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Subscriptions – Tilaukset – Prenumerationer
BirdLife Suomi ry / BirdLife Finland
Annankatu 29 A 16, FI-00100 Helsinki, Finland
Phone: +358 9 413 533 00
Telefax: +358 9 413 533 22
E-mail: office@birdlife.fi
Sähköposti – E-post: toimisto@birdlife.fi

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

Jan Ove Bustnes*, Morten Helberg & Bård-Jørgen Bårdsen

*J. O. Bustnes, Norwegian Institute for Nature Research, High North Research Centre on Climate and the Environment (FRAM), NO-9296 Tromsø, Norway * Corresponding author's e-mail: Jan.Bustnes@nina.no*
M. Helberg, BirdLife Norway, Sandgata 30 B, 7012 Trondheim
B.J. Bårdsen, Norwegian Institute for Nature Research, High North Research Centre on Climate and the Environment (FRAM), NO-9296 Tromsø, Norway

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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, Hallgrimsson & 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.

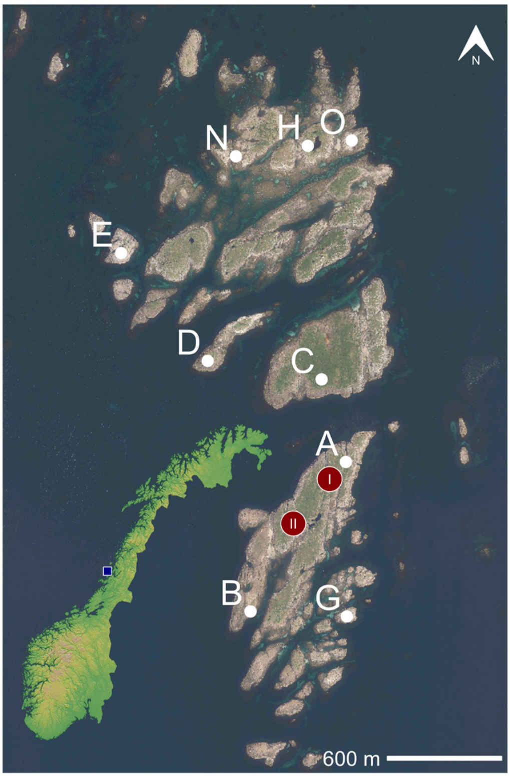

Fig.1. Aerial photo of Horsvær, on the Norwegian Coast, showing the position of 9 different sub-colonies of Lesser Black-backed Gulls (A–O) occupied between 2005 and 2020. The A-, D-, and H-sub-colonies have been mostly abandoned after 2014, whereas N and O sub-colonies were largely established after 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://norgeibilder.no/ (a collaboration between the Norwegain Mapping Aurthorties 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. graellsi*), 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 (65º19’N, 11º37’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 (65º15’10’’N, 11º41’31’’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 Horsvær, 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 Horsvær 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 Horsvær 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 Horsvær, 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 Horsvær. A license to kill the Ravens was granted by the Sømna 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 Horsvær 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: $\log_e$(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 Horsvær 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 Horsvær (2005–2019) being predated 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	1.783	0.366	4.874	<0.001
($R^2 = 0.38$, $\Delta_i = 3.32$)				

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 Horsvær 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.

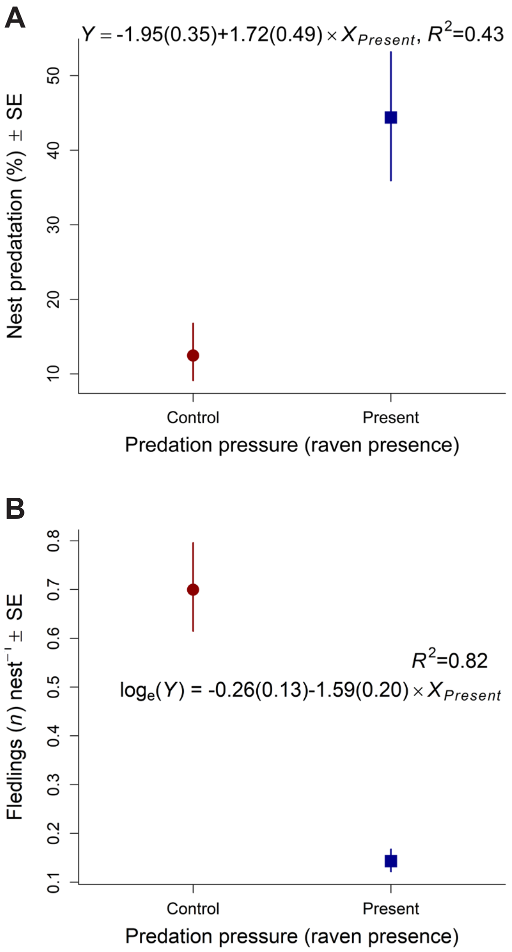

Fig. 3. (A) Predicted proportions (re-calculated into percentages) of nest predated as a function of Predation pressure (Control: years where breeding Ravens were absent; Present: years where breeding Ravens was present at the archipelago; Table 1) in the beta-regression model reported in Table 2. (B) 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 theirs precision in parentheses): the difference between when Ravens were present ($X_{present}$) and the control situation when Ravens were absent (Intercept).

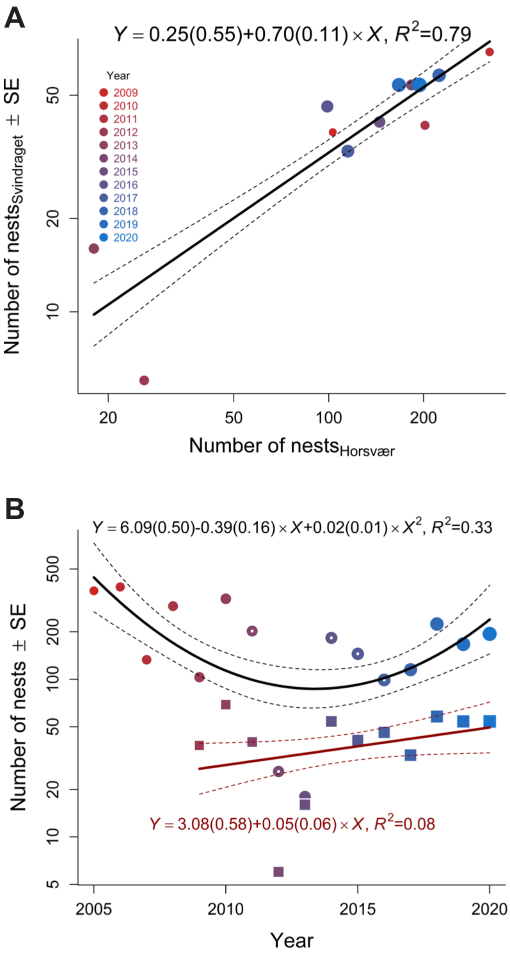

Fig. 4. (A) The relationship between number of Lesser Black-backed Gull nests at Horsvær and Svindraget (both axis at $\log_e$-scale), where the distance from Horsvær's center colony (C-colony, Fig. 1) and Svindraget is 7.8 km, in the period between 2009 and 2020 (see Table 1 for the underlying data). (B) The temporal dynamics for the same response in each area (Horsvær and Svindraget in circles and squares, respectively). Svindraget showed no evidence of any temporal dynamics whereas Horsvær 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) $\log_e$(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 Horsvær (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) Hosrvær (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	*t*	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, Horsvær)	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, Δ_i=3.19)				
(d) Number of nests, Horsvær ($\log_e$-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, Δ_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 Horsvær 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 Horsvær 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 Horsvær, 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 (Δ_i = 3.19), and the second-order polynomial model using the data from Horsvær (Δ_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_i) 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	*t*	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 Horsvær 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 Horsvær 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 Horsvær. There might be several differences between Fjordholmen and Horsvær, 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 Horsvær, 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 Horsvær 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 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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Individual variation in song of Black-throated Divers (*Gavia arctica*)

Pekka J. Lehtonen* & Jyrki Lappalainen

*P. Lehtonen, Toppelundintie 5 F 33, FI-02170 Espoo, Finland * Corresponding author's e-mail: pelehtonen@gmail.com*
J. Lappalainen, Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, P.O. Box 65, FI-00014 University of Helsinki, Finland

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The intention of the study was to determine whether male Black-throated Divers (*Gavia arctica*) can be distinguished individually by their vocalization. The songs of 19 male Black-throated Divers (BTDs) were recorded in their territories in the same lake area in 2018–2021 in Finland. The songs were recorded in one year in nine territories and in 2–4 consecutive years in ten territories. The song consists of one introductory phrase and one or more repeat phrases. Seventeen variables were measured from the spectrograms of the introductory phrase and the first repeat phrase. These variables included the frequencies and duration of different parts of the spectrogram. The discriminant analyses were used to examine the recognition of individual BTDs based on the spectral analysis of the male yodels (n = 297) in different territories (n = 19). The discriminant analysis showed that when using 14 of the variables of the yodels, the discriminant analysis classified the yodels to correct territories at a rate of almost 98% based on the cross-validation of all data. This suggests that the same individuals defend their territory from year to year.

1. Introduction

Vocal individuality is useful in situations where visual signals cannot be used, such as in rainforests, meadows with tall grass, or at night (Yee *et al.* 2016, Zsebők *et al.* 2017**,** Chang *et al.* 2018**,** Raymond *et al.* 2020). By recording birds, an assessment of abundance can be made without disturbing the natural behavior of the birds **(**Zsebők *et al.* 2017). Individual recognition of acoustic signals is useful for birds because it enables communication over a longer distance than visual observation (Raymond *et al.* 2020). Vocal discrimination can also be used, for example, for the purposes of a neighbor-stranger discrimination (Vogel 1995, Mager *et al*. 2010, Raymond *et al.* 2020).

Many recent articles have dealt with the individual identification of birds by vocalization. Zsebők *et al.* (2017) explored the individuality of the calls of male Common Cuckoos (*Cuculus canorus*). They conducted a discriminant function analysis on the acoustic variables to distinguish individuals and observed that individuals differ in both the frequency and time of their calls. Discrimination of the male calls of 26 individuals was almost 100% accurate. Budde (2010) analysed the vocal repertoire of the Grey Crowned Crane (*Balearica regulorum gibbericeps*) and showed that individuals and sex identification are possible in the unison call.

Gilbert *et al.* (1994) concluded that spectrograms of the yodel vocalizations of BTDs showed clear qualitative differences between individuals. However, the within-year stability of BTD yodels could not be systemically investigated because of the limited range of recordings. Four BTDs were recorded in the same location in 1991 and 1992 and the spectrograms were very similar. Another *Gavia*-species, Common Loon (*Gavia immer*), has been studied thoroughly and reported to be recognized for their dynamic vocal repertoire (Miller 1988, Vogel 1995, Walcott *et al*. 1999, Mager & Walcott 2007, 2014, Mager *et al*. 2007a, 2012). Walcott *et al.* (1999, 2006) have shown that the male yodel of Common Loon is quite consistent and stable from year to year.

Structural analyses of vocalization (*e.g.*, Barklow 1979, Vogel 1995, Walcott *et al.* 1999) have shown considerable variability among the yodels of territorial Common Loon males. Some elements within the yodel exhibit low intra-individual variability and high inter-individual variability, and territorial loons respond differently to yodels from territorial neighbours and non-neighbours (Vogel 1995, Mager *et al*. 2010). They also change their vocalizations when they change territories to distinguish themselves from the previous owner after taking over the territory (Walcott *et al.* 2006). This suggests that one of the functions of the yodel is to inform others about their identity.

Mager *et al.* (2007a, 2007b) found geographic variation in the body size and vocal behaviour of Common Loons across North America, and that the dominant frequencies of yodels are partly influenced by the body size of males. Mennill (2014) showed that Common Loons called when the abiotic conditions were ideal, *i.e.*, calm weather, no rain, or other distracting noises, for long-range signalling.

Black-throated Diver (BTD) (*Gavia arctica*) is a widely distributed species that breeds on freshwater lakes and ponds in Arctic and Subarctic regions across Eurasia, extending east to the westernmost Alaska (Russell 2020). Individual identification of BTDs is a crucial issue for prioritizing behavioural studies. It can be used to estimate whether the same individuals occupy the same territories from year to year when they return to their territories in spring. Individual identification can also be used to estimate the age of the bird by following them in their territories for long periods of time. Identifying birds individually makes it possible to examine the differences in their social behaviour for example in the company of other BTDs in flocks where social interactions are powerful and versatile. However, visual identification of BTDs during the breeding season is questionable because it can disturb nesting. Therefore, other methods are needed for identification. After the breeding season when visual identification is less disturbing, the summer plumage of BTDs can be used for individual identification (Lehtonen & Lappalainen 2017).

BTDs defend their breeding territories from both conspecific and interspecific intruders (Sjölander 1968, Lehtonen 1970, Eriksson *et al.* 2008). BTDs produce most yodels just after ice break when they have returned to the lake and occupy their territories. At that time, it is possible to hear hundreds of yodels in one day from a single location. In the following weeks, the number of yodels is steady. During breeding, male gives loud, rhythmic, *kuuik-kukuuik-kukuuik*… This territorial call (yodeling) is one of the most well-known features of this species and may under favourable conditions be heard at the distances of 4–6 km (Lehtonen 1970). If the breeding is successful, the BTDs continue regular yodeling till August. In late summer, BTDs are most active after sunset (Lehtonen 1970, Lehtonen & Perämäki 2019).

With a territory song (yodel), male BTDs express their ownership of a certain area and warn other conspecific partners to come to the scene (Lehtonen 1970, Lehtonen & Lappalainen 2017). It is also believed to be a long-range threat signal given during aggressive situations and territorial encounters (Sjölander & Ågren 1972). The song consists of one introductory phrase and one or more repeat phrases (Fig. 1).

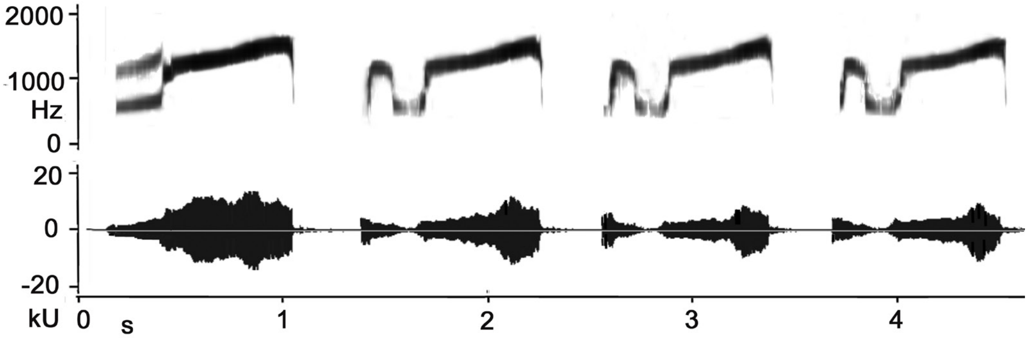

Fig 1. Sound spectrogram (above) showing the change in in frequency (in Hz), and waveform (below) showing the change in energy (kU, kilounits, dimensionless) of a typical yodel over time (in seconds). The yodel consists of an introductory phase of two notes that rise in frequency and repeat phrases of two syllables that follow the introductory phrase.

Lehtonen and Lappalainen (2017) found that individual identification of BTDs can be done based on the details of the breeding plumage. Following that study, one male BTD was photographed regularly over four summers, and based on the plumage, the same male occupied the same territory during the years 2018–2021. However, the use of plumage needs visual observations of the BTDs. In other *Gavia*-species, yodel has been suggested to be used as a tool for identifying different individuals (Walcott *et al.* 1999, 2006). Therefore, here the aim was to examine the territory-specific variation in male BTD yodel based on spectral analysis in order to understand between-individual variation in yodelling in this species. First, the yodel was divided into different, measurable parts and frequencies were measured at certain points of the yodel, and the variability of each of these measurements in each BTDs was compared with the variation of all BTDs (Mager & Walcott 2007). This procedure enables an estimation of the originality of the different parts and frequencies of the yodel and helps to identify which parts of the yodels vary the most. Secondly, these different measured variables of the yodels were analysed in discriminant analysis to estimate if these can be used to identify different BTD males in different territories.

2. Material and methods

2.1. Study site and yodel recording

This research was conducted on Lake Suontee (61˚39’N, 26˚31’E) in Finland. Lake Suontee covers an area of 150 km^2 and has 500 islands and islets, supporting about 120 BTD pairs (Virtanen *et al.* 2011, Lehtonen *et al.* 2013, Virtanen 2013, Lehtonen & Lappalainen 2017). The yodels were recorded on 19 territories between May and August in 2018–2021 (Fig. 2). The territories were located within an area of 21 km^2 and were usually 500–1000 meters apart from each other.

The yodels were recorded onto digital memory card using an Audio-Technica AT897 shotgun microphone connected to Zoom H4nPro or to

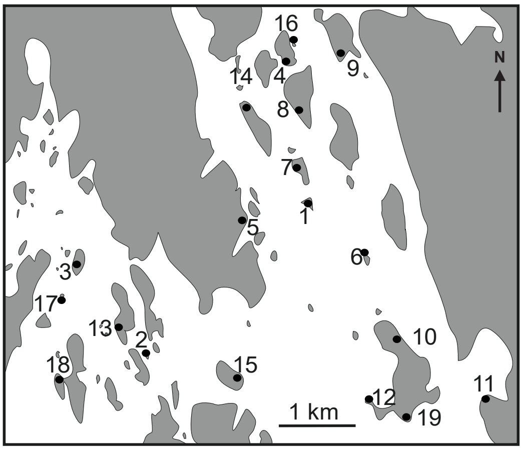

Fig. 2. The study area (Lake Suontee, 61˚39’N, 26˚31’E). The locations of different territories are marked with corresponding numbers, and the sites for recordings with black circles.

Zoom H5 hand recorder. The recordings were in 16 bits WAV format. To acquire an adequate sample of yodels from each individual while minimizing disturbance, the recordings were made leaving the recorder as discreetly as possible on the territory of BTDs overnight to perform continuous recording approximately from 7 pm to 7 am. The recording device was installed right next to the water so that the sound would not bounce off the beach terrain but comes directly from the lake to the microphone.

Total recording time was about 1000 hours and about 5000 yodels were recorded. Only recordings made close enough (less than 400 m distance) gave a high-quality spectrum from which all the variables used in the statistical analysis could be measured. High quality spectra were obtained from 297 yodels. Annually 5 to 15 yodels per territory were used for statistical analysis. Playback was not used.

Spectrograms were generated using the Cornell laboratory Raven Pro (version 1.6) bioacoustic analysis software. The frequency (the nearest Hz) and duration (the nearest milliseconds, ms) variables of the introductory phrase and the first repeat phrase of each yodel were measured (Table 1, Fig. 3).

2.2. Statistical analyses

Following previous work by Mager & Walcott (2007), the coefficient of variation (CV) was calculated from different yodel variables first within individuals (CV_i) and then between individuals (CV_b). The CV was calculated as:

$$CV = (s \times 100)/ Y \tag{1}$$

where s is the standard deviation and Y is the arithmetic mean of the data set. The ratio between individuals (CV_b) was compared with the average

Table 1. Definitions of measured and calculated variables of yodels recorded from Black-throated Divers. Duration is in ms, and frequency is in Hz

Variables	Definition
Measured	
DI	Duration of the introductory phrase
DI1	Duration of first note of introductory phrase
DI2	Duration of second note of introductory phrase
DGAP	Duration between introductory and first repeat phrase
DR1	Duration of first repeat phrase
DR11	Duration of first note of first repeat phrase
FI1	Frequency with highest intensity at end of second harmonic of first note of introductory phrase
FI2C	Centre frequency of second note of introductory phrase
FI2B	Frequency of beginning of second note of introductory phrase
FI2E	Highest frequency at the end of introductory phrase
FR11C	Centre frequency of first syllable of first repeat phrase
FR11	Highest frequency of first syllable of first repeat phrase
FR12B	Frequency of beginning of second note of repeat phrase
FR12E	Highest frequency at the end of second note of first repeat phrase
FR12C	Centre frequency of second note of first repeat phrase
Calculated	
FIBE	Difference in frequency during second note of introductory phrase (FI2E minus FI2B)
FR1BE	Difference in frequency during second note of first repeat phrase (FR12E minus FR12B)

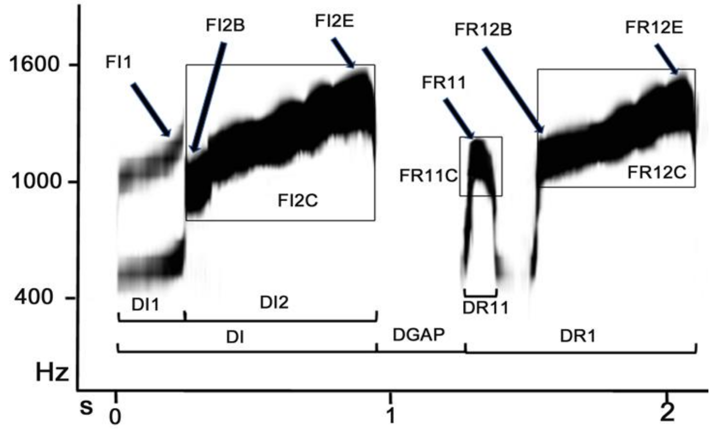

Fig. 3. Sound spectrogram of the introductory phrase and first repeat phrase showing the change in frequency of a typical yodel over time. In x-axis time is in seconds, and in y-axis is the frequency in Hz. Measured variables are explained in Table 1.

CV within individuals (CV_i) as:

$$\text{Ratio} = CV_b/CV_i \qquad (2)$$

to determine those acoustic variables that exhibit a low within-individual variability yet high between -individual variability. These, in turn, could help determine which variables could discriminate individuals.

The identification of male yodel in each territory was done with the discriminant analysis (SAS 2014). First, the best set of measured variables of the yodel were selected using stepwise selection with all the data in the discriminant analysis. The discriminant analysis using stepwise selection of variables removed three variables from the analysis, when all the 17 variables were included. The removed variables were DI2, FIBE and FR12B (see Table 1 for variable definitions). The correlation analysis showed that the variable DI2 was strongly correlated with DI ($r = 0.80$, n = 297), and FIBE with FI2E ($r = 0.96$, n = 297) and FR12B ($r = 0.86$, n = 297). If the stepwise analysis was started excluding the variables DI and F12E, the variable FR12B was still removed. The ASCC values suggested that these two discriminant analyses showed similar potential discriminatory power ($p < 0.0001$, ASCC = 0.424 in both analyses) (SAS 2014).

The best set of selected variables and all the data were then analysed with discriminant analysis using territory as a class. Here, the prior group size probability was used, and the misclassification estimate was based on cross-validation, *i.e.*, the leave-one-out option. The data were also divided into train and test data so that the train data included all territories, but the test data were selected among those territories that had more than one year of data. Because there were some territories that had only one year of yodels, those were put in the train data, and all territories that had data over several years, only the last year was placed in the test data (territories 1, 3–6, and 13–17) (Table 2). Here, both the options in the prior group size effects were compared (no prior group size vs. prior group size).

3. Results

3.1. Structure of the song

In a typical yodeling position, the male head was at a 40 degree angle (± 3 degrees, n = 9, Fig. 4).

Table 2. The number of analysed yodels in different territories during the studied years.

Study year	Territory number	Yodels
2018	1	8
2019	1, 2, 5–7, 17	54
2020	1, 3–6, 8, 13–18	104
2021	1, 3–6, 9–16, 19	131

Structurally, the yodel (*i.e.*, song) is composed of two distinguishing features: an introductory phrase of two notes that rise in frequency, and a series of 2-syllable repeat phrases that follow the introductory phrase (Fig. 1). There are most often 2–4 repeat phrases, but sometimes even 5–10. Depending on the number of repeat phrases the song lasts from two seconds to ten seconds. The duration from beginning of the introductory phrase to the end of the first repeat phrase varied from 1.63 seconds to 2.58 seconds (n = 297).

The duration and frequency of different measured variables in yodels varied considerably (Table 3). Some frequency variables, such as FI1, FI2B, FI2E, FR11, FR12B and FR12E (Table 1 and 3) showed very little within-individual variability (CV_i, Table 3). Some variables, such as DI, DR and FIE exhibited high between-individual variation (CV_b, Table 3). The CV_b/CV_i score of all variables was in the range 2.2–7.0 showing a large difference between CV_i and $CV_{b.}$

In most cases the song of different BTDs is much alike and the identification of the individual in question can be made only by spectral analysis. The easiest way is to look at frequency at the end of introductory phase (FI2E, Table 1, Fig. 3). This frequency is exceptionally stable (CV_i = 1.42) within and between years and gives a rapid information of the bird in question. Although the introductory and the repeat phrases have most often two notes, the frequency (in Hz) of the second note rises abruptly in yodelings of some individuals. If this happens, then the end frequency of the second note (FI2E and FR12E, Table 1) and the difference between the end and start frequency of the second note (FIBE and FR1BE, Table 1) are exceptionally high.

3.2. Discriminant analyses

The stepwise discriminant analysis removed three variables, DI2, FIBE and FR12B, from the analysis, thus including 14 variables (Table 4). The misclassification rate of these 14 variables was 2.02% based on cross-validation in all data. In the analysed data, six different yodels from four different territories were misclassified. Notably, there was misclassification of the yodel from territory 6 into territory 16 and *vice versa*, both recorded in the summer of 2021, and two yodels that were misclassified from the territory 7 into territory 15 both recorded in the summer of 2019. In spite of these, the correct classification was almost 98% in 19 territories and in 297 yodels analysed (Fig. 5).

The manual division of the data into the train (n = 201) and test data (n = 96) showed that the misclassification rate was 16.40% in the test data, when the prior group size probabilities were not considered. From the five yodels recorded in territory 3, three were misclassified into territory 19. The distance between the territories in yodels that were misclassified were in general more than


Fig. 4. Black-throated Diver male in a typical yodeling position.

Table 3. Mean and standard deviation (std) of yodel variables recorded from individual males. CV_i and CV_b are variance variables within-individual and between individual, respectively. Ratio is CV_b/CV_i.

Variables	Mean	Std	Range	CV_i (%)	CV_b (%)	Ratio
Duration (ms)						
DI	965	119	715–1273	3.2	12.3	3.83
DI1	244	72	121–510	9.6	29.6	3.08
DI2	722	83	507–963	4.0	11.5	2.86
DGAP	297	40	200–423	6.0	13.4	2.22
DR1	822	113	572–1095	3.4	13.7	4.04
DR11	113	30	49–214	11.8	27.0	2.27
Frequency (Hz)						
FI1	1337	51	1212–1473	1.77	3.8	2.17
FI2C	1324	136	1034–1809	4.06	10.3	2.53
FI2B	1118	44	1037–1252	2.03	3.9	1.93
FI2E	1677	151	1417–2064	1.42	9.0	6.31
FR11C	1084	57	947–1292	3.12	5.3	1.69
FR11	1230	56	1103–1438	2.08	4.5	2.17
FR12B	1218	49	1059–1333	1.71	4.0	2.34
FR12E	1640	153	1358–2024	1.33	9.3	7.04
FR12C	1340	136	1026–1809	4.41	10.1	2.30
Calculated variables (Hz)						
FIBE	559	146	254–987	5.60	26.2	4.68
FR1BE	421	144	198–813	7.03	34.3	4.87

3 km (mean 3.5 km, range 1–5.5 km). The shortest distance in which the yodel was misclassified was between the territories 13 and 18 (Fig. 2). When the prior group size probabilities were considered, the misclassification rate was 10.46%.

4. Discussion

The obtained results on BTD vocalization suggest, that the BTD males in each territory are the same individuals even in different years. In a similar study, Walcott *et al.* (1999, 2006) ringed individuals of the closely related Common Loon to verify the individual characteristics of the yodeling. In BTDs individuality can be verified by photographing the breeding plumage of BTDs and by examining whether the plumage remains the same from year to year (Lehtonen & Lappalainen 2017) or by ringing the BTDs and recapturing them annually to check their identity. However, the BTD is a highly sensitive species and both methods impose strong disturbance on them, as the former would require photographing the BTDs close enough in nesting time when they are hiding. Photographing requires a long presence in the vicinity of the nest and is not advisable due to interference to nesting. Annual catches near the nest in open waters is extremely difficult and can harm the BTDs. In our view the only safe way to catch the BTDs is during dark nights in August–September while capturing during the breeding season can cause major disturbance for nesting and probably abandonment of the nest. Thus, there is no safe way to visually ensure the individuality of BTDs during the breeding season.

Table 4. The order of selected variables in classification of the male yodels into different territories based on stepwise discriminant analysis. Variables DI2, FIBE and FR12B were removed ($p > 0.05$).

Number in	Variables	Partial r^2	F	P-value
1	FR12E	0.98	743.4	<0.0001
2	DR1	0.92	179.4	<0.0001
3	DI	0.87	99.7	<0.0001
4	FI2E	0.86	94.1	<0.0001
5	FR1BE	0.70	35.3	<0.0001
6	DR11	0.69	34.1	<0.0001
7	DGAP	0.69	33.5	<0.0001
8	DI1	0.67	30.1	<0.0001
9	FI1	0.63	25.9	<0.0001
10	FR11	0.53	17.1	<0.0001
11	FR12C	0.32	7.1	<0.0001
12	FI2B	0.30	6.4	<0.0001
13	FR11C	0.18	3.3	<0.0001
14	FR12CA	0.10	1.6	0.0500

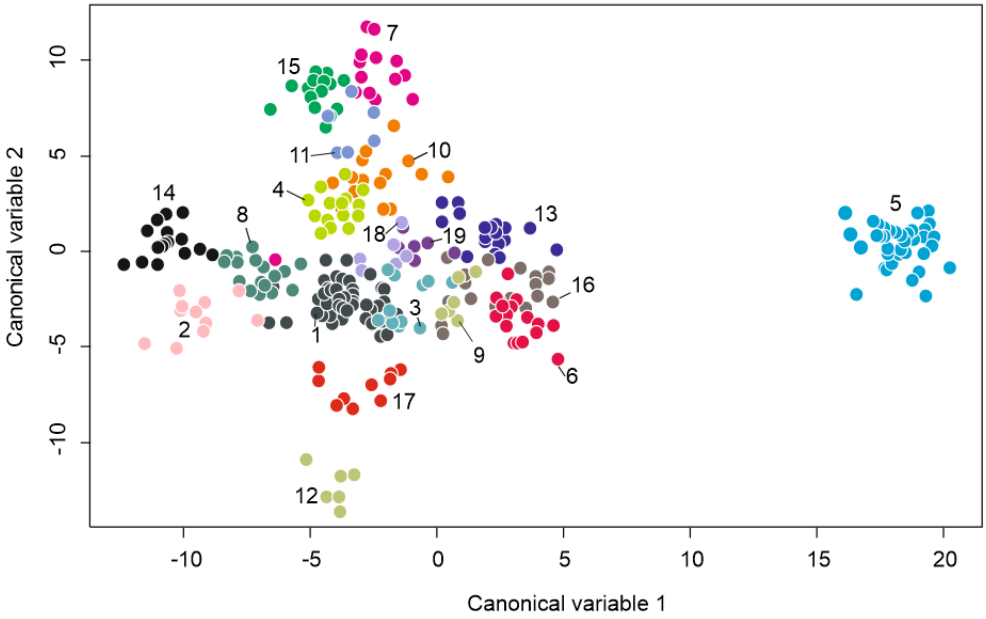

Fig. 5. The two canonical variables of all yodel data. The yodels in each territory are marked with different colours and the number refers to each territory. The yodel of BTDs in territory number 5 is clearly different compared to other yodels and territories (recording is available in the online supplementary materials). Color figure is available in the online version of this article.

Based on our results, the BTDs vocalization in specific territories remain the same from year to year. Thus, yodel characteristics are either territory-specific or individual-specific. The previous sounds unrealistic, and studies with the Common Loons show that the vocalization in specific territories remain the same from year to year. We have shown that the same BTD pair occupied the same territory during nine consecutive years (Lehtonen & Lappalainen 2017). On these findings, we assume that the yodeling is individual-specific and can be used to identify different males. At some point the males will be replaced and this yodel approach could be used to test if the yodel deviates from the previous.

The discriminant analyses showed that the individual males of Black-throated Divers can be differentiated from each other by their yodel in different territories. The overall misclassification rate was 2.02% based on cross-validation in all data. The highest misclassification rate, 10.46%, was observed in test data that included those territories that had two or more years of yodel data, and where only the last year of data was tested. The difference between these two analyses and misclassification rates (2.02 and 10.46%) is that on cross-validation only one song is classified at the same time against all other songs, while in the manual division all 96 songs are tested at the same time. The latter mimic situation, where the yodels were recorded in several territories over one summer and were then all classified based on earlier recorded yodels and thereby obtained discriminant functions.

The recent research on different bird species have shown that the spectral and acoustics variables of songs can be used to identify individual birds. Favaro *et al.* (2015) measured 31 spectral and temporal acoustic variables of the calls of the African penguin (*Spheniscus* sp.). The acoustic variables were used in a stepwise discriminant analysis, which classified correctly 66.1% of the contact calls and 62.5% of display songs to the correct individual bird. Similarly, Chang *et al.* (2018) showed that discriminant analysis classified correctly 94.5% of the individuals of Large-tailed Nightjar (*Caprimulgus macrurus*) based on nine vocal variables. In another nightjar species, *Caprimulgus europaeus*, Raymond *et al.* (2020) found that the male songs were correctly classified at a maximum of 73.5% within one season, rising to 75% if full-length calls and 13 acoustic variables were used. Yee *et al.* (2016) showed that the individual territorial calls of Sunda Scops-owls (*Otus lempiji*) can be correctly classified with 97.1% accuracy with discriminant function analysis.

In the BTD male yodel, duration and frequencies of the different parts of the introductory phrase and the first repeat phrase (Table 1) were found to be the most important in the identification. The repeat phrases, usually 2–4, are very similar to each other. When experimenting with the data, the variables also from the second repeat phrase were included in the analyses, but it was found that these have no added value in the individual identification of BTDs and therefore these were excluded from further analyses.

The success of the recording is affected by the size of the territory and the choice of the recording location. The size of the territory of the BTD pair varies from ten to one hundred hectares, depending on the environment and the nesting phase (Lehtonen 1970). Recording is only possible in calm and rainless weather, otherwise the sound of waves and rain will interfere. The maze of territory with its small islands can weaken the quality of recorded yodels. Often the territory is the whole island, and when a BTD circumnavigates its territory, the yodel may come from behind the island, making it unusable.

The duration from the beginning of the yodel to the end of first repeat phrase varies considerably in different territories. It was difficult for the human ear to distinguish the voices of most other BTDs, but it was possible to perceive the pace of the introductory phrase and the first repeat phrase as slow or fast. Another example of yodel that can be distinguished by human ear is the yodel of the territory 5. This is due to sudden change in frequency during the second note of the introductory phrase and the second note of the first repeat phrase: The sudden change rises the frequency about 350 Hz.The male of the territory 11 also raises his song during the second note of the introductory phrase.

Walcott *et al.* (2006) observed that male Common Loons changed their yodels either the first or second year on the new territory when they changed their territory. Furthermore, this change increased the difference between the new resident's yodel and that of the previous resident. This result implies that loons not only change their vocalizations as the birds change territory, but also that the new owner is familiar with the yodel of the resident that it replaces. Such a change was not observed in the present study, and therefore the results suggest that no territory changes occurred during the study period.

The results here based on male yodels suggested that the same male BTDs occupy the same territory from year to year. Similar results were found for both male and female BTDs based on their breeding plumage in an earlier study in the same area (Lehtonen & Lappalainen 2017). Thus, these two studies are mutually supportive. However, individual identification by the vocal repertoire of males gives lower misclassification rates than using the breeding plumage based on discriminant analyses. Further, recording the yodels are much easier to carry out and causes minimal disturbance to BTDs than using the breeding plumage. However, the use of breeding plumage is valuable if data are also needed from females.

The main reason for using vocalization for individual identification is that the technique causes minimal interference, making it particularly suitable for BTDs that are sensitive to interference. The vocalizations in specific territories remain the same which probably suggests that these are the same individuals from year to year. Future studies should assess if yodels can be used to identify individuals by comparing yodel with other individual characteristics such as plumage or the use of ringed individuals.

Yksilöllinen vaihtelu kuikkien (*Gavia arctica*) reviirihuudoissa

Kuikkien (*Gavia arctica*) kuuluva reviirihuuto on tunnetuimpia luonnonääniä pohjoisilla alueilla. Tutkimuksen tavoitteena oli selvittää, voidaanko koiraskuikkia tunnistaa yksilöllisesti huudon perusteella. Vuosina 2018–2021 äänitettiin 19 urospuolisen kuikan reviirihuuto, 10 niistä 2–4 peräkkäisenä vuotena ja yhdeksän yhtenä vuotena. Äänitykset tehtiin samalla järvialueella Suomessa. Huuto koostuu yhdestä johdanto-osasta ja yhdestä tai useammasta toisto-osasta. Johdanto-osan ja ensimmäisen toisto-osan spektrogrammeista mitattiin 17 eri parametriä. Nämä koostuivat spektrogrammin eri osien taajuuksista ja kestoista. Valitut parametrit analysoitiin tilastollisesti. Erotteluanalyysiä käytettiin tutkittaessa kuikkayksilöiden yksilöllistä tunnistamista reviirihuutojen (n = 297) spektrianalyysin perusteella eri reviireillä (n = 19). Analyysit osoittivat, että käytettäessä 14 muuttujaa ja ristiinvalidointia, pystyttiin reviirit luokittelemaan huudon perusteella lähes 98 prosenttisesti oikein. Tämä viittaa siihen, että samat yksilöt puolustavat reviiriään vuodesta toiseen.

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Online supplementary material

The supplementary material contains information about the average duration (Fig. S1) and the average frequencies (Fig. S2) of yodels in different territories. Possible abrupt changes in frequency of the second note of the introductory phrase and repeat phrases are shown in Fig. S3. Misclassified yodels in the discriminant analysis after cross-validation are presented in Tables S1 and S2. The song/voice recording includes the exceptional yodel of the BTD male in territory 5 compared with the more typical yodel of the territory 1.

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Night-brooding behaviour in provisioning cavity-nesting birds is a trade-off between adult predation risk and nestling thermoregulation needs

Henning Heldbjerg*, Anthony D. Fox, Thorsten J.S. Balsby &
Peder V. Thellesen

*H. Heldbjerg, Department of Ecoscience, Aarhus University, C.F. Møllers Allé 8, DK-8000 Aarhus C, Denmark * Corresponding author's email: hh@ecos.au.dk*
A. D. Fox, Department of Ecoscience, Aarhus University, C.F. Møllers Allé 8, DK-8000 Aarhus C, Denmark
T. J.S. Balsby, Department of Ecoscience, Aarhus University, C.F. Møllers Allé 8, DK-8000 Aarhus C, Denmark
P. V. Thellesen, Møllevej 14, Fåborg, DK-6818 Årre, Denmark

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Night-brooding of nestlings in cavity-nesting avian species carries predation risks to parents. Anecdotally, several species are known to shift from constant adult night-brooding behaviour to leaving nestlings unattended at night during offspring development but the timing, speed of change and sex-specific differences between parents, and the factors shaping this behaviour have rarely been described. Moreover, the location and nature of night roosts used by adults whilst provisioning nestlings has received little research attention. We studied breeding Common Starlings (*Sturnus vulgaris*) and hypothesised that, in such a cavity-nesting species, 1) nestlings would only be night-brooded until they achieved thermal independence, 2) since the species is frequently polygynous, female parents would most likely exclusively night-brood offspring despite provisioning by both sexes and 3) night-brooding would be more likely during nights with lowest temperatures. Nightly video recordings throughout the nestling phase at eight Starling nests together with data from 18 Starlings fitted with GPS-loggers during 26 nights provided support for hypotheses 1) and 2), while we found no support for hypothesis 3). All tagged male Starlings always roosted far from the nesting site (up to 8 km) independent of nestling age; all females brooded nestlings, usually up to the first seven-nine days after hatching (when the nestlings achieve thermoregulation), but roosted with males after day 10, when all tagged Starlings from the same nesting 'colony' roosted together. These results confirm differential sex-related parental effort in provisioning Starlings, suggesting females only night-brood until young achieve homeothermy.

1. Introduction

Nestlings of altricial species have little or no capacity to maintain core body temperature immediately post-hatching, since they are dependent on parental heat until they have reached the stage of development where they can achieve thermoregulation (Andreasson *et al.* 2016). Physiological development of endothermy (metabolic heat generation to self-maintain body temperature) in passerine nestlings is closely correlated with increases in body mass and accompanying decreases in surface-area-to-volume ratio and age, but tends not to be correlated with plumage development (*e.g.*, Andreasson *et al.* 2016, Pereyra & Morton 2001). This implies that small nestlings are completely dependent upon parental care for warmth, food, and protection from the elements (Pereyra & Morton 2001, Wegrzyn 2013), until they attain homeothermy (when they can maintain a stable internal body temperature despite external influence, Andreasson *et al.* 2016).

The developmental pattern of thermoregulation has been studied experimentally by testing how well single nestlings at different ages can thermoregulate at ambient temperatures (Dunn 1976, Pereyra & Morton 2001). The onset of endothermy is species specific, dependent upon length of the nestling period, brood size, nest type and nest location (Clark 1982, Dunn 1975, Morton & Carey 1971). In reality, growing nestlings often benefit from heat provided by other brood members, enabling homeothermy in full broods earlier than would be the case with a single offspring. Clark (1985) showed that parent Common Starlings (*Sturnus vulgaris)* (hereafter Starling) altered their daytime brooding in relation to the average homeothermic capacity within broods and also showed dramatic increases in nest cup temperature 30 seconds after a parent entered the nest box during daytime, suggesting comparable benefits will accrue to offspring during night-brooding and the coldest part of the daily temperature cycle. This begs the question, given the increasing predation risk of being confined to a nest cavity with an ever more noisy brood of nestlings emitting strong olfactory signals accessible to nocturnal predators such as Mustelids (Feare 1984), how do night-brooding parents trade off their own predation risk through incubation with the diminishing need to brood young acquiring endothermy? In this study, we investigate how adult behaviour changes with the development of thermoregulatory abilities in nestlings by studying the degree of night-brooding among adult Starlings, to determine whether there are changes during the nestling rearing phase.

Adult passerine energy expenditure during incubation differs negligibly from that while only resting in a non-incubating posture above an air temperature of 15 °C (Haftorn & Reinertsen 1985). Hence adult birds would have expended much of the heat, which they impart to their young, in their own temperature regulation even if they were not brooding. This means maintenance of nestling endothermy by brooding is trivial energetically compared to, for example, the energy costs of intensive feeding (Wegrzyn 2013). Rather than leave the nest box, brooding adult Starlings may also benefit from staying overnight in a nest cavity with nestlings in cold environments, by accepting an increased risk of predation as a trade-off to reduce their own energetic costs of thermoregulation (Nilsson & Nord 2017). Several species are known, anecdotally, to show changes in adult brooding behaviour during nestling development, particularly shifting from initial constant adult brooding behaviour to later leaving nestlings on their own at night during the development of offspring (Katzenberger *et al.* 2015). However, details of the timing, the speed of the changes and parental sex-related differences, and the factors shaping this behaviour have rarely been described. Moreover, knowledge about the night roosts used by adults whilst provisioning nestlings has received little research attention.

The Starling is a cavity-nesting, widespread and numerous but declining breeding species associated with farmland and human settlements in western Europe (Feare 1984, Heldbjerg *et al.* 2019). The migration has been well studied throughout much of its breeding range (Fliege 1984), showing Danish breeding Starlings to be short distance migrants, mainly wintering in the British Isles and the Netherlands arriving early to the breeding sites, often in late winter, the majority in March (Bønløkke *et al.* 2006). They breed across the entire country with highest densities associated with large grassland areas and grazing dairy cattle (Heldbjerg *et al.* 2016, Vikstrøm &

Moshøj 2020). Typically, the species lays only one clutch but in years with early springs, two clutches are recorded in some areas. At the study site, the mean number of fledglings at the time of ringing (age 12–14 days) was 5.56 ± 1.01 SD (1971–2015: 857 clutches). The breeding period, which is highly synchronous has advanced by *ca.* 0.2 days year^{-1} during 1971–2015 with a mean first egg laying date in the most recent years at *ca.* 24 April and a corresponding fledgling date at *ca.* 30 May (Thellesen 2017). Starlings often breed in loose 'colonies' combining suitable nest sites with available feeding opportunities within a few hundred metres (Heldbjerg *et al.* 2017).

Cavity nest sites provide multiple benefits from environmental protection to avian parents over incubating and brooding in open nests (such as thermal insulation and protection from large predators that cannot access the cavity), yet confinement also brings risks (for instance from predation by species that can gain access to the nesting cavity). However, the chance of surviving a predator at night may still be better outside the nesting cavity than inside for adult birds. Starling nestlings in nest boxes are known to occasionally be predated by, for example, domestic cats (*Felis catus*), stone martens (*Martes foina*) and Magpies (*Pica pica*) but whether this is also a risk for the adults is unknown to us. If the predation risk is higher inside than outside the nest box, adult Starlings face a conflict between the need to maintain body heat in newly hatched nestlings that have yet to achieve effective homeothermy in the nest cavity *versus* the risk of their own predation from staying with nestlings at night (especially from mustelids, *e.g.*, Dunn 1977, Sorace *et al.* 2004). These factors shape our three hypotheses relating to night-brooding behaviours in Starlings for which we attempt to find support in this investigation.

Firstly, 1) Starling parents should night-brood offspring only as long as needed to maintain the body temperature of nestlings when ambient temperature falls at night, ceasing when the nestlings reach the age, weight and development to achieve effective homeothermy (generally seven to nine days after hatch, Clark 1982). In other words, the adult Starling behaviour should change in accordance to the nestling homeothermy. To test this, we assumed that our nestlings attained homeothermy at the same age as the Clark study (given this is metabolically determined) and examined whether night-brooding behaviour was dependent on offspring age, with an expectation that night-brooding declined after age seven days.

Secondly, Starlings are frequently polygynous (Merkel 1978, 1980); estimated at 20–60% of all males (Pinxten *et al.* 1989), and male birds in general tend to provide parental care when the fitness derived via offspring survival is greater than benefits of abandoning nestlings to seek out new mates (Balshine 2012). We therefore hypothesise that Starling males potentially divide parental investment between more than one brood, and hence 2) would be less likely to roost in nest boxes than females associated with a given brood. Males might rather benefit from association with local communal roosts (Feare 1984), to which we might expect females to resort once they ceased night-brooding homeothermic nestlings and we hypothesize that only females undertake brooding.

Finally, we hypothesized 3) that brooding would be more likely on cold nights, because regardless of the nestlings' own age and thermoregulatory abilities, nestlings would expend more energy in the absence of night-brooding by adults on cold compared to warmer nights, which would also be beneficial for the brooding adult.

2. Material and methods

Our studied colony comprised 15–17 Starling pairs breeding annually in nest boxes on a dairy farm with grazing cattle and mixed crops of spring barley, winter wheat, grass and fodder beet, owned by one of the authors (referenced as PVT from now on) in Hjortkær, near Esbjerg (55°32'N, 8°43'E) in southwest Denmark (Fig. 1), the subject of study since 1971 (Thellesen 2017). All breeding attempts were followed in detail in each nest box and the nestling age in each nest was recorded in days from day one (hatching date).

During the study of breeding Starlings over fifty years at the study site, PVT has observed that while female Starlings tended to brood newly-hatched nestlings in their nest boxes, nestlings over *ca.* one week old rarely had brooding adults in the nest box with them at night.

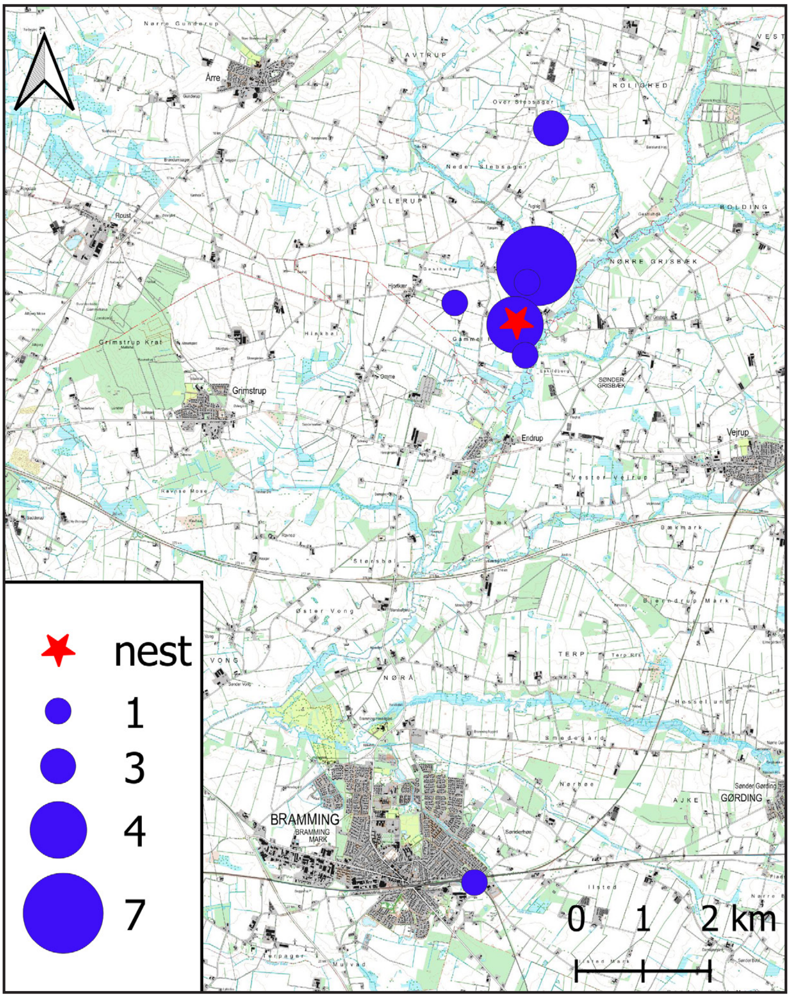

Fig. 1. Map of different overnight roosting sites used by parental provisioning Starlings (*Sturnus vulgaris*) (blue dots) breeding at the study dairy farm (red star). Increasing size of the symbols indicate the number of Starlings (one-seven) at each site. The Coordinate system is WGS84, UTM zone 32N (EPSG:25832). The map source is DTK25 – Danmarks Topografiske Kortværk 1:25 000 (www.kortforsyningen.dk)

2.1. Video surveillance

We used video surveillance of the entrance to nest boxes containing Starling nestlings of known age to determine the presence of a night-brooding adult and to relate presence/absence to ambient temperature and brood age, without disturbing the birds by our presence. Four video cameras were mounted 50 cm from, and focused upon, nest box entrances during the 2015–2017 breeding seasons to continuously monitor arrival and departure of birds throughout the provisioning period. Cameras were set to be triggered to record every movement, including parent birds entering and leaving nest boxes. Cameras were linked to a Digital Network Video Recorder (Handykam, Xvision XR960 HD DVR) which enabled storage of files for later analysis of activities. Activities recorded at eight (ultimately successful) Starling nest boxes are included in this study. Starling nightly presence/absence in a given nest box was registered by checking the last and first movements each day from hatching date (day one) to day 14. Starlings were never observed moving during darkness (recordings of night-active birds and other taxa at Starling nest boxes confirmed that movements were also registered and stored in absolute darkness). Out of the potential 112 camera-nights, 11 camera-nights were lost due to technical difficulties (hard disk capacity exceeded). The final outward movement from a nest box on a given day confirmed the bird was roosting elsewhere, while a final movement into the nest box indicated it was brooding nestlings inside. Similarly, movements were scored for the first movements in the morning (first in constituted roosting elsewhere, first out equated to night-brooding). The primary information from this source were "complete night records", where a given bird was confirmed coming to the nest box both at night and departing the following morning. Of the 101 complete night records, 79 confirmed the presence of an adult at night and morning while 22 were contradictory either as a result of movements potentially not being detected by the video or because visits by other adult Starlings to the nest boxes obscured our interpretation of whether a bird was present overnight or not. This equated to 78.2% of video recordings confirmed brooding on both occasions from all-night camera monitoring (see Supplementary Material Table S1 for details). We included additional data from the nights when the system independently recorded either last ("evening only") or first ("morning only") records only, in a subsequent analysis to assess their effect despite the lack of corroborative recordings.

2.2. Bird tracking protocol

We also tagged provisioning parent Starlings with GPS-loggers to describe their foraging movements and habitat preferences during day-time (Heldbjerg *et al.* 2017). Here, we use data from the same devices to determine sex-based differences in roosting site behaviour of adults, which was not always possible from identification of colour rings (see below) on the night-brooding adults on the video recordings.

Eighteen breeding Starlings provisioning offspring were caught during 5–14 May 2015 and 6–14 May 2016, either in nest boxes by a remote triggered closure of the entrance hole or in mist nets nearby. In a backpack attachment, we used battery powered Gypsy 5 GPS-loggers (Technosmart Europe srl., Rome, mass *ca.* 3.2 g including Teflon harness, *ca.* 3.5–4% of Starling body mass), which recorded with positional accuracy of 2–4 metres one fix per minute during daylight and one fix per hour at night, commencing one day after attachment to exclude behavioural effects of capture and handling (Heldbjerg *et al.* 2017). Tagged birds were recaptured after three–five days to retrieve loggers and data extracted via a cable connection. The recapture timing was chosen to be long enough to enable the full use of the battery capacity and short enough to be confident of recapturing the adults during the nestling phase, consistent with adults bearing loggers for the shortest possible period. All captured adults were sexed and ringed with a metal ring and three coloured rings to enable individual identification from distance and on video recordings. All procedures conformed with Aarhus University codes of research practice and were carried out with permission from the Danish Natural History Museum Ringing Centre.

Each logger provided a data file (.txt) giving position, speed and precision information for every time-stamped fix until battery failure. We filtered data after Horizontal Dilution of Precision (HDOP), which is a good indicator of how accurate the positions are, using only a precision less than *ca.* 10 meters (HDOP > 2.5) to focus on the timing of movements to and from the night roost and its position, defined by the end point of the very last flight of the day to the roost site and by counting back to the first moving point along the first flight out early morning.

We predicted that adult Starlings may be more prone to stay in the nest box at night when the night temperatures are low. Therefore, we included the minimum daily temperatures in our model on the assumption that night temperature was an additional factor that affected decisions by brooding birds to stay or leave the nest box at night. For this purpose, we used temperature data from the nearest Danish Meteorological Institute observation site at Varde (20 km from the study site, accessed 21 August 2020 at https://www.dmi.dk). Sunset and sunrise at the study site for relevant days was obtained from the mobile application software 'Dusk and Dawn' (Stobbe 2016).

2.3. Statistical analysis

We used a generalized linear mixed model (GLMM) with a binomial distribution to test the qualitative response whether a Starling roosted in its nest box as recorded in the video surveillance, since presence/absence (probability) of Starlings in nest boxes at night follows a binomial distribution. We included individual as a random effect to account for the multiple observations gathered from each individual. The logistic regression tested follows this formula:

$$\text{Probability} = 1/(1+\exp(\beta*\text{day}+\text{intercept})) \quad (1)$$

The inflection point (*i.e.*, where the probability for spending the night at the nest box was 0.5) was therefore estimated as: –intercept/β (after isolating day in the equation 0.5=1/(1+exp(β*day+ intercept))). We tested the three different measures of presence: evening only, morning only and complete nights. In this analysis we aimed at estimating the inflection point and therefore omitted temperature from the model, as the inflection point then would be a function of both day and temperature.

In another logistic regression also based on video surveillance data, we tested the effect of temperature on the likelihood of spending the night in the nest box using a generalized linear model. Here, we included days since hatching and the lowest ambient night temperature in the area as fixed effects, and the individual starling as random effect using three different measures of presence: evening only, morning only and complete nights, which gave three models. We used proc glimmix in SAS version 9.4 (SAS Institute, Cary, NC) to run the models.

3. Results

Video recordings verified whether each Starling stayed in the nest box or roosted away from it on a given night in eight nest boxes, enabling us to establish at what age nestlings were left on their own at night. We found that days after hatching had a significant effect on the likelihood of presence/absence in the nest box at night (GLMM: $F_{1,70} = 15.22$, $P = 0.0002$, $\beta_{day} = 1.2726$, Intercept = –10.01). Based on all eight nest boxes, the inflection point when more than 50% of the adult (female) Starlings spent the night away from the nest was estimated to be 7.9 days after hatching (Fig. 2). Estimated values based on evening behaviour alone (7.7 days) and morning behaviour alone (7.1 days) provided confirmatory results (Table 1). As early as day five, the first female spent the night away and by day 10 all females stayed away from their nest boxes at night (Fig. 2). The lowest ambient temperature did not affect the likelihood of spending the night in the nest box (Table 2).

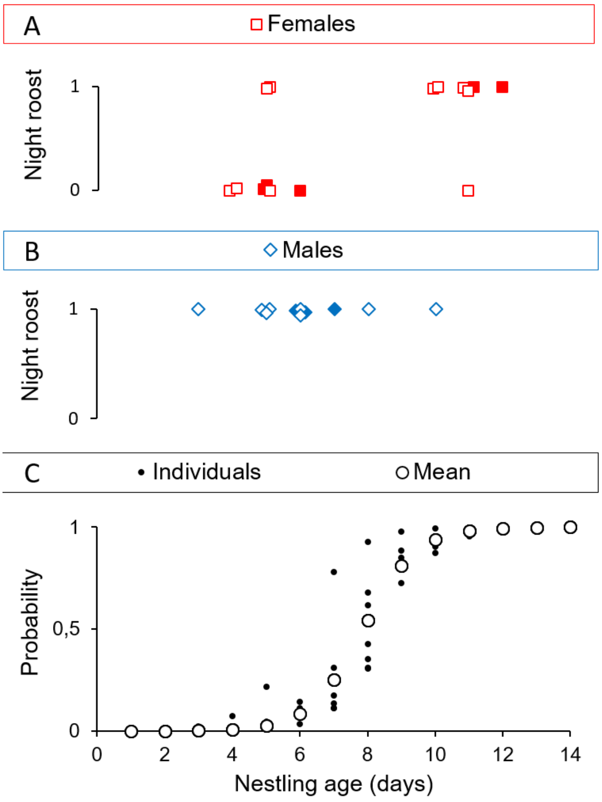

Fig. 2. Panel A shows presence (0) and absence (1) of GPS tagged female Starlings (*Sturnus vulgaris*) (red squares) night roosting in the colony with respect to nestling age; filled symbols indicate 2nd nights of the same individuals. Panel B shows the same for males (blue diamonds). Panel C shows mean fitted logistic curve (open circles) based on the daily probability of presence/absence of night-brooding Starlings (from video recordings) derived from logistic regressions of data from eight individuals (shown by small filled circles from individual models). The inflection point is the nestling age when the probability of night-brooding is 0.5.

Table 1. Generalized mixed model testing the effect of day in relation to the likelihood of the female Starling spending the night in the nest box. β and intercept are parameter estimates and inflection point estimate is the night where 50% of the females did not attend the brood at night.

Dependent variable	df	*F*	*P*	β	Intercept	Inflection point
Combined	1, 70	15.22	0.0002	1.2726	–10.01	7.87
Evening away	1, 95	28.79	<0.0001	0.4569	–3.50	7.66
Morning away	1, 95	29.82	<0.0001	0.5247	–3.73	7.11

Table 2. Generalized linear model testing the effect of day and minimum ambient temperature as fixed factors in relation to likelihood of the female Starling spending the night in the eight nest boxes (N=79).

Variable	Combined			Evening away			Morning away		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Day	1, 69	10.94	0.0015	1, 94	23.59	<0.0001	1, 94	26.92	<0.0001
Temperature	1, 69	2.55	0.1147	1, 94	0.36	0.5506	1, 94	1.06	0.3058

We derived positions for 18 GPS-tagged Starlings from 26 nights. This included eight birds with data from two consecutive nights (Supplementary Material Table S2). All eight males (during 11 nights) consistently roosted away from the colony (Fig. 2, see Supplementary Material Table S3), the furthest *ca.* 8 km away in a group of coniferous trees at the edge of an urban area (Fig. 1). Four females (on seven nights in all) roosted in their nest boxes (Fig. 2). The remaining six females (eight nights) roosted 0.5–3 km from the nest (Fig. 1). Males roosted away from the colony independent of nestling age (day 3–11). The four females roosted (seven nights) in the colony with nestlings of day 4–11 (4–6 and one from day 11). The six other females that roosted (eight nights) away from the colony had nestlings of day 5–12 (10–12 and two at day five). All eight birds (five females, three males) with information on roosting site from two consecutive nights roosted at the same site.

Of nine birds tracked on the same night (7–8 May 2016, when all broods were five to seven days old), all six males roosted together in a willow thicket *ca.* one kilometer north of the colony, while all three females roosted in the colony. Two females (10–12 day old nestlings) also used the willow site on two consecutive nights (14–16 May 2016). The only pair with positions from the same night (10 day old nestlings) roosted together in a willow *ca.* three kilometers north of the colony.

Starlings arrived at roosts shortly before sunset (mean = 22.8 minutes ± 18.4 SD, n = 10) and departed again shortly before sunrise (mean 17.3 minutes ± 6.0 SD, n = 13) with no significant differences between the sexes in either arrival or departure.

4. Discussion

The video recording results confirmed that female Starlings always night-brooded nestlings in nest boxes at the beginning of brood rearing but this behaviour changed when the nestlings were *ca.* eight days, when they are downy and the flight feathers are about to emerge from the sheaths (Supplementary Material Fig. S1) and after ten days all females stayed away from the nest at night. Effective homeothermy was found in experiments to be attained at lower mean individual nestling weights in larger broods (Clark 1982), but at our study site and for Starlings in general, clutch sizes varied little, hence the variation between the nests were small and confirmation of the effect of brood size on night-brood cessation date must await larger samples with larger brood size variation. Starlings with GPS-loggers confirmed the pattern of a behavioural change in night-brooding. Data from loggers showed only females roosted at the colony, confirmed by the fact that no tagged males roosted at the colony (and hence never in nest boxes). The precision of the GPS positions is too low to identify the exact night roost (*i.e.*, whether or not in the nest box), especially because the positional precision is reduced when the GPS is located inside a nest box. However, despite the fact that we did not have irrefutable proof (*e.g.*, by observing a given female based on leg rings in the nest boxes on each given night), we are confident that Starlings night roosting in the colony were actually roosting in their nest boxes. This judgement is based on our observations of colour ringed females witnessed entering and leaving nest boxes when caught on the video recordings and on the extensive experience of PVT, which confirmed that Starlings were never found roosting in other nest boxes during the nestling phase nor at any other roost site away from their own nest box at the farm (*e.g.*, in buildings or trees in the immediate vicinity).

These observations support our hypotheses that 1) Starlings (specifically females) only brooded nestlings at night until *ca.* eight days of age and 2) that provisioning males never roosted in nest boxes (also confirmed by PVT from ringing studies). Hence, males were not tied to the nest site at night, but instead shared communal roosts with other males at different roost sites at night a significant distance away from the nests. We found no support for hypothesis 3) that the lowest ambient night temperature affected brooding in nest boxes.

The nature of night roosts used by birds whilst breeding has received very little attention (see Jirinec *et al.* 2016). Those authors found that the nocturnal roosts of Wood Thrush (*Hylocichla mustelina*) males were on average 121.8 meters from their active nests in habitats with denser canopy, often outside the diurnal home ranges. Similarly, Hill and Cresswell (1997) found male Eurasian Blackbirds (*Turdus merula*) at a communal roost several hundred metres away from nests and were accompanied by females once the nestlings were 11 days old. However, night-roosting of male Starlings, unexpectedly up to eight km away from nests, while provisioning nestlings has hitherto been unreported. The fact that roosts were several kilometres away from the nest may imply that once the adults have decided to leave the nest, they seek the best quality night roost, and that the distance moved is negligible in terms of energy use in comparison to value of using such a site. Whether this is due to the communal benefits of roosting with other birds (*e.g.*, learning of alternative rich feeding opportunities or dilution of predation risk) remains unclear and warrants further investigation. The general trend for an overall decline in brooding behaviour during the course of the nestling phase is well known from several other avian species, such as pigeons (Saxena *et al.* 2008), hawks (Wreford *et al.* 2017), falcons (Rejt 2004), tits (Tinbergen & Dietz 1994) and swallows (Marsh 1980, Winkler *et al.* 2011) but in all cases, these studies lack detail on the nestling age when the change occurs and the variation in this behaviour.

4.1. Changing needs and behaviour during the nestling phase

Results showed that females brooded their offspring overnight during the period when the nestlings are considered to be unable to self-regulate their own temperature, but ceased to do so once they had reached an age when it is considered that they have attained homeothermy. This confirms that night-brooding only continues as long as necessary to protect nestlings against heat loss, a risk adults must trade off against their own risk of predation in the cavity at night. We have no data to compare the risk for the female to be predated in the cavity to being predated away from the nest but these results clearly demonstrate that after nestlings attain homeothermy, females choose to desert them at night in the cavity in favour of a collective roost with other adult conspecifics. It is however important to note that females showed some variation in when they left the nest box at night, but we have no data on factors that could cause this variation.

Another change that may be related to the achievement of homeothermy can be seen in the behaviour of the provisioning adults. Until the nestlings are ten days old, adult Starlings remove faecal sacs from the nest, but when nestlings are feathered, this activity ceases (Feare 1984). Faecal sacs remaining in the nest will potentially result in damp and colder nestlings but Feare (1984) suggested that after this developmental stage, it is less critical to the maintenance of the thermal insulation properties of nest cavities.

Clark (1982) showed that, in general, Starling brooding behaviour decreased in relation to the effective homeothermic capacity of nestlings within broods. Temperature loss in Starling nestlings is inversely correlated with brood mass and air temperature, *i.e.*, the lower the temperature and the smaller the brood size the greater the loss (Clark 1982). As brood age and weight increase, loss of body temperature declines until day seven-eight when homeothermy is attained for a given brood size and air temperature. By day eight (when our data confirms that females change their brooding behaviour) nestlings have attained body mass of *ca.* 50 g compared to *ca.* 6 g at hatching (Feare 1984). Our birds tended to have a mean clutch size of five, resulting in total brood mass at day eight of *ca.* 250 g, the brood weight at which Clark (1982) found that Starling nestlings were able to self-regulate their body temperature at air temperatures, which lay somewhere between 6.5 and 13 °C (the temperatures experienced at our study site in the nestling period).

In this case, it is difficult to differentiate between the effective homeothermy and individual endothermy of a brood (*i.e.*, nestlings in a large brood can be effectively homeothermic due to high thermal inertia while still failing individually to maintain body temperature in the face of cold ambient conditions, *e.g.*, Dunn 1976, 1979). However, in Starlings, the age of effective homeothermy and endothermy appear strongly correlated, at least at low ambient temperatures (Clark 1982), but the difference here is perhaps not significant, as seen from the perspective of the parent, the brood has attained the ability for individuals to regulate their body temperatures in situ. For this reason, we suggest that once their offspring attained homeothermy, our female Starlings ceased brooding nestlings in the colony and joined males at communal roosts. Unfortunately, we have no GPS recordings from females with nestlings at day seven to day nine, *i.e.*, around the time of inflection.

The videos were recorded from outside the nest boxes and hence gave no information about the actual behaviour of the female in the nest box (*i.e.*, whether it was actually brooding or not). Studies on tits by Nilsson and Nord (2017) have shown that females often spend the night in the nest box late during nestling development when nestlings are endothermic, sleeping at the rim of the nest-cup and with no contact to the nestlings. They interpret this as a behaviour that mainly functions as a thermoregulatory benefit to the female. However, this behaviour may be species specific since in a Starling nest, there is no rim of a nest-cup and no space for the adult female to avoid contact to the nestlings. Hence at the nestling age of *ca.* eight days (*i.e.*, the inflection point, when the clutch typically weighs 250 g and cover almost all nest box ground surface) she will functionally be night-brooding and we cannot exclude that leaving the nestlings on their own is simply a matter of limited space in the nest box when the nestlings have grown large. Recordings inside nest boxes would describe any variation in the female behaviour during the nestling phase.

4.2. Differential sexual parental investment

Video records rarely enabled us to sex the bird (based on coloured leg rings) entering or leaving the nest box due to rapid movements under difficult light conditions. Nevertheless, in the small sample of GPS-tagged birds all those identified were females, confirming the pattern from ringing data compiled during the 50 year long breeding bird studies, that males were never retrapped in nest boxes at night during the nestling phase. Following the statement by Feare (1984) that females exclusively incubate eggs at night, it seems reasonable that the same sex invests in the initial nocturnal brooding of young nestlings.

Our data support our hypothesis that males and females differentially invest in their offspring. Starlings are frequently polygynous, hence males are likely to simultaneously have nestlings in more than one nest while females attend only their own clutches (Feare 1984). We suggest this explains her acceptance of a greater risk from predation to enhance her offspring survival by keeping nestlings warm prior to the onset of their own thermogenesis. Equally, the results suggest a willingness to trade-off her own survival versus that of their offspring. It is unlikely that the daily risk of nest predation changes during the nestling phase, so the decision to leave the nestlings on their own with increasing age is likely related to their probability of thermogenesis, rather than any real change in predation risk.

Nattruvningsbeteende hos fåglar som häckar i håligheter är en avvägning mellan egen predationsrisk och ungarnas termoregleringsförmåga

Nattruvning ökar predationsrisken hos fåglar som häckar i håligheter. Det är känt att flera arter verkar byta från fullständig nattruvning till att helt övernatta utanför håligheten och lämna ungarna i boet obevakade över natten. Man vet dock mindre om tidpunkten då detta sker, hur snabbt det sker, samt om det finns könsspecifika skillnader i dessa beteenden mellan föräldrafåglarna. Även kunskapen om var de övernattar då de matar på dagarna är begränsad. Vi undersökte häckande starar Sturnus vulgaris och lade fram hypoteserna att 1) nattruvning av ungarna skulle bara fortlöpa tills ungarna kan termoreglera, 2) enbart honorna nattruvar trots att båda könen matar ungarna, eftersom staren är polygyn, och 3) nattruvning är vanligast under de kallaste nätterna. Vi fann stöd för hypoteserna 1) och 2) men inte för hypotes 3) med hjälp av data från nattlig videoinspelning under hela ungomvårdnadstiden och data från 18 starar med GPS-loggers under 26 nätter. Alla GPS-försedda hanstarar övernattade långt från häckningsplatsen (upp till 8 km) oberoende av ungarnas ålder medan alla GPS-försedda honor nattruvade sina ungar vanligtvis sju till nio dagar efter kläckning (då ungarna kan termoreglera), men övernattade med hanarna efter dag 10, då alla starar från samma ”koloni” övernattade tillsammans. Dessa resultat bekräftar att det finns könsspecifika skillnader i ungomvårdnad hos matande starar och att honorna bara nattruvar tills ungarna själv kan termoreglera.

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Online supplementary material

Supplementary material available in the online version of the article includes Tables S1–S3 and Fig. S1.

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