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Research

Multiple stressors: negative effects of nest predation on the viability of a threatened gull in different environmental conditions

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The majority of the world's seabirds show substantial population declines, but a detailed understanding of the phenomenon is lacking. A potentially important mechanism that has received momentum lately is nest predation. This study aimed to assess the population viability of a threatened population of the lesser black-backed gull *Larus fuscus fuscus* under different scenarios for nest predation and environmental conditions. We merged results from statistical analyses of 16 years of empirical data with a Leslie model, emphasising the impact of predation at the nesting stage. In the model, we quantified the effect of multiple stressors on the viability of the lesser black-backed gull according to the IUCN Red List's 'Vulnerable' criteria (30% reductions in population size over < 3 generations). First, the empirical analyses showed that the estimated apparent survival probability, which showed declining temporal trends, was on average 0.862 and 0.470 for adults and juveniles, respectively. The average clutch size in the absence and presence of nest predation was 2.836 and 0.935 eggs nest⁻¹, whereas the average number of fledglings nest⁻¹ was 0.452, respectively. Nest predation and chick production showed a concave-up temporal trend, whereas clutch size showed no trend. Second, based on the predictive models, we documented multiple stressor effects: nest predation was the single-most-important stressor, but its adverse effect was severely amplified when environmental conditions were poor. When important nest predators were present, *L. f. fuscus* met the 'Vulnerable' criteria. Nonetheless, when nest predation was absent or low, the status of our population was following IUCN Red List's 'Least Concern' criteria (its official status). Nest predation played a vital role in limiting population growth – a finding that is likely to be relevant for several other seabirds in northern Europe.

Keywords: climatic vulnerability, Corvidae (ravens (*Corvus corax*), hooded crows (*Corvus cornix*)), Horsvær Nature Reserve, Helgeland, northern Norway, literature review, population viability analysis (PVA), reproductive failure



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Correction added on 08 August 2023, after first online publication:

Supporting Information has been updated in this version

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Introduction

Globally, many seabirds have experienced population declines, and seabirds are more at risk than comparable groups of birds (Croxall et al. 2012). A recent quantitative review of the world's monitored seabirds revealed an overall reduction by 70% from 1950 to 2010, a decline not evenly distributed across taxa and regions: pan-global populations were, for instance, more at risk than short-ranging coastal populations (Paleczny et al. 2015). A recent review of seabirds' breeding success documents a substantial hemispheric variability where pelagic and fish-eating birds in the north experienced the most significant impact of ocean warming and other human impacts (Sydeman et al. 2021). Parallel to this, several studies have documented a dramatic decline of many seabird species in the north. Fauchald et al. (2015) reported that 71% ($n = 17$) of the studied species showed > 50% population declines over the past 25 years (for at least one of the regional populations assessed). They based their review on data from Norwegian territories only. Still, it covered a large area (expanding from the North Sea to the Arctic) that supports a significant proportion of the global populations for many of its breeding seabirds (reviewed by Barrett et al. 2006).

This overall, yet highly varying, negative trend in seabird numbers do not have a common explanation (Dias et al. 2019). Instead, a complex interplay between both extrinsic processes, including anthropogenic and natural stressors, and intrinsic causes, such as selection of breeding and feeding habitats, explain seabird population dynamics (reviewed by Barrett et al. 2006, Croxall et al. 2012, Fauchald et al. 2015, Paleczny et al. 2015). Nonetheless, climate change and adverse weather conditions at the breeding sites affected as much as 40% of all the threatened species, but even more worrying is that the adverse effects of climate will probably become more severe in the future (Croxall et al. 2012). Many studies also show that climate plays an indirect role and may act in concert with other stressors like pollution (Kimberly and Salice 2015, Mbaka et al. 2015) and nest predation (Prop et al. 2015, Bårdsen et al. 2018). Dias et al. (2019), who report that ca 70% of the threatened seabirds face multiple stressors, support this. For the three most threatened groups, i.e. albatrosses, petrels and penguins (Croxall et al. 2012), it is pertinent to tackle marine and terrestrial stressors to reverse population declines (Dias et al. 2019). The top-three threats for these species were invasive alien species, bycatch in the fisheries and climate (Dias et al. 2019). Another example of the complexity and the challenges involved in understanding seabird population trends is the delayed effects of sea surface temperature (and other climatic measures) on adult survival: this has been viewed as a signal of changed feeding conditions more than a direct link to climate (Reiertsen et al. 2012, Guéry et al. 2017, Bårdsen et al. 2018). However, impaired adult survival is bad news no matter the causal mechanisms involved. The reason for this is that long-lived iteroparous species, such as many seabirds, show little variation in adult survival compared to other vital rates, while this is the most

significant vital rate affecting population growth (seabirds: Erikstad et al. 1998, reviewed by Gaillard et al. 2000).

The lesser black-backed gull is a species of 'Least Concern' (LC) in both the 2019 IUCN Red List and the 2022 Norwegian Red List (assessed 2 Feb 2022: <www.iucnredlist.org>; <www.artsdatabanken.no>). Nonetheless, for two of its subspecies, the Norwegian population comprises a large proportion of the world's breeding population: 8–9% (i.e. the nominate subspecies: *Larus fuscus fuscus*) and 37–49% (*L. f. intermedius*; 13–49% for the other gulls; Barrett et al. 2006). The nominate subspecies is considered threatened over most of its distribution range: especially in northern Norway (Barrett et al. 2006) and Finland (Hario et al. 1998). The two most likely factors explaining declines of northern-European seabirds (including *L. fuscus*) were predation in the breeding colonies and ecosystem changes affecting prey availability (Fauchald et al. 2015).

Population dynamics are emergent properties of processes acting on individuals over time (Bårdsen et al. 2011, DeAngelis and Grimm 2014). Insights about demographics commence from longitudinal studies following marked individuals (Reiertsen et al. 2012, Guéry et al. 2017). Even though gaining precise estimation of population vital rates (demographic processes averaged over groups of individuals with similar states: Caswell 2001) is challenging, obtaining abundance estimates with sufficient accuracy and precision to infer changes in population size in space or time can be even more demanding (Bårdsen and Fox 2006, Morellet et al. 2007, Rughetti 2016). Models projecting population-level information, such as the future number of individuals, based on estimated vital rates (Caswell 2001, Morris and Doak 2002) can provide management with information about population viability cost-efficiently compared to long-term monitoring of population size (Rughetti and Festa-Bianchet 2014). Models also have added utility as they may be used: 1) as means to explore relationships without reverting to real-world manipulation (computer experiments) that may be impossible, unethical or illegal to perform (Gilbert 2008); 2) to identify knowledge gaps, such as estimated mechanisms or patterns (parameters) for which we currently lack precise information (Bårdsen et al. 2018).

Our objective was to use IUCN's 'Vulnerable' (VU) criteria to assess if the population viability of *L. f. fuscus* was affected by nest predation and environmental conditions at Norway's largest breeding site. Specifically, we aimed to 1) estimate annual juvenile and adult apparent survival and reproduction and their temporal trends; 2) assess how nest predation affected fecundity; and 3) perform a population viability analysis based on the estimated population demographics. We parameterised an age-structured (Leslie) model to perform computer experiments. First, we treated nest predation as a two-level factor: 'Control' (nest predation occurred at natural level) versus 'No predation' (all eggs survived). We kept predation constant while the frequency of good and poor years continuously increased or decreased. Second, we manipulated nest predation continually, keeping the environment constant. These computer experiments aimed to test the multiple stressor hypothesis on *L. f. fuscus*.

Material and methods

Study protocol

We conducted our study on several sub-colonies at Horsvør Nature Reserve (Supporting information S1), where the protection of the breeding areas of the lesser black-backed gull has been given particular importance (Bustnes et al. 2020; Supporting information for details). The fieldwork has been conducted annually at two separate periods. First, an intensive period in June (1–12 days) recording clutch size and predation. Second, a shorter visit (1–2 days) in late July or early August where the fledglings have been tagged with unique IDs and counted. In both periods, we have recorded previously marked individuals. The raw data contained the following variables (Supporting information):

- ID: A colour plastic ring, enabling unique recognition through an alphanumeric code, which can be read from a distance, enabling us to estimate survival and resighting probabilities.
- Clutch size and fledglings: The number of observed eggs and chicks nest⁻¹ across colonies along with a count of the number of nests and the date of recording across two visits per year.

Statistical analyses

Survival

We fitted Cormack–Jolly–Seber (CJS) models to estimate apparent survival (Φ) and encounter probability (p) in R (<www.r-project.org>) using the marked-package (Laake et al. 2013; Supporting information). We assumed two age-classes for Φ and p representing a juvenile (j) and an adult (a) age-class for Φ with different binning intervals for Φ and p : Φ_a , Φ_j , p_a and p_j represent ≥ 2 and ≤ 1 , ≥ 4 and ≤ 3 years of age, respectively (Supporting information S1). We performed both data formatting and processing, e.g. creating age classes, using built-in functions in the marked package. Before fitting the CJS models, we also performed Goodness-of-Fit tests using R2ucare (Gimenez et al. 2018) (Supporting information). We ran the survival analyses in two steps where we: 1) created 30 candidate models with various time- and age-structures for both Φ and p (modelled as factor variables; Supporting information S1 provides details regarding additional covariates); and 2) selected the candidate model with the smallest Akaike's information criterion (AIC; Anderson 2008) and extracted estimates from the selected model (Supporting information). We calculated mean life span (MLS) based on the annual estimated Φ_a and its corresponding 95% CIs (according to Seber 1982): $\div 1/\log_e(\Phi_a)$. Consequently, this indicates how the annual estimated survival affected MLS.

Reproduction

Our estimation of clutch size in the absence of nest predation was running in several steps using the clutch size and the

recording date to predict the average number of eggs laid each year (Supporting information S2). First, we defined a baseline model that contained the additive effects of year (a factor variable) and date (a centred numerical variable: subtracting the average). Second, we used the same model structure in a linear mixed effects (LME) model, using NewColony as a random effect (random intercepts only). We used the generalised least squares (GLS) model as the standard linear model fitted using the same likelihood as the LME models (Supporting information). Third, as the residuals for both models showed evidence of heteroscedasticity, we assessed four different variance structures in addition to the baseline GLS and LME. We thus ended up with ten candidate models where we selected one based on the second-order AIC (AICc; Anderson 2008). Fourth, we formulated two additional models with different fixed effects (again selecting one final model using AICc: a model selection strategy inspired by Zuur et al. 2009). One model with date as the only fixed effect (testing if clutch declined as a function of date), and one where we also included year (Supporting information S2).

Then, we predicted the annual laying clutch size, defined to occur on 1st June. We base this theoretical measure of reproduction in the absence of predation on a few assumptions. First, we determined the laying date based on the fact that 75% ($n=59$) of the nestlings had hatched by 27 June in 1985 (median = 23; range = 13 June–15 July) in a lesser black-backed gull colony close to our study area (Figure 2 in Bevanger and Thingstad 1990). Second, the incubation time for Norwegian lesser black-backed gulls is 24–26 days (Helberg 2020). Third, we assume that our estimated linear relationship between date and clutch size holds for the extrapolation (nine days) from our minimum first recording date to 1st June (Supporting information S2). Fourth, the date of laying is assumed constant.

Nest predation

We assessed nest predation by visiting the nests twice [average (\bar{x}) = 5.39; range = 3–12] days apart and by creating a response that was the number of eggs lost to predation day⁻¹. We used the same modelling approach as in the analyses of laying clutch size except that the model's baseline structure consisted of year (a centred numerical variable) and year² (i.e. the second-order polynomial; Supporting information S2). When we selected the fixed effects, i.e. in the final model selection stage, we assessed whether a simple linear (regression) model had merit over the more complex polynomial model. Our estimate of nest predation was conservative for several reasons. First, three years (2012–2013 and 2016; $n=86$) were excluded from the analyses as not a single chick was produced in these years even though nest predation rates probably were high. Second, even though we excluded 7.108% of the nests with a positive clutch size development ($n=2040$), eggs could be lost to predation unnoticed as the birds may have compensated their losses by producing extended clutches (Nager et al. 2000). Third, our observations do not separate between partial and complete nest

predation occurring before our first visits: nests losing all eggs before our first visit were, for instance, not included. Fourth, we chose the model that gave the most conservative estimated daily predation rates (Supporting information S2). The total number of eggs lost to predation for each year was calculated by multiplying the year-specific predicted number of eggs lost day⁻¹ with an assumed incubation time of 24 days (above). Subtracting the average number of eggs lost to predation from the laying clutch size predicted in the model above resulted in a calculated annual hatching clutch size.

Temporal trends and imputation

We tested for temporal trends (2005–2019) in estimated survival, laying and hatching clutch size, as well as the number of fledglings nest⁻¹. We used the estimates from the CJS model as the response in linear models (Supporting information S2) as 1) Φ_a was uninformative in 2013 (it's 95% CIs practically covered both zero and one), 2) Φ_j was lacking for 2012–2013 and 2016 and 3) such a statistical modelling approach opened for imputing the missing estimated survival rates in the matrices below (Supporting information S2). For all the responses, we selected one model from a set of two candidate models using AICc: 1) a straightforward model that only contained the linear effect of year; and 2) a model that, in addition, also included year² (as in the analyses of nest predation above). Hence, we used the prediction from these models to impute adult and juvenile (values used in the matrix models) survival in 2013 and 2012–2013 and 2016, respectively. Removing these years from the simulations, or imputing values using the average, would have resulted in higher survival (since the imputation models revealed negative temporal trends) and, consequently, an over-optimistic viability assessment in our models.

Model description

We created an age-based (Leslie) matrix model (Caswell 2001, Morris and Doak 2002) based on the estimated apparent survival and reproduction. Our model assumed four age classes: a juvenile (j : ≤ 1 -year-old), two pre-breeding classes and an adult class (a : ≥ 3 years old). In simple terms, the model may be expressed as follows (details in Fig. 1):

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t) \tag{1}$$

Here, $\mathbf{n}(t)$ represents a vector of the number of individuals from each age class within a given point in time (t), $\mathbf{n}(t+1)$ means the same for the following year. \mathbf{A}_t is a time-varying transition matrix consisting of the annual estimates for survival (P) and fecundity (F) (Caswell 2001, Morris and Doak 2002).

We used annual estimated apparent survival (for age class i) as P_i ($P_0 = \Phi_j$ and $P_1 = P_2 = P_{3+} = \Phi_a$). Hence, we cannot separate mortality and emigration in our matrix models. This, however, has limited practical implication as we aimed to assess population viability within our study area, so it did

not matter if the disappearing birds were dead or permanently emigrated. Only the adults (3+) reproduced, meaning that F_{3+} was the only positive fecundity rate, which was why we used four age classes instead of the two used in the CJS-models. Fecundity rates in matrix models are the fraction of individuals produced that survive and thus are recruited into the population from t to $t+1$ (Morris and Doak 2002: 207). Hence, we base F_{3+} on the average clutch size (multiplied by 0.5; assuming a 1:1 sex ratio). We then multiplied this estimate of the average number of females produced per nest with Φ_j . In the model, predation occurs in-between laying and hatching, whereas the estimated survival for chicks marked as fledgling was applied as the survival from hatching and onwards (Fig. 1C). The transition matrix varied in time (\mathbf{A}_t) through a random selection of years and their associated values for P_i and F_j . Our model assumes a simple form for regulation to prevent unlimited growth (Supporting information).

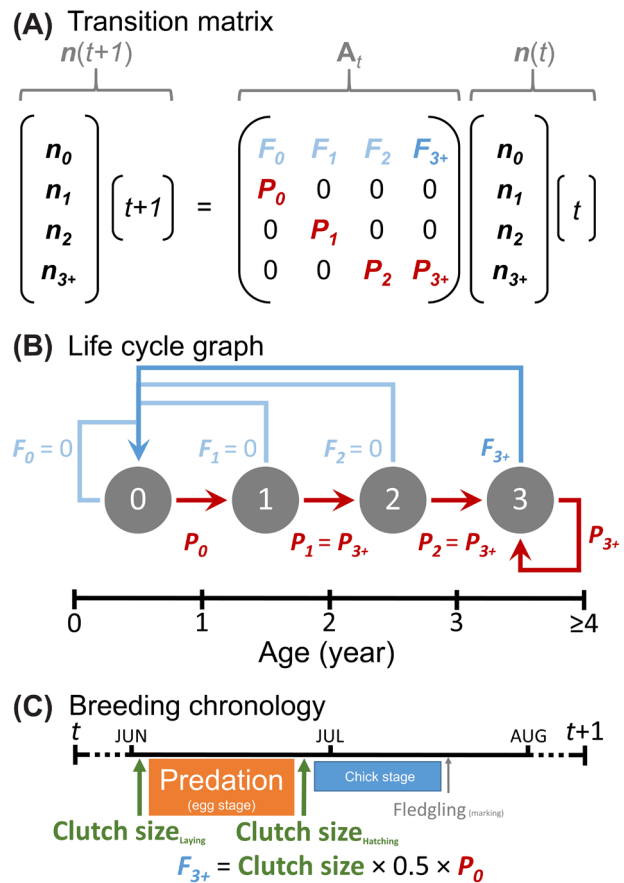


Figure 1. Schematic overview of the model showing: (A) the transition matrix (\mathbf{A}_t); (B) the life cycle graph; and (C) the timeline for the breeding season. The four age classes consist of individuals being ≤ 0 , 1, 2 and ≥ 3 years (3+) old and their associated fecundities (F) and survival probabilities (P). We manipulated nest predation either by using clutch size at hatching (Control: estimated clutch size after predation has taken its toll) or at laying (No predation: a predator-free estimate) as the basis for calculating F_{3+} (C).

Computer experimentation

We used computer experiments to create scenarios for future environmental conditions and nest predation (Supporting information S3). Initial conditions were based on the stable age-class distribution for the average matrix and were kept similar across all simulations as $n_0=43$, $n_1=20$, $n_2=19$ and $n_{3+}=218$, so $n(t_0)$ was 300 (Supporting information S3). We ran our simulations and analysed the output in R using the popbio-package (Stubben and Milligan 2007).

Long-term (asymptotic) effects

We ran 200 different population trajectories in each run to visually check if the output was consistent across populations. We defined terminal time to 200 years; the output was medians, including the 25th and 75th quantiles across all the simulated populations, for the 100 last years of each simulation. We fitted generalised additive models to each response variable (median values), such as population growth rates (λ) and abundance (N), using environmental conditions or nest predation as single predictors (Supporting information). In all simulations, the selection of a given year (and its associated fecundity and apparent annual survival) formed the basis for creating F_{3+} and P_s in \mathbf{A}_t (Fig. 1B). Hence, we simulated environmental scenarios by manipulating the: 1) environmental goodness index (EGI) and 2) environmental harshness index (EHI). We simulated 80 scenarios with equally spaced values for EGI and EHI varying from 0 to 1/15. Bigger values for these indices mean increased probability of selecting good (EGI) and poor (EHI) years as defined by ranked Φ_a . The rationale for this is that theory predicts that environmental stress has an insignificant effect on Φ_a in long-lived organisms compared to other vital rates (Gaillard et al. 2000). In the control run, the probability distribution for sampling years was uniform: i.e. each year had an equal probability of being selected (status quo). Previously, the increased frequency of poor or good environments has formed the basis for scenarios for future climate change (Bårdsen 2017) with the rationale that climate models predict increased frequencies of extreme events (Tebaldi et al. 2006, Benestad 2007, Sun et al. 2007).

Moreover, we manipulated nest predation rates differently, resulting in two different quasi-experiments. First, we contrast zero predation (No predation) with our study area's observed predation rates (Control). This result in Experiment I, where we kept environmental conditions constant while manipulating nest predation continuously as follows:

1. Control: We manipulated nest predation rates from zero (predation was absent) to 0.75 (75% of all eggs were removed by predators) while keeping environmental conditions at status quo (EGI = EHI = 0).
2. Good: Nest predation rates manipulated as in the Control-scenario, but good years had an increased probability of being selected as EGI = 0.5/15 (~0.030).

3. Poor: The same as the Good-scenario except that poor years had an increased probability of being selected (EHI = 0.5/15).

Second, in Experiment II, we added two levels of nest predation while manipulating environmental conditions along a gradient:

1. Control-EGI: Nest predation rates were present as we estimated and calculated them from the empirical data. Consequently, we used the estimated clutch size at hatching (Supporting information S2) as the basis for calculating F_{3+} (Fig. 1). Then, we assessed the effect of improved environmental conditions by varying EGI from zero (control) to 1/15. In the extreme run, the probability of selecting the poorest year became zero. In contrast, the probability of selecting the best year was 2/15 or twice the probability compared to the status quo (Supporting information S3).
2. No predation-EGI: Same as the first scenario except that no nest predation occurred. Hence, we used laying clutch size (Supporting information S2) as the basis for calculating F_{3+} (Fig. 1).
3. Control-EHI: Nest predation was like the first scenario, but we manipulated EHI to increase the probability of selecting poor years.
4. No predation-EHI: Same as the third scenario except that no nest predation occurred.

Quasi-extinction: transient dynamics

We assessed quasi-extinction based on stochastic growth functions (using \mathbf{A}_t as input) using the cumulative probability for population reductions of 30% within 36 years based on 50 000 runs (initial conditions similar as above; Supporting information). We calculated stochastic populations growth rates using both a simulation (λ) approach and Tuljapurkar's (λ_T) approximation (Morris and Doak 2002: ch. 7), and we based them on matrices, with (Control) and without (No predation) nest predation, for 1) 2005–2018, 2) 2005–2010 (early) and 3) 2011–2018 (late).

Prospective and retrospective analyses

We performed stochastic sensitivity and elasticities analyses and fixed life table response experiments (LTBR: Caswell 2001; details in Supporting information S3). We completed the LTRE in several steps. First, we defined a reference matrix using the average vital rates for when predation was present (Control) and compared it to when predation was absent (No predation) and matrices based on data from the literature. Second, we used matrices based on the absence of predation as the reference. Third, we used period-specific matrices comparing the No predation (reference) to the Control scenario using data from our study area.

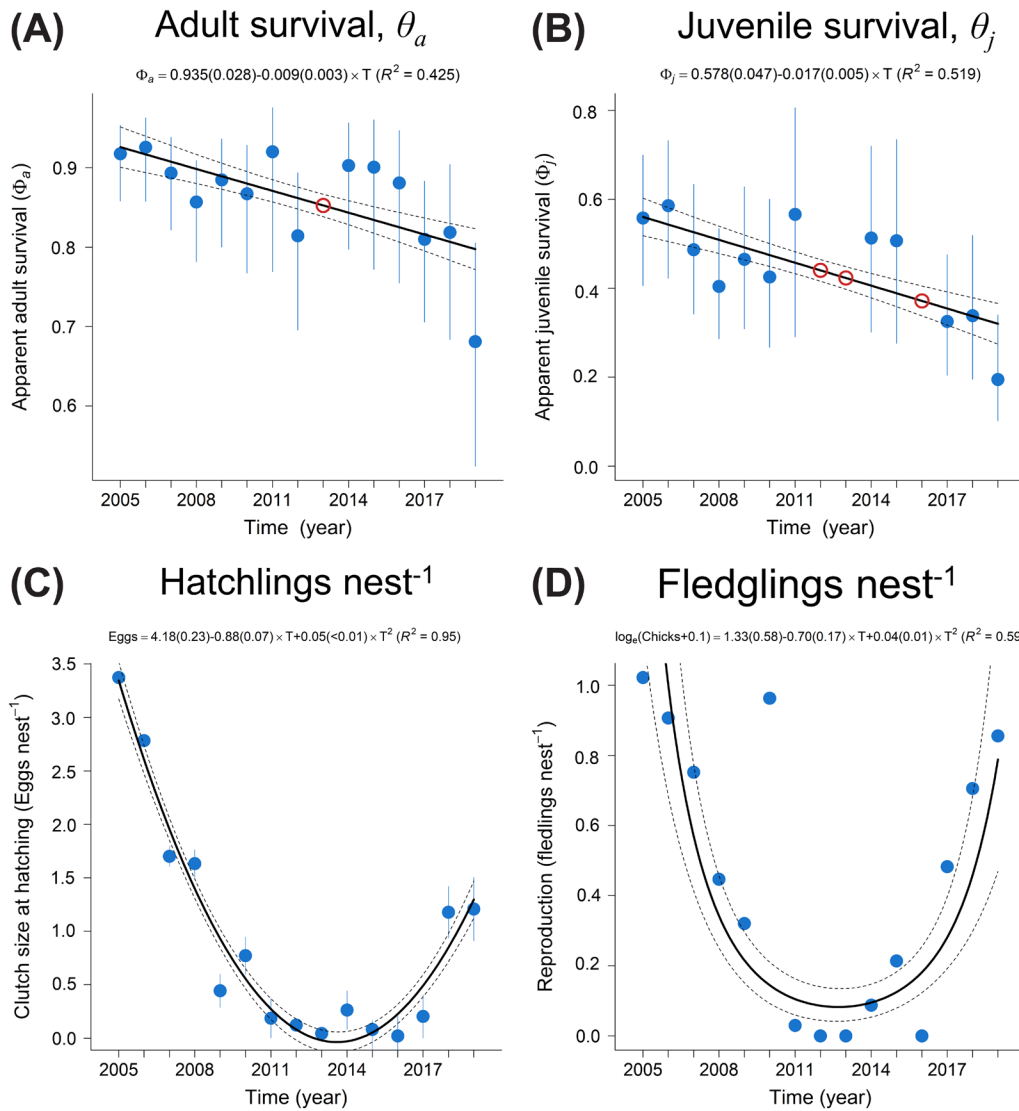


Figure 2. The temporal trends for estimated apparent survival of (A) the adults (Φ_a) and (B) the juveniles (Φ_j); (C) the number of hatchlings nest⁻¹; and (D) the log_e (number of fledglings nest⁻¹). Red dots show imputed values used in the matrix models for Φ_a and Φ_j (Supporting information S2).

Results

Empirical results

Survival

The selected model contained a time- and age-varying structure for both Φ and p , where the difference in AIC for this and the second-ranked model was > 200 . The average estimated Φ_a from the selected model was 0.876 [coefficient of variation (CV) on probability-scale ($CV_{\text{Prob.}}$) = 4.635%; CV on logit-scale (CV_{Logit}) = 18.370%] and varied from 0.810 (95% CI = 0.706, 0.883 in 2017) to 0.926 (95% CI = 0.858, 0.963 in 2006). For the juveniles, the average estimated Φ was 0.470, and varied from 0.325 (95% CI = 0.204,

0.475 in 2017) to 0.586 (95% CI = 0.422, 0.732 in 2006; $CV_{\text{Prob.}} = 18.829\%$; $CV_{\text{Logit}} = 294.151\%$; Fig. 2A and B). These estimates excluded 2019 as the last year always results in the lowest estimated Φ , and for Φ_a we excluded 2013 due to its low precision (the 95% CI covered all possible outcomes). These estimates resulted in an MLS that varied from 12.98 (95% CI = 6.51, 26.35) to 4.74 (95% CI = 2.87, 8.05) years. Using the average Φ_a , this resulted in an MLS of 7.82 years. The estimated p varied from 0.201 (95% CI = 0.147, 0.269 in 2013) to 0.939 (95% CI = 0.802, 0.983 in 2020) with an average of 0.623 for the adults; and 0.023 (95% CI = 0.015, 0.035 in 2012), and 0.420 (95% CI = 0.160, 0.734 in 2020) with an average of 0.116 for the juveniles (Supporting information S1). In the analysis solely consisting of birds marked

as adults, estimated Φ was 0.890 (95% CI=0.869, 0.908) and time-invariant, whereas p was both 'Trap dependent' and varied over time (Supporting information S1).

Reproduction

In the analyses of laying clutch size, we selected an LME model with an exponential variance function and both date and year as fixed effects (Supporting information). This model supported the hypothesis that clutch size decreased as a function of the day of our visit in June (-0.038 eggs day $^{-1}$) and varied across years (Supporting information). The result of this model was that we could predict clutch size at laying, which showed evidence of a temporal variation: $\bar{x} = 2.836$; CV=18.422%; range=1.708, 3.491 (Supporting information S2). Our theoretical laying clutch size was 0.683 (0.030 SE), or 32%, larger than the empirical estimate ($\bar{x} = 2.153$; CV=22.069%; range=1.083, 2.743).

Nest predation

In the analyses of egg predation rate day $^{-1}$, we selected a GLS with a power-variance function including both year and year 2 as fixed effects (Supporting information S2). This model supported the hypothesis that daily nest predation rates were low at the start of the study, highest in the middle years (2012–2013) and decreased again at the end of the study (Supporting information S2). Based on the annual difference between the predicted clutch size at laying and hatching, we estimated that an average of 70.53% (range=1.70–99.16%) of the eggs disappeared from laying to hatching (63.99% if we remove 2012–2013 and 2016; Supporting information). The predicted clutch size at hatching was smaller than at laying [$\bar{x} = 0.935$ (1.153 excluding 2012–2013 and 2016)]. Despite the presence of a temporal variation in hatching clutch size, it was > 6 times more variable than laying clutch size (CV=112.206%; range=0.022, 3.374 (Fig. 2C; Supporting information)). The number of fledglings nest $^{-1}$ was 0.452 (SD=0.388; CV=85.802%), or 0.565 (SD=0.349) excluding years without chick markings.

Temporal trends and imputation

We documented simple linear and negative temporal trends for Φ_j ($R^2=0.52$) and Φ_a ($R^2=0.43$; Fig. 2A and B) and the polynomial model in the analyses of clutch size at hatching ($R^2=0.95$) and fledglings nest $^{-1}$ ($R^2=0.59$; Supporting information S2). The shape of these non-linear relationships was somewhat different. The number of eggs nest $^{-1}$ at hatching decreased until 2014; then, it increased to around a third of the maximum clutch size of ~ 3.5 eggs at the beginning of the study (Fig. 2C). In contrast, the number of fledglings nest $^{-1}$ decreased from 2005 until 2012–2013 and then increased towards the end of the period (Fig. 2D). The effect of time on laying clutch size was negative but not statistically significant (Supporting information S2). The number of fledglings nest $^{-1}$ was ≤ 0.087 in five out of 15 years (30%; Fig. 2D), and in 60% of the years, each pair produced < 0.5 chicks.

Long-term effects

Experiment I: continuous manipulation of nest predation

Extinction always happened when nest predation was present since the long-term stochastic population growth (λ) eventually became negative (Fig. 3). We did, however, document an environment–predation solid interaction. In the 'Good' environment (EGI=0.5/15) – predators could remove $\sim 50\%$ of the eggs without causing extinctions (Fig. 3A). In the 'Control' (status quo) environment, extinctions occurred when $\geq 29.5\%$ of the eggs were predated (Fig. 3B). This was in contrast to the 'Poor' environment when only $\geq 2.3\%$ of the eggs lost to predation caused extinctions (Fig. 3C). This multiple-stressor effect was also evident when looking at the median abundance at the end of the simulations (N ; Fig. 3).

Experiment II: continuous manipulation of the environment

We documented a strong interaction between environmental conditions and the presence ('Control') and absence ('No predation') of predation. First, in improved environments, extinctions occurred in the presence of predation except for the very best environments (EGI ≥ 0.061 ; Fig. 4A), and this was in contrast to the 'No predation' scenario where growth always occurred (Fig. 4A). Second, the presence of predation always resulted in extinctions under worsened conditions (EHI > 0), whereas in the absence of predation, extinctions only occurred in the worst environments (EHI ≥ 0.036 ; Fig. 4B).

Quasi-extinction

Based on matrices covering 2005–2018, the probability of quasi-extinction was ~ 0.75 after nine years when predation was present ['Control': $\lambda_5 = -0.044$ (95% CI = $-0.046, -0.042$); Fig. 5A], but extinctions never occurred in the absence of predation ['No predation': $\lambda_5 = 0.060$ (95% CI = $0.059, 0.061$); Fig. 5B]. In 2005–2010 when both survival and reproduction was high (Fig. 2), the probability of quasi-extinction was low irrespectively of whether nest predation occurred ['Control': $\lambda_5 = 0.041$ (95% CI = $0.039, 0.043$); Fig. 5C] or not ['No predation': $\lambda_5 = 0.104$ (95% CI = $0.103, 0.104$); Fig. 5D]. Finally, the probability of quasi-extinctions reached 0.75 after four years in 2011–2018 when predation was present ['Control': $\lambda_5 = -0.121$ (95% CI = $-0.123, -0.121$); Fig. 5E], whereas the risk of quasi-extinction was very low when predation was absent ['No predation': $\lambda_5 = 0.026$ (95% CI = $0.025, 0.027$); Fig. 5F].

When we assessed the long-term behaviour of the system based on a constant transition matrix (using **A** based on the annual vital rates), 12 (80%) versus five (33%) out of 15 years eventually resulted in extinctions (i.e. $\lambda > 0$) when predation was present and absent, respectively (Supporting information S4). In the absence of predation, the only year that resulted in an actual collapse ($\geq 80\%$ declines after 36 years) was 2017 due to its low fecundity combined with low survival estimates. However, when predation was present, the 11 years post 2008 resulted in collapses. Similarly, bonanzas ($\geq 80\%$

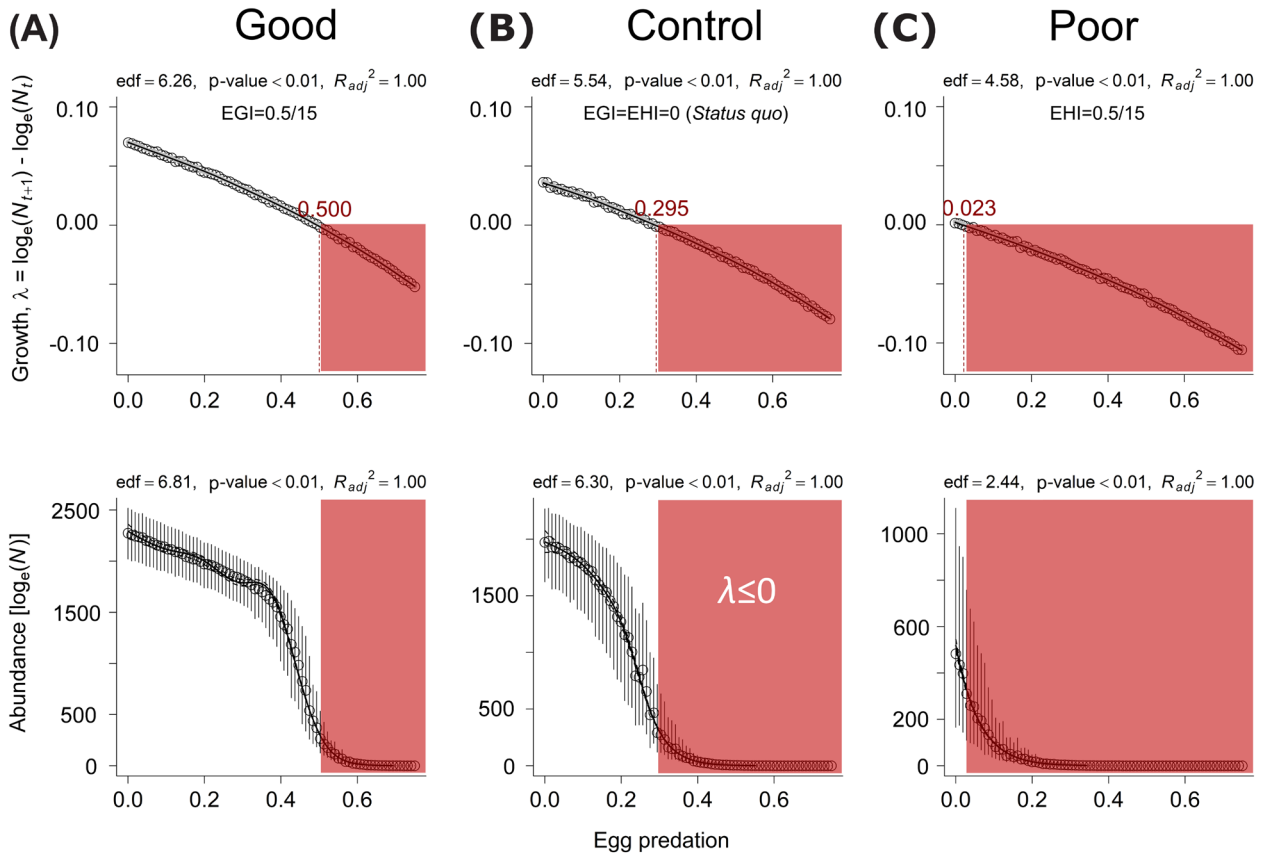


Figure 3. Upper panel: Stochastic population growth rates using both a simulation approach (λ ; bars representing 95% CIs) and Tuljapurkar's (λ_T) approximation for scenarios where nest predation varied from zero to 0.75. This manipulation of nest predation was crossed with manipulation of the environmental goodness index (EGI) and environmental harshness index (EHI), creating three different environments: 1) *Good* where an increased probability of selecting years with high (adult) survival occurred ((A); EGI=0.5/15); 2) *Status quo* where all years had a fair chance of being selected ((B); EGI=EHI=0); and 3) *Poor* where the probability of selecting years with low survival increased ((C); EHI=0.5/15). Red polygons show the range in which population declines ($\lambda < 0$ as defined by the simulations), and we ultimately predicted extinction using generalised additive models (GAMs). Lower panel: median population abundance (bars shows 25th–75th quantiles), on \log_e -scale (Supporting information provides technical details). GAM-specific details include the effective degrees of freedom (edf); statistical significance for the degree of smoothing; (P) and the adjusted coefficient of determination (R_{adj}^2). Note the difference in the range of the Y-axis.

increases) occurred in three (20%) and ten (70%) years when predation was present and absent, respectively (Supporting information S4). Moreover, keeping one vital rate at its average and varying the others within their observed range, extinctions occur when nest predation occurs.

Prospective and retrospective analyses

The sensitivity and elasticity analyses showed that λ was affected mainly by P_{3+} . The relative importance of F_{3+} and P_0 depended on whether predation was present or not. In the 'No predation' scenario, juvenile survival was more important than fecundity, whereas the opposite was true in the 'Control' scenario (Supporting information). In contrast, the LTRE showed that fecundity had the most significant influence on λ (even though its effect varied). Removing the impact of nest predation resulted in a minor difference

in λ between our study area and matrices defined by literature-based averages (Supporting information S4). Finally, linear regressions revealed that λ was positively related to all the rates but that fecundity and adult survival was more important than juvenile survival (Supporting information S4).

Discussion

Both nest predation and environmental conditions affected the population viability of the lesser black-backed gulls, but nest predation was the most important stressor. Our computer experiments revealed that if predators removed ~30% or more of the eggs laid, extinctions would occur under present-day environmental conditions. This threshold predation-value, after which extinctions happened, changed to 50% and

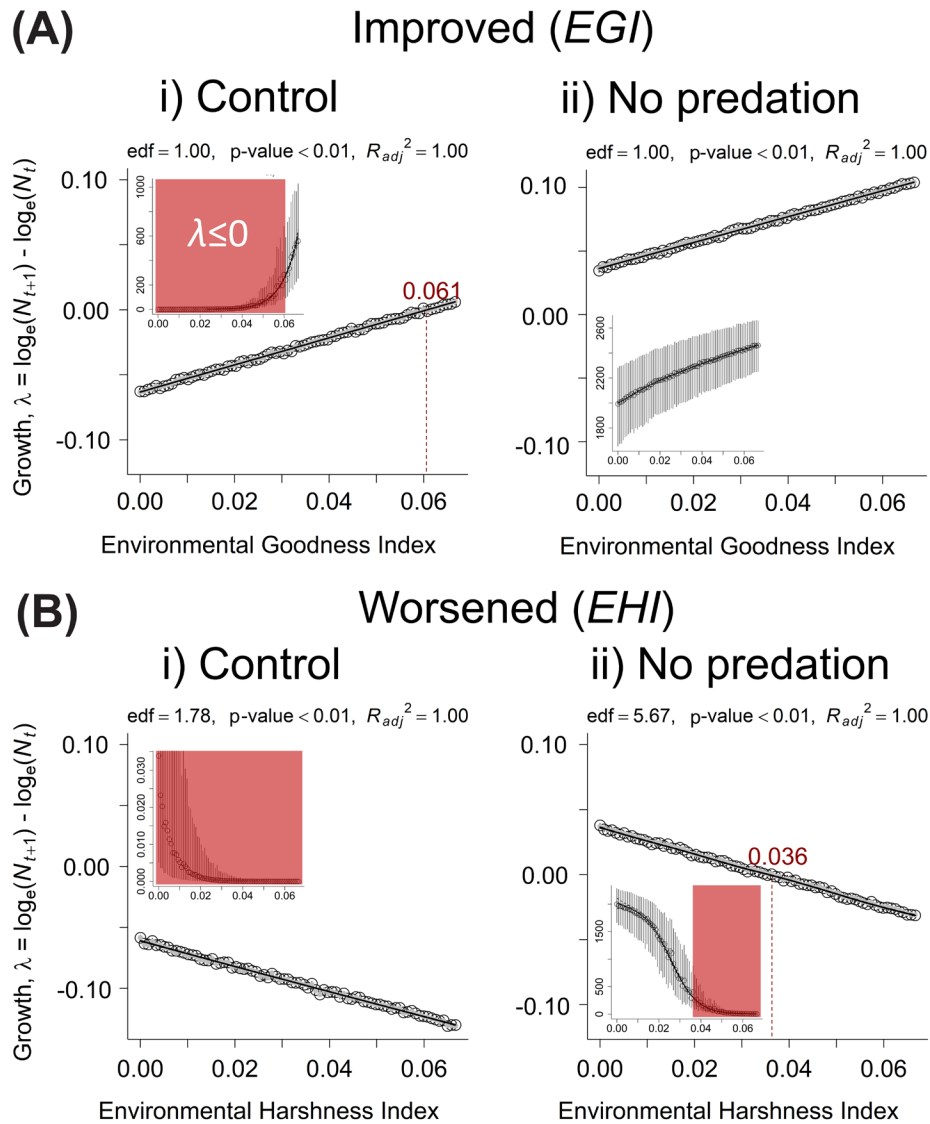


Figure 4. Stochastic population growth rates along gradients of improved (A) and worsened (B) environmental conditions (details provided in Fig. 3). In both cases, zeros simulate *status quo* where all years had a similar probability of being selected. We crossed environmental scenarios with manipulation of predation where either hatching ('Control') or laying ('No predation') clutch size formed the basis for calculating the fecundities (Fig. 1C). Small sub-plots show the resulting population abundance, and red polygons indicate the range in which long-term population declines ($\lambda < 0$) were predicted (Supporting information S4).

2% if the environment was improved and worsened, respectively. Nest predation also had a dramatic effect in the experiments where we manipulated the frequency of good and poor years, combined with the presence or absence of nest predation. In the presence of nest predation, the populations avoided extinction if the frequency of good years increased relative to present-day conditions. More importantly, based on all matrices, it was highly probable that quasi-extinctions occurred within less than ten years when nest predation was present. In contrast, when predation was absent, extinctions only happened if the frequency of poor years increased. In sum, our study supported the multiple stressor hypothesis for *L. f. fuscus*.

Demography

The average estimated apparent adult survival (0.88) was lower than previous studies (Other studies = 0.90; Supporting information). We could not find other reports of juvenile survival, so we would not compare our results with the literature. Both estimates showed negative and linear temporal trends from 2005 to 2019. The low estimated encounter probability for the youngest age class (≤ 3 years; $\bar{x} = 0.12$) supports the hypothesis that few birds visit their breeding sites before maturity. We have no records of yearlings (individuals hatched the previous year), whereas the encounter probability for the adults (≥ 4 years) was higher in our study

($\bar{x} = 0.62$). Still, this estimate was lower than the other study reporting this ($\bar{x} = 0.94$: Camphuysen and Gronert 2012). Our study included younger individuals in the adult age class compared to the other study (where the average age was 12 years: Camphuysen and Gronert 2012: 116), which may explain the discrepancy between the studies. The youngest segments of our adult class thus probably consisted of more non-reproducing birds (see Wanless et al. 1996 who assumed no breeding until four years), which is consistent with the higher estimated encounter probability in the analyses solely based on adults (Supporting information).

The number of fledglings nest⁻¹ is negatively biased as an unknown proportion of the chicks are unobserved during marking (due to hiding or escaping offshore). Still, reproduction was low in our study as less than 0.5 fledglings left an average nest in the majority of years. Even though the number of fledglings nest⁻¹ was small, it was not statistically different from other studies ($\bar{x} = 0.59$). Nonetheless, the average clutch size was larger in the literature ($\bar{x} = 2.78$) than in our study area. Interestingly, we did not document any temporal trends in clutch size at laying. Reproductive allocation at the start of the breeding season was thus highly variable but unaffected by predation in the coming breeding season (which is the case for many long-lived organisms who adjust their reproductive effort in a risk-sensitive manner when faced with unpredictable environments: Bårdsen et al. 2008, 2014, Bårdsen 2017). The gulls either chose to breed without information about predation pressure, or the cost of breeding (up to the laying stage) was too low for the gulls to take nest predation into account when choosing how many resources to allocate into reproduction at the laying stage.

Early life mortality

Over the years, we estimated that predators removed 70.53% of the eggs laid, and this number is larger than the literature ($\bar{x} = 11.91\%$; Supporting information S5). An additional decrease of 32.82% happened from hatching to fledgling, and an average pair lost 85.29% of the eggs they laid (Supporting information S2). Predation may be challenging to estimate, particularly if the goal is to separate predation pressure for different stages. We urge caution when comparing effects across studies. Yet, we know that predation plays a significant role in limiting the breeding success in our study area. Common egg and chick predators, reported in the literature, include the herring gull (*Larus argentatus*: Bevanger and Thingstad 1990, Hario 1994), the great black-backed gull (Lif et al. 2005), red fox (*Vulpes vulpes*: Spaans 1998, Davis et al. 2018a) and intra-specific predation from neighbouring individuals (Bevanger and Thingstad 1990). Our estimate is thus higher than Hario (1994:5), who reports that only 6% of the chicks hatched survived and reached the fledgling stage.

Our mortality estimates used in the model are conservative (Supporting information S6) as we assumed that nest predation is the only source of mortality from egg-laying until hatching and no mortality from hatching to fledgling.

At the same time, we know that some eggs are non-viable. Chicks may die from causes other than predation, such as diseases, pollution, starvation and bad weather (Bevanger and Thingstad 1990, Bolton 1991, Hario and Rudback 1996, Lif et al. 2005). Predation is, according to Hario (1994), not the most common cause of death among chicks: 73% died from diseases, but among those subject to predation, most of the deaths (36%) occurred in the first five days of life (21% of them caused by predation). In a follow-up study, however, 37% of the chicks were lost to predation by herring gulls (and as much as 90% if we add the chicks categorised as 'most probably taken': Hario and Rudback 1999:74). Yet another study highlights the importance of parental quality by showing that chick mortality was much lower for high- versus low-quality adults (Bolton 1991; see Supporting information for details).

The most common egg predators in our study were breeding ravens (*Corvus corax*) present from 2011 to 2016 (not observed in 2013), but we also documented one pair of nesting hooded crows (*Corvus cornix*) in 2015. According to the presence and absence of corvids had a dramatic effect on reproduction (hence having similar effects on reproduction as previously been documented for red foxes: Davis et al. 2018b). Moreover, nest predation showed a concave-up temporal trend (like hatching clutch size and fledglings nest⁻¹) – the most significant losses observed in the mid-period – practically no predation occurred at the beginning and last year of the study. On average, 95% of the eggs were predated in 2011–2016, meaning that the gulls only produced 0.031 fledglings nest⁻¹ when the ravens were breeding. To our knowledge, this is the first study documenting that nest predation by ravens may be the direct cause of reproductive failure, which indirectly can cause the decline of *L. fuscus*. Nonetheless, both previous analyses of observational data from our study area and anecdotal accounts (Davis et al. 2018b, Bustnes et al. 2020) have shown adverse effects of nest predation by ravens.

Long-term effects

Nest predation inevitable caused extinctions in our simulations even though its negative effect on population growth, and hence viability, interacted with environmental conditions. This interaction documents a multiple-stressor effect involving both predation and environmental conditions. First, extinction in the long run ('Experiment I') occurred when predators took $\geq 29.5\%$ of the eggs under present-day environmental conditions, but when the frequency of good and poor years increased, extinctions occurred at much higher ($\geq 50.0\%$) and lower ($\geq 2.3\%$) predation rates. Second, nest predation resulted in negative growth in all environments except the top 10% of the best environments ('Experiment II'). In the absence of nest predation, population growth was always positive in the improved simulations, whereas negative growth only occurred in the worst 45% environments. More importantly, under present-day environmental conditions, nest predation resulted

in negative population growth and extinctions after < 100 years ($N_{t=200} < 1$), whereas a population increase of 564% ($N_{t=200} > 1993$) relative to the initial population size occurred in the absence of predation.

Interestingly, a similar model on common eider *Somateria mollissima* documented a multiple-stressor (interaction) effect involving nest predation and climate. In this model, the threshold for when predation induced extinctions was 25.81% under present-day conditions (Bårdsen et al. 2018). The threshold beyond which nest predation caused extinctions

was thus very similar for these two distantly related species breeding in Northern Norway. Bårdsen et al. (2018) documented that human presence could prevent extinctions if they saved $\geq 19\%$ of the eggs normally taken by predators (assuming predators took 29% of the eggs laid). Empirical studies on common eiders also documented this: human protection of breeding birds from predation leads to rapid population growth (Hanssen et al. 2013, Prop et al. 2015). This is relevant for our population, where human absence has increased nest predation.

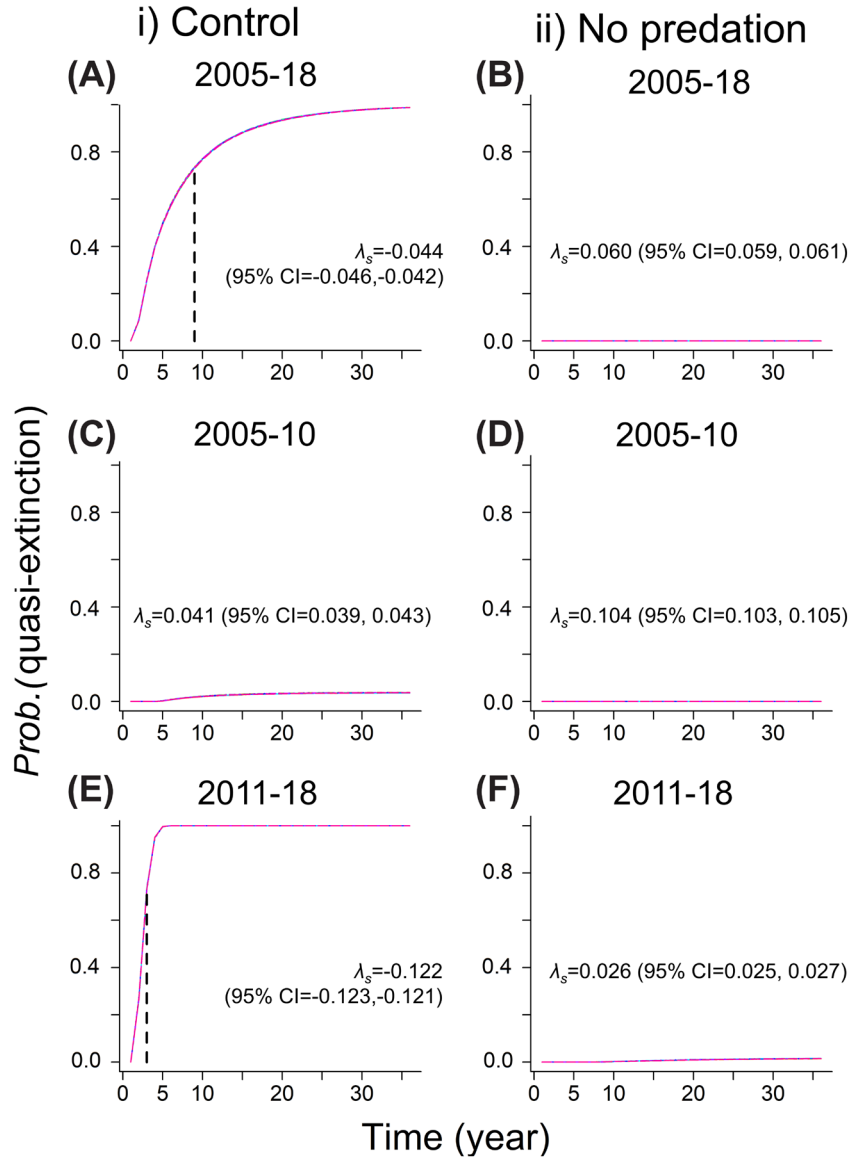


Figure 5. Probability of quasi-extinction (30% reductions from an initial size of 300 individuals over 36 years) for the whole time series (A and B), the early (C and D) and (E and F) late period. In the *Control* scenario (left panel), nest predation was at its natural level. In contrast, the *No predation* manipulation (right panel) used clutch size at laying as the basis for calculating the fecundities. Dotted lines indicate the time that gave an average probability of quasi-extinction closest to 0.75. Stochastic long-term population growth (using simulation; λ_s) and its associated 95% Confidence Intervals (CI) are also shown for each scenario.

Quasi-extinction

In the assessment of quasi-extinction, we are concerned with more transient and management-relevant dynamics instead of the long-term (asymptotic) behaviour discussed above (Ezard et al. 2010). Our assessment of the probability of quasi-extinction revealed that nest predation by corvids caused our study population to meet the VU category of the IUCN Red List (IUCN 2012; Supporting information). When we included predation, it was highly likely to meet the VU criteria after four and nine years using data from 2005–2018 and 2011–2018, respectively. Nonetheless, the extinction risk was practically zero in the earliest years and the absence of nest predation. The negative effect of nest predation on the fecundities was low in the earliest years before the ravens were breeding. Nonetheless, population declines for the lesser black-backed gull are not just a local phenomenon as the number of breeding pairs in the North Sea and Skagerrak decreased from > 50 000 breeding pairs in 1984 to < 25 000 in 2013 (Fauchald et al. 2015:26). As deduced by long-term behaviour based on annual matrices, it was also clear that nest predation harmed population viability: 20% and 67% of the years resulted in growth in the presence and absence of predation, respectively. The most significant difference in these constant growth rates coincided with the estimated predation rates in the latest period. We explain this as long-term growth happened irrespectively of whether nest predation occurred or not using data from the literature, but only in the absence of predation in our study area. In sum, when faced with nest predation by ravens, the status of the nominate subspecies of the lesser black-backed gulls (*L. f. fuscus*) is of greater conservation concern than indicated by the LC status that *L. fuscus* currently holds (BirdLife International 2019).

Prospective and retrospective analyses

The impact of fecundity, induced by predation, was always the most important factor affecting population growth in the fixed LTRE than the hypothetical effect of adult survival as revealed in the sensitivity and elasticity analyses (Supporting information S4). The retrospective analyses revealed a significant difference in population growth comparing our study population to the literature-based average vital rates, but only when we based our matrices on the situation when nest predation was present.

Conclusions and prospects

Even though nest predation should act in concert with multiple other natural and anthropogenic stressors, it was singled out as the most critical stressor as it caused extinctions at a rapid pace. For instance, when we parameterised our models with data from a period when one breeding pair of ravens, the status of the simulated populations went from being viable to facing serious

extinction risk. We thus support earlier studies where egg and chick predation has been put forward as an explanation for decreasing population trends (Davis et al. 2018a) and to be forceful enough to affect the geographical distribution (Spaans 1998), including urbanisation (Spelt et al. 2019), of the lesser black-backed gull. Previous studies have also shown that management actions, such as human presence and the protection of breeding birds, may have positive effects (Spaans 1998, Hanssen et al. 2013, Bårdsen et al. 2018, Davis et al. 2018a). In line with this, Hentati-Sundberg et al. (2021) report that the absence of tourists due to Covid-19 increased the presence of predators. It is essential to follow the Horsvær population in the future to cover more generations than we do in the present study. This will enhance our understanding of the *L. f. fuscus*'s long-term dynamics, including its conservation status. Yet another issue to further pursue in the future is to test the relative importance of nest predation, climate (Bårdsen et al. 2018) and food availability (e.g. due to reduction of fish discards Votier et al. 2004) – potentially important stressors for seabirds in general (review: Fauchald et al. 2015). Following the multi-stress hypothesis (Bustnes et al. 2015, Bårdsen et al. 2018, Kvie et al. 2019), interactions are expected (also see a recent review of threats to seabirds: Dias et al. 2019) and call for the combined use of experiments and continuous development of process-oriented models (Supporting information S6).

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Author contributions

Bård-Jørgen Bårdsen: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (supporting); Methodology (lead); Software (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jan Ove Bustnes:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (supporting); Project administration (lead); Software (supporting); Validation (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.d7wm37q19>> (Bårdsen and Bustnes 2022).

Supporting information

The supporting information associated with this article is available with the online version.

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