

Reproductive success of threatened northern Lesser Black-backed Gulls (*Larus fuscus fuscus*) in relation to nest predation by Ravens (*Corvus corax*)

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Many seabird populations suffer heavily from the destruction of nests by generalist predators. In this study, we analyzed 16 years of data (2005–2020) on the reproductive output of the northern Lesser Black-backed Gull (*Larus fuscus fuscus*) at Horsvær, the largest assemblage of this subspecies in Norway (up to ~400 pairs), in relation to the occurrence of breeding Ravens (*Corvus corax*). A pair of Ravens were firstly discovered at Horsvær in 2010, and between 2011 and 2016 they were observed with broods (2–5 fledglings) in most years. Between 2017 and 2020, human intervention prevented the Ravens from breeding in the colony. However, in 2020 a pair of Ravens brought their fledglings over from a neighboring island in the middle of the incubation period for the gulls. On average, the nest predation rate was 43% when Ravens had fledglings within the study area. In contrast, only 10% of nests were depredated in years when Ravens did not reproduce successfully or were absent. Moreover, only 0.07 fledglings were on average produced per nest in years when Ravens bred successfully, compared to 0.71 fledglings per nest in years with no Raven reproduction. A high level of nest predation led to a decline in the number of nesting gulls, which was not observed in a neighboring Raven-free colony. Finally, in years with high Raven predation at Horsvær, production of fledglings was still high in yet another nearby Lesser Black-backed Gull colony. The Ravens were established at Horsvær in the absence of people in the spring, and the only option to save these threatened gulls may be to prevent the Ravens from nesting successfully in or near their colonies.



1. Introduction

Predation on nests has long been identified as a primary source of reproductive loss in various bird species (Ricklefs 1969, Martin 1993). It is, however, debated how important nest predation by generalist predators, such as corvids, is for the productivity and abundance of birds (Madden *et al.* 2015). However, there are several examples of Ravens (*Corvus corax*) having substantial negative impacts on the nesting success of seabirds (e.g. Maccarone 1992, Avery *et al.* 1995, Peery & Henry 2010, Carle *et al.* 2017, Ekanayake *et al.* 2015). Seabirds such as gulls may be fierce nest predators themselves, but some species are also vulnerable to nest predation (Massaro *et al.* 2001, Kazama 2007, Scopel & Diamond 2017, Mills *et al.* 2018), including the Lesser Black-backed Gull (*Larus fuscus*) (Calladine 1997, Bukacinski *et al.* 1998, Hario 1994, Hallgrímsson & Hersteinsson 2012).

A large proportion of the Lesser Black-backed Gull population in northern Norway consists of the nominate subspecies (*L. f. fuscus*) which is threatened over its whole distribution range, especially in Finland and Norway (Hario *et al.* 1998, Helberg *et al.* 2009, Juvaste *et al.* 2017). The Norwegian population has declined strongly since the early 1970s (Bustnes *et al.* 2010a), which has mostly been attributed to the crash in the Atlantic herring (*Clupea harengus*) stock in the late 1960s (Myrberget 1985, Røv 1986, Bevanger & Thingstad 1990, Strann & Vader 1992), although other species of fish may also be important in the gulls' diet (Bustnes *et al.* 2010b).

In 2005, a demographic study of the northern Lesser Black-backed Gull was started at Horsvær, a small archipelago in the southern part of Nordland County (Fig. 1), which was the largest assemblage of this subspecies in Norway (Bustnes *et al.* 2010a). Anecdotal evidence suggests high breeding numbers at Horsvær in the 1950s (S. Jørgensen, pers. comm.). The first nest counts in 2005 and 2006 recorded close to 400 nests, distributed over seven sub-colonies (Bustnes *et al.* 2020). Subsequent studies have shown that adult Lesser Black-backed Gulls frequently move between these sub-colonies, permanently or visiting, but rarely move to other colonies once established at Horsvær (Bustnes *et al.* 2020, J.O.

Bustnes *et al.* unpublished data).

The northern Lesser Black-backed Gull has been found to behave differently from other gull species regarding feeding ecology and migration (Strann & Vader 1992, Juvaste *et al.* 2017, Helberg *et al.* 2009, Bustnes *et al.* 2013). In this study, we noted that these gulls were less aggressive than the other gull species, such as Common Gull (*L. canus*), Herring Gull (*L. argentatus*) and Great Black-backed Gull (*L. marinus*). When we were present, the Lesser Black-backed Gulls mostly flew high and rarely feigned attacks at us, or they only sat in flocks in the tidal zone.

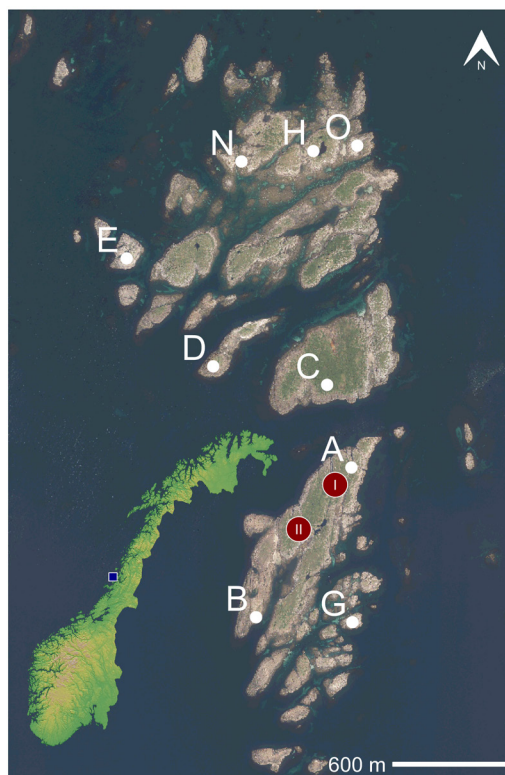


Fig. 1. Aerial photo of Horsvær, on the Norwegian Coast, showing the position of 9 different sub-colonies of Lesser Black-backed Gulls (A–O) occupied between 2005 and 2020. The A-, D-, and H-sub-colonies have been mostly abandoned after 2014, whereas N and O sub-colonies were largely established after 2014. In addition, the positions of two Raven nests are given in red (I = first nesting site; II = second nesting site). The aerial photo was generated through three projects (Nordland Sør 2014, 2010 and 2009) and was downloaded from <https://norgebilder.no/> (a collaboration between the Norwegian Mapping Authorities and Geovekst).

They also appeared to show low aggression toward potential nest predators, such as corvids and other gulls. This contrasts with another subspecies of Lesser Black-backed Gulls (*L. f. graellsii*), which may be very aggressive in encounters with herring gulls (Garthe *et al.* 1999).

The number of Lesser Black-backed Gulls attempting to nest varied dramatically among the years, as did their reproductive output. For example, in 2005 and 2006, more than 350 fledglings were produced, whereas in 2012 and 2013, less than 30 pairs nested, and no fledglings were produced (Bustnes *et al.* 2020). We firstly attributed this to variation in feeding conditions, but we also noted an increasing decoupling between the number of birds attempting to nest and the production of young over the years. Hence, eggs and chicks seemed to be lost at a higher rate.

People inhabited Horsvær for hundreds of years, and subsistence exploitation of natural resources, such as seabird eggs and Common Eider (*Somateria mollissima*) down, was important. People kept generalist predators such as corvids at bay. However, after the permanent settlements were abandoned in the 1970s, and people gradually ceased visiting the islands, Ravens could successfully establish (*i.e.* get through their vulnerable nesting phase). We firstly noted a pair of Ravens in 2010, and between 2011 and 2016, they reproduced successfully at or in close vicinity of Horsvær in most years. In 2017, we were permitted to remove the Ravens, and they were consequently prevented from breeding at Horsvær in the subsequent years.

This study aimed to analyze the relationship between the reproductive success of northern Lesser Black-backed Gulls and the occurrence of breeding Ravens. We applied a natural experimental design where we: 1) contrasted the depredation of nests and fledgling production in years with and without breeding Ravens; 2) contrasted the number of nests at Horsvær with Svindraget, a Raven-free neighboring colony located 8 km apart. This allowed us to estimate the temporal trends in the number of nests both at Horsvær and Svindraget, and the extent to which the temporal dynamics in the number of nests differs across these two areas. The contrasts between Svindraget and Horsvær has the potential to estimate the effect of Raven predation in the context of overall

environmental conditions; 3) contrasted Horsvær with the fledgling production in Fjordholmen, a Raven-free colony 46 km from Horsvær (data available for the years: 2015, 2017–2018 and 2020). A key point in our study design was that the distance between the colonies is far enough to prevent Ravens from making routine trips, but short enough for environmental conditions to be similar.

2. Material and methods

2.1. Study area

The study location was Horsvær (65°19'N, 11°37'E) an archipelago at Helgeland (Nordland County) in northern Norway. Totally, nine different sub-colonies (A–O) were included in this study (Fig. 1), two being on the same island (A and B) whereas all other sub-colonies were on different islands. There were seven sub-colonies when the study started in 2005 (A–H; Fig. 1), but all nests in the G-colony were depredated in 2008 and the sub-colony was subsequently abandoned (Bustnes *et al.* 2020). After 2014, the A, D and H sub-colonies have more or less vanished (usually 0–2 nests per years), and the N- and O-colonies were established (Fig. 1). In addition there were a varying number of gulls nesting outside of the established sub-colonies, which has been included in the total number of nests in Table 1. Four of the sub-colonies (B, E, G, H and N) were dominated by open-rocky habitats and had no vegetation taller than a few cm, and nearly all nests were openly exposed (> 90%). The other colonies (A, C, D and O) were dominated by dense vegetation (~50–80 cm tall) consisting of meadowsweet (*Filipendula ulmaria*): in the A- and D-colony more than 70% of the nests were in the vegetation, and more than 90% of the nests were located in the vegetation in the C-colony.

Since 2009, we have monitored the number of nests at Svindraget (65°15'10"N, 11°41'31"E), a Lesser Black-backed Gull colony on a flat open rocky island located ~7.8 km southeast of Horsvær, which is presently not inhabited by people. In addition, in the years 2015, 2017–2018 and 2020, we visited Fjordholmen (65°37'27"N, 12°18'13"E) in Vevelstad Municipality (~46

Table 1. Reproductive variables of Lesser Black-backed Gulls from Horsvær in relation to occurrence of breeding Ravens, and the number of nests at a nearby colony, Svindraget, where Ravens were absent.

Year	No. of nests	Nests depredated	Fledglings	Percent depredated	Fledglings nest ⁻¹	Breeding Ravens	Nests at Svindraget
2005	364	5	372	1.37	1.02	Absent	–
2006	385	1	349	0.3	0.91	Absent	–
2007	133	17	100	12.8	0.75	Absent	–
2008	291	28	130	9.6	0.45	Absent	–
2009	103	28	33	27.2	0.32	Absent	38
2010	324	25	312	7.7	0.96	Absent	69
2011	202	58	6	28.7	0.03	Present	40
2012	26	23	0	88.5	0	Present	6
2013	18	14	0	77.8	0	–	16
2014	183	24	16	13.1	0.09	Present	54
2015	145	55	31	37.9	0.21	Present	41
2016	99	50	0	50.5	0	Present	46
2017	114	23	55	20.2	0.48	Absent	33
2018	224	19	158	8.5	0.71	Absent	58
2019	166	12	142	7.2	0.86	Absent	54
2020	193	7	20	3.6	0.10	Present *	54

*Arrived after we left Horsvær

km northeast from Horsvær), after banding fledglings at Horsvær. The Lesser Black-backed Gull colony at Fjordholmen consists of three sub-colonies, within a limited vegetated area, with 100–150 pairs in total. Importantly, people still inhabit Fjordholmen in the gulls' breeding season.

2.2. Study protocol

In 2005, the fieldwork lasted from mid-June to late July. In the subsequent years, the fieldwork was divided in two field trips: 1) a period of 6–10 days in mid-June; and 2) 1–3 days in late July early August. This set-up was chosen to reduce the human disturbance of this threatened subspecies. During the first period, all colonies were searched, and all nests were recorded and marked with a numbered wooden stick, and eggs were marked with a waterproof pen. After 4–6 days (3–7 days), we revisited all the nests again, and new nests were recorded. Some nests were

depredated when found (*i.e.* destroyed eggs in or near the nest), and the rate of nest predation was assessed as the percentage of nests depredated (either when found or between nest checks) of the total number of nests. During both nest checks (searches), we recorded clutch sizes. Egg laying starts in early June, and is primarily finalized in the latter half of June when we were present. We are thus confident that our estimate of the number of nests in the colony is reasonably accurate. However, we sometimes found a few nests with eggs during our second visit, which we recorded. Each year during our second field trip, all islands were visited once and carefully searched for chicks (fledglings). The chicks were laid on the ground (in the grass or close to rocks) to calm them while still handling other chicks. Chicks that we were unable to catch, *e.g.* escaped to the sea, were counted. The exception was 2005, when banding of chicks was conducted over a two week period. This year we assumed that nearly all chicks were found and banded, and no counts of unmarked



Fig. 2. Photos showing the Raven nest on a scaffold on a building at Horsv er, and egg remains found under the Raven nest and a roosting site: Lesser Black-backed Gull, Common Eider and Greylag Goose.

chicks were conducted. Fledgling production was assessed as the number of juveniles banded, in addition to the number of unmarked juveniles counted, in relation to the number of nests. This also includes nests found when banding chicks since we assumed it was implausible that nests hatching later than 25th of July would successfully produce fledglings. In the middle of our first stay, we went to Svindraget and made a single nest count, covering the whole island. At Fjordholmen, due to vegetation and limited time in the colony, an exact number of fledglings is challenging to achieve, but acceptable estimates of production status can be achieved. Since 2017, the Horsv er archipelago has also been visited in April to record the presence of Ravens.

2.3. Occurrence and behaviour of Ravens

We recorded the first pair of Ravens in 2010. In 2011 and 2012 they were observed with two fledglings each year, but they may have had more fledglings. In 2014, a Raven nest was discovered on a scaffold on an abandoned building amidst the Horsv er archipelago (Fig. 1 and Fig. 2). In 2015, we removed the scaffold, and in 2016 the Ravens moved to another abandoned building 500 m further south of the same island (Fig. 1). Between 2014 and 2016, the Ravens produced five fledglings annually. In 2017 the Raven nest, including the eggs, was removed in April, and no relaying occurred. After 2017, no nest was found at Horsv er, although a non-breeding pair of Ravens was observed in 2018 and 2019. In 2020, however, a brood of Ravens (six birds in total)

was observed on a small neighboring island when we arrived 8th of June. On the 14th of June, when we left, the Ravens were observed to bring their brood of four fledglings from this neighboring island over to Horsv er. A license to kill the Ravens was granted by the S mna Municipality in 2017, but was never effectuated.

2.4. Statistical analyses

We performed all statistical analyses and plotting in R (R Core Team 2021). Our tests were two-tailed (rejecting the null hypothesis at an α -level of 0.05), and Wald statistics were used to test the hypothesis that the estimates were not significantly different from zero. We used the treatment contrast whenever predator pressure was included in a model: a two-level factor comparing years with the presence of Ravens (Present: treatment) to years when breeding Ravens was absent (Control) from the Horsv er Archipelago. Testing our biological hypotheses required several different statistical methods. The proportions of nests being predated (the number of nests predated divided by the number of nests; see Table 1) were analyzed using beta regressions, while linear models (LMs) and Linear Mixed Effects (LME) models were used on responses that either were normally distributed (clutch size; the number of eggs nest⁻¹) or when log_e-transformation made them fulfill the normality assumption [number of fledglings nest⁻¹, nest counts (see Table 1), and date (days since June 1st); see below for details].

2.4.1. Nest predation and reproductive success

We used beta regression (Cribari-Neto & Zeileis 2010) and the `betareg`-package (Zeileis *et al.* 2020) in the analyses of the proportion of nests being predated as a function of the predation pressure. In this analysis, we used a logit- and a log-link for the mean- and precision-model, respectively (Cribari-Neto & Zeileis 2010). There were two reasons why we chose this modelling approach over standard LMs: 1) the residuals plots revealed potential violations of the assumptions behind LMs (*e.g.* Zuur *et al.* 2010); 2) the response represent proportions (defined within an interval between zero and one). The average of the beta-distribution is estimated by the α - and β -parameters [$E(Y) = \mu = \alpha / (\alpha + \beta)$], whereas the variance is modelled by estimating the precision parameter [$\phi = \alpha + \beta$, where the variance is $VAR(Y) = \mu(1 - \mu)/(1 + \phi)$: Cribari-Neto & Zeileis 2010]. We fitted two different models: 1) one with the same structure for the precision and the mean and precision sub-model (both were a function of predation pressure); 2) another one where the precision sub-model only included the constant (*i.e.*, assumed similar across the two levels of predation pressure). We selected the candidate model with the lowest second-order Akaike's Information Criterion (AICc where Δ_i represents the difference in AICc value between model i and the model with the lowest AICc value: (*e.g.*, Burnham & Anderson 2002, Anderson 2008) value using the `AICcmodavg`-package (Mazerolle 2020). In the analyses of fledgling success, we fitted standard LMs, using the `lm`-function in R, but with a transformed response to fulfil the normality assumption: $\log_e(\text{fledglings nest}^{-1} + 0.1)$. Like in the analysis above, we used predation pressure as the only predictor.

2.4.2. Spatial synchrony

To assess the spatial synchrony in the number of nests at Horsvær (our control area; subject to Raven predation – at least some years) with the number of nests to a neighboring colony (Svindraget) where Ravens were absent, we used: 1) log-log models; 2) LMs assessing temporal dynamics (both fitted using the `lm`-function).

First, in the log-log model, both the number of nests at the Raven-free colony (Svindraget; response) and at our control area (predictor) were \log_e -transformed. We did this for two reasons. First, we realized that the diagnostics for the model without \log_e -transformation was poor (results not shown). Second and more importantly, the log-log models have the desired property that the slope for the predictor is approximately interpreted at a percentage increase in the response relative to one percent change of the predictor (Gelman & Hill 2007). Second, we ran two different linear models assessing the temporal dynamics of the number of nests – in analyses of the data from each colony separately: 1) a simple linear regression model where we predicted the number of nests based on year (setting the intercept to 2005; *i.e.*, 2005 = 0); 2) a second-order polynomial where we added year^2 to the first model. We did model selection similar to in the analyses of nest predation above.

2.4.3. Confounding effects

There were two crucial confounding factors related to our study design that we wanted to test for. First, it was important to assess if clutch size at laying was confounded by the presence of Ravens. For example, if clutch size was small in the years when Ravens were present for reasons other than predation that could seriously affect our results. In line with B.J. Bårdsen *et al.* (unpublished) who predicted clutch size at laying (June 1st; from a model where annual clutch size was predicted based on date and year of recording) and used it as a predator-free measure of reproduction, we used clutch size at our first visit as our closest empirical measure of laying clutch size. We fitted several LME models (Pinheiro & Bates 2000) – all with predator pressure as the only fixed effect, but with three different random effects (random intercepts only): 1) Year; 2) Colony and 3) Colony nested within Year. These models were fitted to nest-level annual data using the `lme`-function, in the `nlme`-package (Pinheiro *et al.* 2020), with a Restricted Maximum Likelihood (*i.e.*, setting the method-argument to “REML”) as the fixed effects were constant (Pinheiro & Bates 2000). We selected one model and used it for inference, adopting the same model selected

procedure as in the other analyses. Second, we measured predation by visiting the nests twice, it was important for us to assess if the number of days in-between the visits were confounded by the presence of breeding Ravens. We used LME models and the same set-up as in the analyses of clutch size above in this analysis.

3. Results

3.1. Nest predation and fledgling success

The number of Lesser Black-backed Gull nests found at Horsv ar varied from 18 (2013) to 385 (2006), on average 185.8 (SE = 27.5). Of these, between 0.26% (2006) and 88.5% (2012) were depredated (Table 1). In the subsequent analysis of predation pressure, we removed 2013 because of extremely poor feeding conditions and that we did not know the status of the Ravens in that year, as we did not observe them.

Defining 2020 as a year where Ravens were absent (as they moved into the study area the day we left and hence did not affect the number of nests observed), 43.1% (SE = 12.8, range = 13.1–88.5%) of the nests on average were depredated in the five years when Ravens reproduced. In comparison, the nest predation rate was only 9.6% (SE = 2.5, range = 0.26–26.2%) in the ten years when Ravens did not reproduce (Table 1). This 4-fold increase in the average nest predation rate in years with breeding Ravens present compared to control years (with only baseline predation levels; *i.e.* predators other than Ravens)

was statistically significant in the beta-regression model ($R^2 = 0.36$, Table 2, Fig. 3). The alternative model, including a similar structure for the precision model as the mean model, had poor support in our data (Table 2).

In the analysis of the production of fledglings, we included 2020 as a year with the presence of breeding Ravens. The estimated number of gull fledglings produced varied from 0 to 372, whereas the mean number of fledglings per nest varied from 0 to 1.02 (Table 1). In the six years when breeding Ravens were present, on average 0.07 (SE = 0.033, range = 0–0.23) fledglings were produced per nest, which was significantly lower than the average of 0.71 (SE = 0.083, range = 0.33–1.02) produced in the nine years when breeding Ravens were absent (Table 3a, Fig 3).

3.2. Raven behaviour and predation

Raven parents and their brood were observed to operate as a unit, attacking sub-colonies systematically and clearing large proportions of the nests within a few days. In 2011, 53% of 73 nests in the C-colony (Fig. 1) were lost before the second nest check, compared to only 10% of 50 nests in the H-colony. However, in 2011 only two fledglings were produced in the C- and none in the H-colony. Similarly, in 2015, 84% of 31 nests were depredated in the E-colony before the second nest check, compared to only 20% out of 15 nests in the N-colony. However, no fledglings were produced in N- and the E-colony in 2015. In 2016, all out of 21 nests were depredated in the C-colony before the

Table 2. Estimates from the beta-regression model relating the proportions of nests at Horsv ar (2005–2019) being depredated as a function of predation pressure using the logit- and log-link for the mean- and precision-model, respectively. We used the treatment contrast, estimating the difference between years when Ravens were present (treatment) and control-years when Ravens were absent (Intercept; see main text for details regarding how predation pressure was defined). R^2 is the pseudo- R^2 reported in the output from models fitted in *betareg*-package. The difference in AICc-values (Δ_i) between this an alternative models where the precision was modelled in the same manner as the average structure.

Parameter	Estimate	SE	z	P-value
Intercept	-1.883	0.329	-5.726	<0.001
Predation pressure (Ravens present)	1.591	0.466	3.411	0.001
Precision (Phi): intercept ($R^2 = 0.38$, $\Delta_i = 3.32$)	1.783	0.366	4.874	<0.001

second nest check whereas the E-, N-, O-colonies (13, 21 and 29 nests, respectively) lost ~38% of the nests, each. However, no fledglings were produced

at Horsv ar in 2016. Hence, the Ravens continued to clear the remaining nests in these years after we left the area in the second half of June.

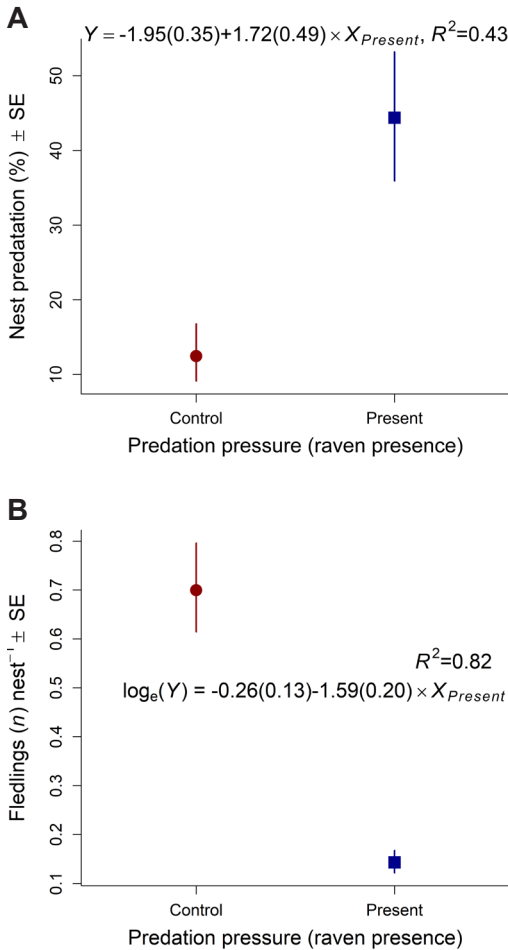


Fig. 3. (A) Predicted proportions (re-calculated into percentages) of nest predated as a function of Predation pressure (Control: years where breeding Ravens were absent; Present: years where breeding Ravens were present at the archipelago; Table 1) in the beta-regression model reported in Table 2. (B) Similarly, predicted fledglings nest⁻¹, back-transformed from log_e(fledglings nest⁻¹+0.1) to normal-scale, as a function of predation pressure in a linear model (*i.e.*, a one-way Analysis of Variance; see Table 3 for details). In both figures, text shows the coefficient of determination (R^2 ; please note that this was estimated differently across the models) and the estimated parameters (including their precision in parentheses): the difference between when Ravens were present ($X_{Present}$) and the control situation when Ravens were absent (Intercept).

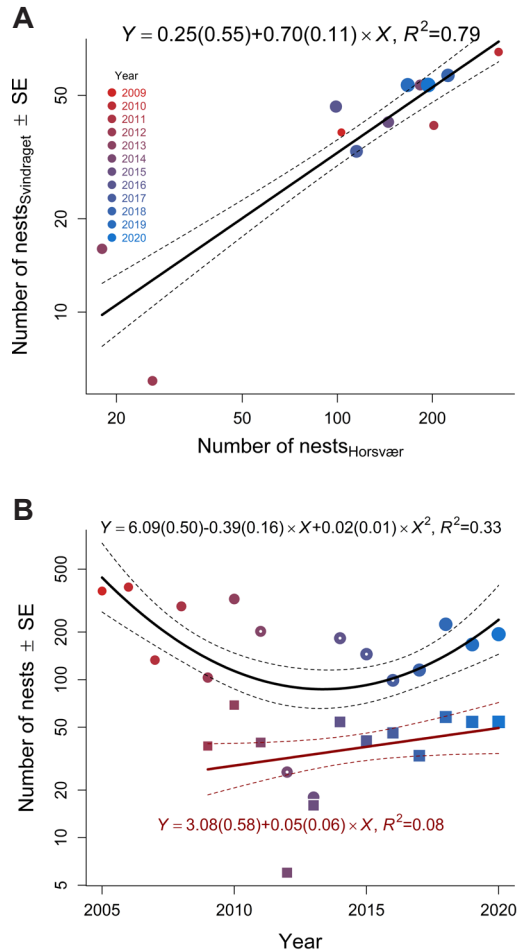


Fig. 4. (A) The relationship between number of Lesser Black-backed Gull nests at Horsv ar and Svindraget (both axis at log_e-scale), where the distance from Horsv ar's center colony (C-colony, Fig. 1) and Svindraget is 7.8 km, in the period between 2009 and 2020 (see Table 1 for the underlying data). (B) The temporal dynamics for the same response in each area (Horsv ar and Svindraget in circles and squares, respectively). Svindraget showed no evidence of any temporal dynamics whereas Horsv ar showed evidence of a curved relationship – being at its lowest in the 2012 (*i.e.* after Ravens started to breed in the area; see Table 3b–d for the underlying statistical analyses). Color figure is available in the online version of this article.

Table 3. Estimates from linear models relating: (a) $\log_e(\text{number of fledglings nest}^{-1} + 0.10)$ to Predation pressure (Table 2 provided details regarding the predictor variable and how to interpret its effect; Table 1 provides the underlying data); (b) the temporal dynamics of the number of nests at Horsv  r (where Ravens were present some years); (c) the temporal dynamics of the number of nests at Svindraget (where Ravens have not been observed) and (d) Horsv  r (where breeding ravens have been observed some years). R^2 is the coefficient of determination, and the difference in AICc-values (Δ_i ; b–c) represents the difference between the selected model presented here and the alternative model (see main text for details).

Parameter	Estimate	SE	<i>t</i>	P-value
(a) Fledglings nest⁻¹ + 0.10 (log_e-scale)				
Intercept	-2.031	0.089	-22.950	<0.001
Predation pressure (ravens present)	2.406	0.158	15.280	<0.001
$(F_{1,14} = 233.30, p > 0.01, R^2 = 0.94)$				
(b) Number of nests, Svindraget (log_e-scale)				
Intercept	0.413	0.583	0.708	0.495
log _e (Number of nests, Horsv��r)	0.664	0.120	5.552	<0.001
$(F_{1,10} = 30.82, p > 0.01, R^2 = 0.76)$				
(c) Number of nests, Svindraget (log_e-scale)				
Intercept	3.079	0.578	5.325	0.000
Year	0.055	0.057	0.958	0.360
$(F_{1,10} = 0.92, p = 0.36, R^2 = 0.08, \Delta_i = 3.19)$				
(d) Number of nests, Horsv��r (log_e-scale)				
Intercept	6.107	0.522	11.704	<0.001
Year	-0.376	0.161	-2.332	0.036
Year ²	0.022	0.010	2.136	0.052
$(F_{2,13} = 2.81, p = 0.10, R^2 = 0.30, \Delta_i = 1.76)$				

3.3 Spatial synchrony: the number of nests and fledglings in two nearby areas

The log-log model (2009–2020) revealed a high degree of spatial synchrony in the number of nests at Horsv  r and Svindraget ($R^2 = 0.79, F_{1,10} = 37.84, p < 0.01$, Table 3b, Fig. 4), suggesting that large-scale feeding conditions were an important determinant of the number of gulls nesting. This implies that a 1% change in the number of nests at Horsv  r resulted in a ~0.70% change in the number of nests at Svindraget, but as the upper 95% Confidence Interval (0.45–0.96) for this estimate was close to one, a near 1:1 relationship at the percentage-scale cannot be ruled out (Fig. 4). The untransformed values also show a high degree of linearity in the relationship between

these two areas (Pearson’s product-moment correlation = 0.90, $df = 10, p < 0.01$). There was no evidence of any temporal trends in the number of nests at Svindraget ($R^2 = 0.08, F_{1,10} = 0.92, p = 0.36$, Table 3c), whereas the number of nests at Horsv  r, where reproducing Ravens were present in some years, showed a curved temporal relationship as both the linear and the second-order polynomial estimates were statistically significant ($R^2 = 0.33, F_{2,13} = 3.19, p = 0.08$, Table 3d, Fig. 4). Thus, we selected two different models in each analysis: a simple linear model in analyses of data from Svindraget ($\Delta_i = 3.19$), and the second-order polynomial model using the data from Horsv  r ($\Delta_i = 1.91$).

We visited Fjordholmen in two years with the presence (2015 and 2020) and absence of (2017

Table 4. Estimates from linear mixed effect models relating: (a) clutch size and (b) \log_e (number of days in-between visits) to Predation pressure (a two-level factor variable consisting of a Control, or baseline, in which Ravens were absent compared to when Ravens were present; Table 1 provides the underlying data). The difference in AICc-values (Δ_c) between the selected models, which constates of a random effect including both Colony and Year, and the two other candidate models were as follows (for the analyses of Clutch size and days between visits, respectively): 1) 41.451 and 667.659 (Year); and 2) 173.431 and 2482.737 (Colony).

Parameter	Estimate	SE	df	<i>t</i>	P-value
(a) Clutch size					
Fixed effects					
Intercept	2.351	0.079	2237	29.935	<0.001
Predation pressure (Ravens present)	0.089	0.140	13	0.638	0.534
Random effects					
Among-Year SD (intercept)	0.225	(95% CI = 0.140, 0.364)			
Among-Colony (in Year) SD (intercept)	0.201	(95% CI = 0.148, 0.274)			
Within-group SE (residuals)	0.678	(95% CI = 0.659, 0.699)			
(b) \log_e (Days in between visits)					
Fixed effects					
Intercept	1.535	0.082	2213	18.668	<0.001
Predation pressure (Ravens present)	-0.258	0.143	13	-1.800	0.095
Random effects					
Among-Year SD (intercept)	0.250	(95% CI = 0.166, 0.376)			
Among-Colony (in Year) SD (intercept)	0.171	(95% CI = 0.166, 0.378)			
Within-group SE (residuals)	0.201	(95% CI = 0.195, 0.207)			

and 2018) reproducing Ravens at Horsvær. In all four years, the production of the Lesser Black-backed Gull was high at Fjordholmen: *i.e.*, in both 2015 and 2018, minimum estimates for production was more than 110 fledglings (14 and 58 fledglings banded in the two years, respectively). In both 2017 and 2020, the production of fledglings was high, but we could not get a reasonable estimate of the number. Hence, it seemed clear that Fjordholmen had a stable and high production of gull fledglings independent of the presence or absence of breeding Raven at Horsvær.

3.4. Confounding effects

Neither clutch size nor the number of days in-between visits was related to predation pressure and hence do not confound our conclusions regarding the effect of breeding raven presence

on the gulls (Table 4). Calculating the averages based on the models, the average time in-between visits was 4.63 and 4.00 days and 2.34 and 2.44 eggs nest⁻¹ when Ravens were absent and present, respectively.

4. Discussion

This study shows that a single pair of Ravens breeding in, or near a colony of northern Lesser Black-backed Gulls may have devastating impacts on the reproductive output, which has also been documented in other seabirds (Carle *et al.* 2017). Hence, the great need for nutrients for the Ravens' fledglings (up to five) in turn causes a significant reduction in the gulls' reproductive output, and possibly for other species, since we found eggs of species such as Common Eiders and Greylag Goose (*Anser anser*) under the Raven nests and

roosting sites, in addition to eggs of Lesser Black-backed Gulls (Fig. 2).

The relatively dense nesting colonies and low aggression of the gulls, combined with a cooperative hunting tactic, made Ravens able to rapidly clear the sub-colonies. Hence, if unmanaged, a single pair of Ravens could effectively curtail gull reproduction over many years. Moreover, gulls may abandon their colonies completely if all their nests are destroyed synchronously (Coulson & Coulson 2009), which happened to the G-colony (Fig. 1) in 2008. Although the culprit was not identified, we suspect that it was Ravens with a brood coming over from another island (Bustnes *et al.* 2020). Furthermore, the abandonment of the three other sub-colonies (A, D and H, Fig. 1) happened after the Ravens had ravaged most of the reproduction for several years. It is also noteworthy that a large proportion of the colonies of northern Lesser Black-backed Gulls in the region of southern Nordland disappeared between 1980 and 2007 (Bustnes & Helberg 2010c). This happened, although there is little evidence of generally poor feeding conditions in this period (Bustnes *et al.* 2010a).

People have inhabited the Norwegian Coast for millennia and influenced the wildlife populations, but in the post-war era depopulation gained traction, accelerating over the last 60 years. In northern Norway, subsistence exploitation of seabirds, such as gulls, alcids and eiders was important, and to maximize production, people persecuted predators such as corvids and eagles. For White-tailed Eagles (*Haliaeetus albicilla*), conservation efforts have led to population growth, which has caused increased predation on nesting seabirds, also in Norway (Hipfner *et al.* 2012, Hentati-Sundberg *et al.* 2020). Populations of many corvids have increased worldwide in response to human changes to the environment (Marzluff *et al.* 2006), but the population development of Ravens in Norway is poorly known. However, less persecution of Ravens has probably led to birds becoming bolder and increased their numbers in seabird colonies. Hence, when people were leaving their coastal settlements, the Ravens had better prospects of success, as seen at Horsv ar where Ravens only established after people ceased coming regularly there in spring.

The number of Lesser Black-backed Gulls attempting to nest varied dramatically between

years, which seems mainly to be a result of variation in the feeding conditions. This is supported by the high correlation between the number of nests at Horsv ar and Svindraget. For example, in the poor breeding seasons of 2009 and 2013, we noted that the gulls were feeding heavily on Blue Mussels (*Mytilus edulis*), an indication of low fish availability and thus poor feeding condition. Hence, high predation on nests could also be a multiple stressor effect: *i.e.*, if predation increased due to poor feeding conditions, the low prospect of success may have made birds less motivated for defending their eggs, and thus increasing the likelihood that predators gain access to the nests. However, in some years with Ravens (2011, 2014 and 2020), the number of nesting attempts were high, and it is noteworthy that the birds seemed to be highly motivated in 2020. In all years since 2010, it was difficult to catch birds with nest cages, but in 2020 they went straight into the cages, as soon as we withdrew from the sites. However, despite high reproductive investment, the gulls appeared to be unable to avoid nest predation by the Ravens that arrived in the middle of their incubation period. Moreover, our observations from Fjordholmen clearly shows that a Raven-free colony may have a stable and high reproductive output independent of Raven activities at Horsv ar. There might be several differences between Fjordholmen and Horsv ar, such as breeding habitats. However, there is little evidence that this factor is essential for production in these Lesser Black-backed Gulls (Bustnes *et al.* 2020). The most important difference is probably that people still inhabit Fjordholmen.

Open nesting seabird species, such as gulls, terns and guillemots, seem to be more vulnerable to nest predation by generalist predators than species with concealed nesting (McMahon *et al.* 2020, Hentati-Sundberg *et al.* 2020). However, at Horsv ar, both Herring Gulls and Great Black-backed Gulls seemed far less vulnerable to Ravens than Lesser Black-backed Gulls, and we did not observe Ravens in or near the nests of these aggressive gulls. The Common Gull is also a potentially aggressive species, and in 2016 when no Lesser Black-backed Gull chicks were produced, we still found surviving Common Gull fledglings. However, the number of Common Gulls pairs have also declined at Horsv ar over

the last ten years (J.O. Bustnes & M. Helberg, unpublished data), so heavy predation on this species cannot be excluded. A central question is whether these gull species and other potential nest predators, such as White-tailed Eagles, Hooded Crows (*Corvus corone cornix*), Arctic Skuas (*Stercorarius parasiticus*), American Mink (*Mustela vison*) and Common Otters (*Lutra lutra*), could be responsible for some of the heavy predation on the Lesser Black-backed Gulls. All these species are present, except American Mink, and likely to prey on nests of the Lesser Black-backed Gulls. However, they have been there during the whole study period, and the heavy predation only occurred when Ravens were producing fledglings.

This study suggests that an intermediate-sized, colonial nesting gull such as the non-aggressive northern Lesser Black-backed Gull does not have a working defensive strategy when Ravens establish close to their colonies, even when they appear to be highly motivated for breeding. Thus, even the largest Norwegian colony of this subspecies seems to have a gloomy future if no protective measures are taken. As such, our analyses do suggest declining numbers of nesting gulls since the study started, a trend different from the nearby Svindraget. Human beings are an intrinsic part of most ecosystems (Mace 2014), and the Norwegian Coast has been inhabited for thousands of years. People have influenced the ecosystem by their exploitation of seabirds and their control of predators. This has probably laid the groundwork for large populations of some species, including Lesser Black-backed Gulls in some areas. We believe that the only way to protect these northern Lesser Black-backed Gulls is by preventing Ravens from reproducing in or close to their colonies. We propose that people either locate the Raven nests and impairing their reproduction or visit the gull colonies before and at the onset of egg-laying of the Ravens.

Förökningsframgång hos den hotade silltruten (*Larus fuscus fuscus*) i förhållande till bopredation av korpar (*Corvus corax*)

Många sjöfågelpopulationer lider kraftigt av bopredation. I denna studie analyserade vi 16 års data (2005–2020) om silltrutens (*Larus fuscus*

fuscus) häckningsframgång vid Horsvær, den största samlingen av denna underart i Norge (upp emot 400 par), i förhållande till förekomsten av häckande korpar (*Corvus corax*). Ett korppar återfanns för första gången på Horsvær 2010 och mellan 2011 och 2016 producerade de kullar med 2–5 flygga ungar under de flesta åren. Mellan 2017 och 2020 gjordes ingrepp som hindrade korparna från att häcka i kolonin. Under 2020 hämtade ett korppar sina flygga ungar till Horsvær från en närliggande ö, mitt under ruvningsperioden för trutarna. Bopredationsraten var 43% när korparna hade sina flygga ungar i området. Till skillnad från detta skedde bopredation endast i 10% av trutboen när korparna inte häckade eller var borta. Dessutom producerades i medeltal endast 0.07 flygga trutungar per bo när korparna hade ungar, medan det producerades i medeltal 0.71 ungar per bo när korparna inte häckade. En hög nivå av bopredation ledde till en minskning i antalet häckande trutar, medan en minskning inte observerades i en närliggande korpfri koloni. Slutligen, under år med hög korppredation på Horsvær var häckningsframgången fortfarande hög i en närliggande koloni. Korparna etablerade sig på Horsvær när inga människor befann sig på ön, och det enda alternativet att skydda dessa hotade trutar är genom att förhindra att korpar kan häcka nära eller i trutkolonierna.

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References

- Anderson, D.R. 2008: Model based inference in the life sciences: a primer on evidence. Springer Science, New York, United States of America.
- Avery, M.L., Pavelka, M.A., Bergman, D.L., Decker, D.G., Knittle, C.E. & Linz, G.M. 1995: Aversive conditioning to reduce Raven predation on California least tern eggs. — Colonial Waterbirds 18: 131–138.
- Bevanger, K. & Thingstad, P-G. 1990: Decrease in some Central Norwegian populations of the northern

- subspecies of the Lesser Black-backed Gull (*Larus fuscus fuscus*) and its possible causes. — Fauna Norvegica Ser C, Cinclus 13: 19–32.
- Burnham, K. P., & Anderson, D. R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, Inc., New York, USA.
- Bukacinski, D., Bukacinska, M. & Spaans, A.L. 1998: Experimental evidence for the relationship between food supply, parental effort and chick survival in the Lesser Black-backed Gull. *Larus fuscus*. — Ibis 140: 422–430.
- Bustnes, J.O., Anker-Nilssen, T. & Lorentsen, S-H. 2010a: Local and large-scale climatic variables as predictors of the breeding numbers of endangered Lesser Black-backed Gulls on the Norwegian Coast. — Journal of Ornithology 151: 19–26.
- Bustnes, J.O., Barrett, R.T. & Helberg, M. 2010b: Northern Lesser Black-backed Gulls; what do they eat? — Waterbirds 33: 534–540.
- Bustnes, J.O. & Helberg, M. 2010c: What happened to the Lesser Black-backed Gulls in northern Norway. — Ottar 5: 36–42 (in Norwegian).
- Bustnes, J.O., Moe, B., Helberg, M. & Phillips, R. 2013: Rapid long-distance migration in Norwegian Lesser Black-backed Gulls *Larus fuscus fuscus* along their eastern flyway. — Ibis 155: 402–406.
- Bustnes, J.O., Bårdsen, B.J. & Helberg M. 2020: To hide or not to hide: nesting habitat dynamics in a threatened gull. — Waterbirds 43: 163–173.
- Calladine, J. 1997: A comparison of Herring Gull *Larus argentatus* and Lesser Black-backed Gull *Larus fuscus* nest sites: their characteristics and relationships with breeding success. — Bird Study 44: 318–326.
- Carle, R.D., Calleri, D.M., Beck, J.N., Halbert, P. & Hester, M.M. 2017: Egg depredation by common Ravens *Corvus corax* negatively affects pelagic cormorant *Phalacrocorax pelagicus* reproduction in central California. — Marine Ornithology 45: 149–157.
- Coulson, J.C. & Coulson, B.A. 2009: Ecology and colonial structure of large gulls in an urban colony investigations and management at Dumfries, SW Scotland. — Waterbirds 32: 1–15.
- Cribari-Neto, F., & Zeileis, A. 2010: Beta Regression in R. Journal of Statistical Software 34:1–24. <https://www.jstatsoft.org/v034/i02>.
- Ekanayake, K.B., Sutherland, D.R., Dann, P. & Weston, M.A. 2015: Out of sight but not out of mind: corvids prey extensively on eggs of burrow-nesting penguins. — Wildlife Research 42: 509–517.
- Garthe, S., Freyer, T., Huppopp, O. & Wolke, D. 1999: Breeding Lesser Black-backed Gull *Larus graellsii* and Herring Gulls *Larus argentatus*: Coexistence or competition? — Ardea 87: 227–236.
- Gelman, A. & Hill, J. 2007: Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, United Kingdom.
- Hallgrímsson, G.T. & Hersteinsson, P. 2012: Spatial contraction in a large gull colony in relation to the position of arctic fox dens. — European Journal of Wildlife Research 58: 441–450.
- Hario, M. 1994: Reproductive-performance of the nominate Lesser Black-backed Gulls under the pressure of herring gull predation. — Ornis Fennica 71: 1–10.
- Hario, M., Bianki, V. & Zimin, V. 1998: *Larus fuscus fuscus*. — In: Kotiranta, H., Uotila, P., Sulkava, S. & Peltonen S.-L. (eds.). Red Data Book of East Fennoscandia. Ministry of Environment, Finnish Environment Institute and Botanical Museum, Finnish Museum of Natural History, Helsinki, pp. 247–249.
- Helberg, M., Systad, G. H., Birkeland, I., Lorentzen, N. H. & Bustnes, J. O. 2009: Migration patterns of adult and juvenile lesser black-backed gulls breeding in northern Norway. Ardea 97: 281–286.
- Hentati-Sundberg, J., Berglund, P-A., Hejdström, A. & Olsson O. 2020: COVID-19 lockdown reveals tourists as seabird guardians. — Biological Conservation 254: 108950.
- Hipfner, M.J., Blight, L.K., Lowe, R.W., Wilhelm, S.J., Robertson, G.J., Barrett, R.T., Anker-Nilssen, T. & Good, P. 2012: Unintended consequences: how recovery of sea eagles *Haliaeetus* spp. Populations in the northern hemisphere is affecting seabirds. — Marine Ornithology 40: 39–52.
- Juvaste, R., Arriero, E., Gagliardo, A., Holland, R., Huttunen, M.J., Mueller, I., Thorup, K., Wikelski, M., Hannila, J., Penttinen, M.L. & Wistbacka, R. 2017: Satellite tracking of red-listed nominate Lesser Black-backed Gulls (*Larus f. fuscus*): Habitat specialization in foraging movements raises novel conservation needs. — Global Ecology and Conservation 10: 220–230.
- Kazama, K. 2007: Factors affecting egg predation in Black-tailed Gulls. — Ecological Research 22: 613–618.
- Maccarone, A.D. 1992: Predation by common Ravens on cliff-nesting black-legged kittiwakes on Baccalieu Island, Newfoundland. — Colonial Waterbirds 15: 253–256.
- Mace, G.M. 2014: Whose conservation? — Science 345: 1558–1560
- Madden, C.F., Arroyo, B. & Amar, A. 2015: A review of the impact of corvids on bird productivity and abundance. — Ibis 157: 1–16.
- Martin, T.E. 1993: Nest predation and nest sites. — BioScience 43: 523–532.
- Marzluff, J.M. & Natherlin, E. 2006: Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. — Biological Conservation 130: 301–314.
- Mazerolle, M. J. 2020: AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3–1.
- Massaro, M., Chardine, J.W. & Jones, I.L. 2001: Relationships between Black-legged Kittiwake nest site characteristics and susceptibility to predation by large

- gulls. — *Condor* 103: 793–801.
- McMahon, B.J., Doyle, S., Gray, A., Kelly, S.B.A. & Redpath, S.M. 2020: European bird declines: do we need to rethink approaches to the management of abundant generalist predators? — *Journal of Applied Ecology* 57: 1885–1890.
- Mills, J.A., Yarrall, W., Bradford-Grieve, J.M., Morrissey, M. & Mills, D.A. 2018: Major changes in the red-billed gull (*Larus novaehollandiae scopulinus*) population at Kaikoura Peninsula, New Zealand; causes and consequences: a review. — *Notornis* 65: 14–26.
- Myrberget, S. 1985: Breeding of Lesser Black-backed Gulls at Tranøy in Senja [Hekking av sildemåke på Tranøya i Senja]. — *Fauna* 38: 140–145. (In Norwegian, with English summary).
- Peery, M.Z. & Henry, R.W. 2010: Recovering marbled murrelets via corvid management: A population viability analysis approach. — *Biological Conservation* 143: 2414–2424.
- Pinheiro, J. C. & Bates, D.M. 2000: Mixed effect models in S and S-PLUS. Springer, New York, USA.
- Pinheiro, J.C., Bates, D. M., DebRoy, S. & Deepayan, S., Team, R.C. 2020: nlme: linear and nonlinear mixed effects model. R package version 3.1–152.
- R Core Team. 2021: R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricklefs, R. E. 1969: An analysis of nesting mortality in birds. — *Smithsonian Contribution in Zoology* 9: 1–48.
- Røv, N. 1986: Bestandsforhold hos sildemåke *Larus fuscus* i Norge med hovedvekt på *L. f. fuscus*. — *Vår Fuglefauna* 9: 79–84. (In Norwegian with English summary)
- Scopel, L.C & Diamond A.W. 2017: The case of lethal control of gulls on seabird colonies. — *Journal of Wildlife Management* 81: 572–580.
- Strann, K-B. & Vader, W. 1992: The nominate Lesser Black-backed Gull *Larus fuscus fuscus*, a gull with a tern-like feeding biology, and its recent decrease in northern Norway. — *Ardea* 80: 133–142.
- Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A.B., & Rocha, A.V. 2020: betareg: Beta Regression. R package version 3.1–3.
- Zuur, A.F., Ieno, E.N. & C.S. Elphick. 2010: A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.