\mathrm{CI}_{95\%} = –0.881$ to –0.072, $N = 13$).

Time trends in female body condition and breeding schedule

Our ancillary analysis of time trends in female body condition at hatching and timing of breeding revealed that female body condition at hatching increased over time (LMM: b = 0.034, $t = 6.60$, $P < 0.001$, $N = 2523$ observations on 1326 females). There was also a temporal shift towards later timing of breeding (LMM: b = 0.29, $t = 9.55$, $P < 0.001$, $N = 2523$ observations on 1326 females).

Discussion

Our results provided support for our first and third hypotheses (skipping breeding was more common under high predation risk and among younger breeders), but not for our second hypothesis (increasing male bias results in a higher incidence of intermittent breeding). We also detected a strong temporal increase in the incidence of intermittent breeding, with average estimated breeding propensity decreasing from 95.2% in 2004 to only 53.8% in 2016 (Fig. 1). The estimated rate of temporal decrease in breeding propensity may, in fact, be conservative, given the exclusion of (presumed) first-time breeders from our analysis and the fact that declining population size in eiders has been linked to a later onset of first breeding (Hario and Rintala 2009). Breeding propensity also showed a strong negative correlation with population productivity (Fig. 3). With respect to the effects of predation risk, breeding in a high predation risk area (indexed by the time-detrended annual island-specific proportion of depredated nests) had a strong negative association with the probability of breeding. This finding agrees with the theoretical prediction that individuals should refrain from breeding as the mortality cost of reproduction increases (Shaw and Levin 2013). Though in itself, this idea is not new – e.g. Coulson (1984) proposed that eiders refrain from breeding in years of low adult survival – predation risk has not before been invoked as a variable underlying the decision to forgo breeding in this species. Thus, Coulson (2010) ascribed the periodically high incidence of intermittent breeding observed in a sedentary British eider population to food shortage for unspecified reasons. Perhaps surprisingly, we found that annual abundance of white-tailed sea eagles had no independent explanatory effect on the probability of breeding. One possibility is that annual-based indices of eagle abundance 20 km away may not capture local variation in predation pressure. Further, the functional form of the relationship between the two variables may be more complicated than expected here. It is also noteworthy that the eagle abundance index showed a dramatic increase over time (see “Spatial and temporal variation in predation risk”), and so it is conceivable that the likewise very strong temporal increase in intermittent breeding could have masked any effects of eagle abundance *per se* on breeding propensity. Nevertheless, we did find that predation on breeding eider females by eagles was the single most important cause of female mortality during the breeding season, increasing markedly over time, and thus this source of predation is likely to affect the incidence of intermittent breeding in this population (see also Ekroos et al. 2012a).

As our results are based on correlative evidence alone, there is a need to consider alternative explanations. We cannot rule out the possibility that some females observed at sea but not captured at the nest actually nested outside the study area. However, we consider it very unlikely that a significant segment of the breeding population would have settled elsewhere to breed, for two reasons. First, females show a high level of breeding philopatry to specific nesting islands (Öst et al. 2011). Although predator-induced nest failure increases breeding dispersal distances in the subsequent breeding season, these movements occur at a very fine spatial scale (tens of metres), only rarely involving island switching (Öst et al. 2011, Ekroos et al. 2012a). Second, adult females irrespective of their breeding status occur aggregated close (typically < 1 km) to their nesting island throughout the brood-rearing season in this population (Öst and Kilpi 2000).

Intermittent breeding as a response to predation risk is only likely to evolve given substantial survival costs of reproduction and the presence of predictive cues on predation risk prior to the onset of breeding. These two conditions are likely to be met in our study system. First, the apparent survival of breeding eider females in this population is the lowest recorded in this species, which has been attributed to increased predation during incubation (Ekroos et al. 2012a). This, in turn, is believed to be the main reason for the progressively increasing male bias in the entire Baltic/Wadden Sea flyway population (Lehikoinen et al. 2008). Second, nest success shows moderate spatial predictability at the island level (Öst et al. 2011). The main predators on incubating females, in particular the day-active white-tailed sea eagle, are conspicuous elements in the archipelago year-round. Although we were unable to confirm a direct relationship between white-tailed sea eagle-induced predation risk and breeding propensity, prevailing predation risk nonetheless affects the nest-site decisions of female eiders in several contexts. For example, breeding females disperse farther following nest predation, which delays their breeding schedule in the subsequent season (Öst et al. 2011). Second, large spatiotemporal variation in predation risk – as observed in our study population – may in itself favour the evolution of intermittent breeding, and promote annual and individual variability in breeding propensity. Thus, theoretical and empirical work suggests that individuals inhabiting more variable environments tend to show a higher average frequency of intermittent breeding (Nevoux et al. 2010), pronounced inter-annual variation in the extent of intermittent breeding (Cayuela et al. 2016), as well as large individual differences in breeding propensity (Shaw and Levin 2013). Indeed, our results revealed that there was significant variation between individuals in their propensity to breed (ESM Fig. S1), and breeding propensity showed annual variation not captured by a simple time trend.

Our correlative approach prevents us from drawing conclusions about the mechanisms by which predation risk may suppress reproduction. However, one possibility, supported by a growing body of research, is that predatory stress encountered prior to breeding onset could cause abandonment of the current breeding attempt. Predation risk may demonstrably trigger physiological adjustments that induce reproductive suppression. Although the majority of the existing evidence of such hormonal regulation comes from mammals (Sheriff et al. 2009; Cherry et al. 2016), pre-breeding stress can also suppress ovarian function in seabirds through increased glucocorticoid (corticosterone) secretion (Goutte et al. 2010a). Incubating females having elevated baseline corticosterone levels have lower nest success (Jaatinen et al. 2013) and pre-breeding eider females with higher baseline corticosterone levels have a later breeding phenology (Hennin et al. 2016). It is therefore conceivable that predator-induced stress may also affect the fundamental decision of whether or not to breed. However, testing this hypothesis would require manipulation of predation risk and monitoring of stress hormone concentrations in pre-breeding females, which is logistically challenging in a natural population. Our results also showed that breeding propensity increased with age. This result may also fit the notion of predator stress-induced suppression of reproduction, as younger individuals are often more susceptible to stressors than prime-aged breeders (Goutte et al. 2010b, 2011).

One important confounding factor is body condition, because a minimum threshold body mass is required to initiate reproduction (Drent and Daan 1980; Rowe 1994; Warren et al. 2014; Legagneux et al. 2016; also see “Statistical analysis”). According to the ‘reproductive suppression model’ (Wasser and Barash 1983), long-lived species challenged by unfavourable conditions are expected to maximize their lifetime reproductive success by suppressing their reproduction until a more favourable time. Empirical tests of this model have shown that experimentally challenged individuals refrain from breeding only in unfavourable years (as indexed by nest success) (Griesser et al. 2017). Consequently, only individuals of high quality and/or condition may opt to breed under unfavourable conditions, a prediction recently corroborated in eiders (Jean-Gagnon et al. 2017). Indeed, the observed increase in the body condition of breeding females at Tvärminne appears to match this prediction (see “Results”). Furthermore, the potential deterioration of breeding conditions is reflected in a concomitant temporal shift towards later timing of breeding. The environment may have become less favourable due to intensifying predation, reduced nutrient load affecting mussel stocks

(Laursen and Møller 2014), and/or a shift in the relative importance of wintering versus breeding areas for acquiring the energy reserves needed for reproduction. The increasing mean body condition in the breeding pool is perhaps surprising, given that excess body mass may jeopardize escape performance (Freed 1981; Norberg 1981). However, apparently such effects, if present, are overshadowed by the generally positive relationship between body condition (reflecting individual quality) and survival in this population (Ekroos et al. 2012a). The change in climate forcing, in turn, may be associated with warming winters, which are related to blue mussels of lower nutritional value for wintering eiders (Waldeck and Larsson 2013). Such conditions may cause greater reliance on food resources gathered at the breeding grounds, forcing females to breed later (Jaatinen et al. 2016). Regardless of the reason for the time trend in body condition of breeding females, an increasing fraction of potential breeders may be unable to build up sufficient body reserves for successful breeding under current conditions. To conclude, temporal changes in the energetic requirements for successful reproduction may have contributed to the steep increase in the incidence of intermittent breeding over time (Fig. 1).

In this study, we have demonstrated that spatiotemporal variation in predation risk and breeder age had a profound influence on breeding propensity, which also showed substantial annual and individual variation. The current unprecedented high level of intermittent breeding should cause serious management concern, as this species, although still common, is now classified as endangered in Europe (BirdLife International 2015) due to the recent steep decline over the entire Baltic region (Ekroos et al. 2012b, Öst et al. 2016). Failing to account for the pool of non-breeders may lead us to seriously overestimate the effective reproductive output per mature female, which may obscure alarmingly low levels of population growth (Lee et al. 2017). Consistent with this notion, we found that high incidence of non-breeding was associated with low fledging success (Fig. 3). As for the next steps in this research, we suggest population-wide modelling of the relative role of increased intermittent breeding versus changes in fecundity and offspring survival in contributing to the population-wide decline of eiders in the Baltic Sea. At the individual level, it would be a logistically challenging, yet important, endeavour to develop non-invasive means to monitor the body condition of pre-laying females that skip breeding. Furthermore, it would be illuminating to explore whether the observed between-female variation in breeding propensity is linked to personality traits such as risk-taking, and whether females skipping breeding in dangerous years really achieve a fitness benefit compared to those birds nesting on a more regular basis.

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Figure captions

Figure 1. The probability of presumed breeding in female eiders as a function of time-detrended annual island-specific proportion of depredated nests (for definitions, see text). The lines illustrate the model fit for 2004–2016 (two-year intervals; lighter grey indicate more recent time), when all non-displayed variables are set to their averages. The data points are displayed as open circles in grey (darker colour meaning more overlap) and with added jitter along the y-axis to facilitate viewing the distribution of raw data (actual data are zeros and ones).

Figure 2. The probability of presumed breeding in female eiders (for definition, see text) as a function of minimum age (years since first capture as a breeding bird). The black solid line is the model fit when all non-displayed variables are set to their averages, while the dashed lines are 95% CIs. The data points are displayed as open circles in grey (darker colour meaning more overlap). Jitter is added to the raw data (zeros and ones) along the x- and y-axes to facilitate viewing their distribution.

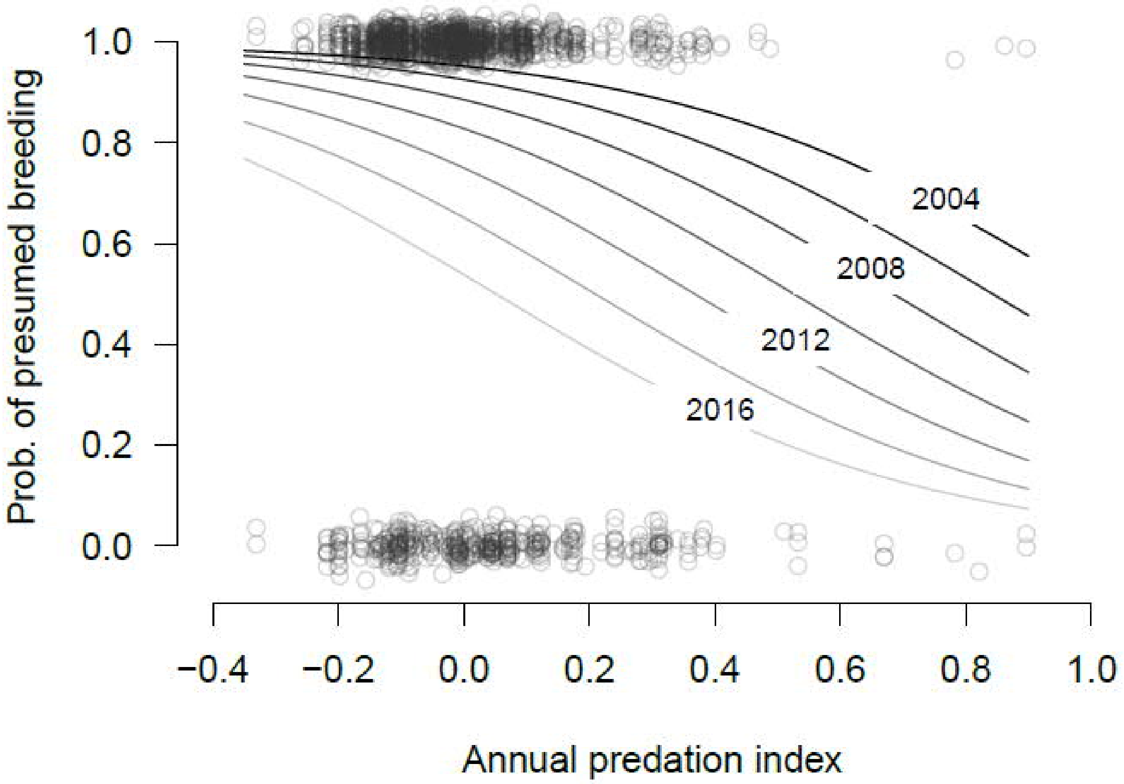
Prob. of presumed breeding
1.0
0.8
0.6
0.4
0.2
0.0
2004
2008
2012
2016
−0.4
−0.2
0.0
0.2
0.4
0.6
0.8
1.0
Annual predation index

Figure 1.

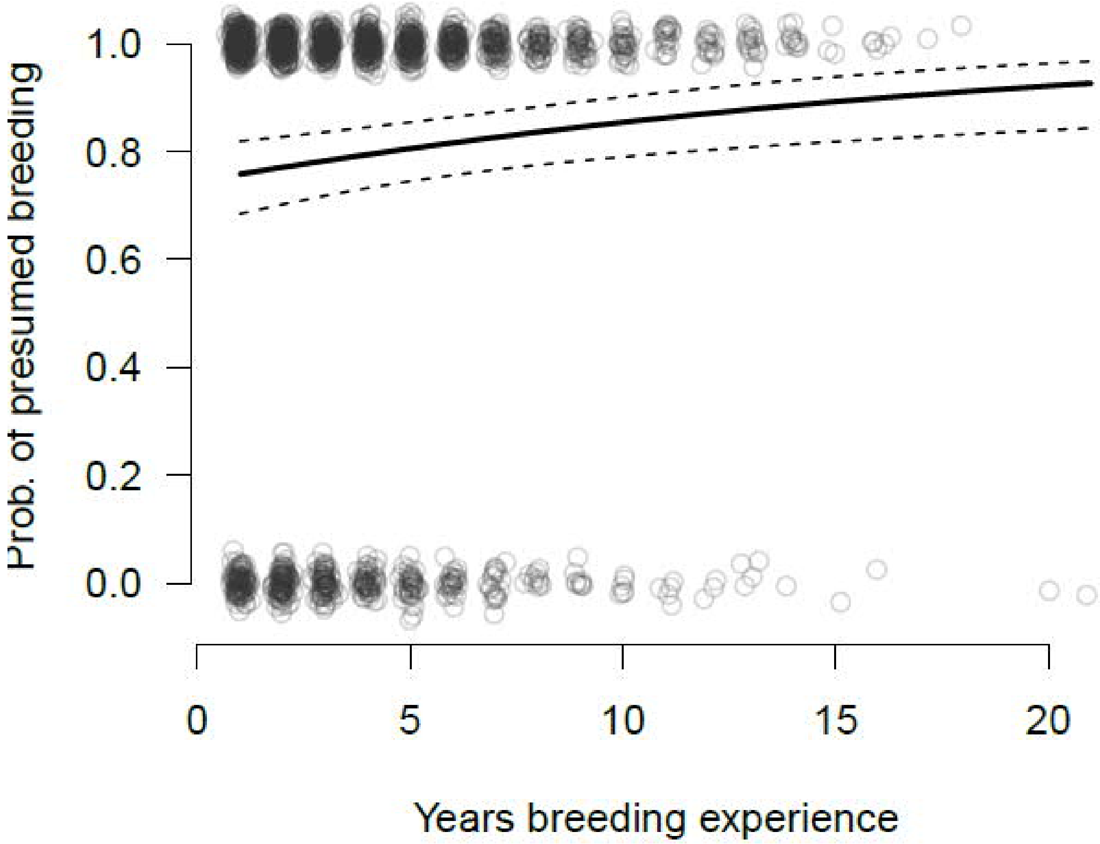
Prob. of presumed breeding
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
Years breeding experience

Figure 2.