

Effects of predation pressure and nest-site selection on the breeding success of terns in a Finnish archipelago

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Studying and quantifying the breeding success of species can help to understand population trends and provide conservation guidance. Here, we studied the breeding success of Arctic Tern (*Sterna paradisaea*) and Common Tern (*Sterna hirundo*) colonies in a Natura 2000 site of the Western archipelago of Finland aiming to understand which factors related to nest-site selection and predation pressure best explain breeding success. We monitored 72 tern nests at 4 colonies and observed them during standardized monitoring sessions to record predation attacks on the tern nests. We ran generalized linear models to determine the factors which impact breeding success (hatching and fledging success). Hatching success was high across the 4 colonies with 69% of the eggs hatching, whereas fledging success was low with only 1 colony producing 14 fledglings while all other colonies had zero fledglings surviving (12% total fledging success). Regarding nest-site selection, our results demonstrate that a greater proportion of vegetation cover increases breeding success, likely through better nest concealment against predators. Nests in smaller colonies with a higher nest density and located closer to the colony center also produced more hatchlings and fledglings. Most predation likely happened during the chick stage, while our extrapolation predicted that predation accounts for at least 94% of all chick losses, indicating that predator control would aid breeding success of tern colonies in West Finland substantially.



1. Introduction

Anthropogenic stressors, including climate change, lead to drastic biodiversity change

globally, including marine species and ecosystems (O'Hara *et al.* 2021). Seabirds especially are facing a combination of threats such as avian influenza wiping out entire colonies (Knief *et al.*

2023) or human encroachment (e.g. Carney & Sydeman 1999), introduced predators (Towns *et al.* 2011), as well as elevated populations of natural predators (Scopel & Diamond 2017). Threatened seabird species have received more attention for conservation actions, but many species of least concern are also affected by climate and anthropogenic change (Dias *et al.* 2019). Two seabird species that could be classified in the latter group having currently globally a favorable conservation status (Red List Category “Least Concern”) are the Arctic Tern (*Sterna paradisaea*, BirdLife International 2024) and the Common Tern (*Sterna hirundo*, BirdLife International 2024). Even so, they are both influenced by climate and global change (Burthe *et al.* 2014) and need thus to be monitored and studied in order to keep their populations stable through e.g. understanding their reproductive success and habitat selection patterns (Morris 2003, Zeale *et al.* 2012). In Finland, both species are listed as Regionally Threatened (Common Tern: Regionally Threatened 2020 – 4c Northern boreal, Forest Lapland; Arctic Tern: Regionally Threatened 2020 – 4a Northern boreal, Kuusamo district, 4b Northern boreal, North Ostrobothnia, 4c Northern boreal, Forest Lapland, 4d Northern boreal, Fjeld Lapland; Hyvärinen *et al.* 2019) and thus require special attention for this region.

Even though common monitoring programs reveal species population trends, they do not describe reasons for potential population changes which are necessary for effective conservation. Breeding success is a fast, direct, and informative indicator for species experiencing environmental change (Rönkä *et al.* 2011) such as food quality (Cairns 1988, Piatt *et al.* 2007), which can help provide insight into population threats. Many factors can influence breeding success: while it is most often used as a bioindicator of diet quality (Piatt *et al.* 2007), predation pressure is shown to be crucial, especially to ground-nesting birds (Lima 2009, Seibold *et al.* 2013) such as terns (Scopel & Diamond 2018). Nest predation can be particularly significant for certain bird colonies, such as in Greenland, where Arctic foxes strongly impact the breeding success of Arctic Terns (Burnham *et al.* 2017). In other colonies, gulls are among the most important predators of tern nests (Burger & Lesser 1978), and it has been

demonstrated that controlling predator populations can benefit tern populations and hence their breeding success (Nordström *et al.* 2003, Scopel & Diamond 2017).

Overall food availability (Monaghan *et al.* 1989, Hatch & Hatch 1990, Suddaby & Ratcliffe 1997) as well as environmental conditions such as sea surface temperatures or climatic conditions (Dunn 1975, Scopel *et al.* 2018) impact reproductive success in seabirds (Pinaud & Weimerskirch 2002). The weather (e.g. rain and temperature) has a significant impact especially during the first week of chicks’ lives when they are more vulnerable (Scopel & Diamond 2018). Sufficient food supply is not only crucial for the chicks (Braasch *et al.* 2009) but also both parents (Suddaby & Ratcliffe 1997) to secure good breeding success. Thus, parental behavior can also influence breeding success for some species (Allen Smith *et al.* 2007, Nisbet *et al.* 2020). This may be particularly crucial for colonial breeders such as terns, where a low availability of food can lead to an increase in kleptoparasitic behavior within colonies (Schreiber & Kissling 2005) and result in breeding failures at some nests. Another important component of breeding success is the timing of egg laying. Tern pairs that lay eggs early in the breeding season have a greater chance of success compared to pairs that lay later (Arnold *et al.* 2004). In the latter case, the fitness of the parents determines the survival chances of the chicks (Arnold *et al.* 2004), which in turn is largely dependent on the age of the birds: an older bird has more experience in finding food and providing parental care compared to a young and inexperienced breeder (González-Solís *et al.* 2004).

Finally, the nest location can be a decisive factor for the breeding success of birds (Hawksley 1957, Buehler *et al.* 2017). When establishing a territory, breeding birds have to integrate several biotic and abiotic factors which may impact breeding success (Parker 1986, Ardia *et al.* 2006) and thus make nest-site selection a critical step in the habitat selection process of birds (Martin 1993). Nest concealment through vegetation around the nest, as well as nest position within the colony can lower the detectability and accessibility to predators (Donehower *et al.* 2007, Gómez-Serrano & López-López 2014, Buehler *et*

al. 2017), such that experienced birds modify their nest-site depending on the prevailing predation pressure to maximize reproductive success (Martin 1993, Latif *et al.* 2012).

The objective of this study was to investigate the breeding success of Arctic and Common Tern colonies in a Natura 2000 site in West Finland. Natura 2000 is a network of protected areas for rare and threatened species and stretches across all 27 European Union countries. The network aims to protect Europe's most valuable and threatened species and habitats, listed under both the Birds Directive and the Habitats Directive (European Commission 2015). Most past research has focused on tern colonies in North America and the UK (*e.g.* Suddaby & Ratcliffe 1997, Arnold *et al.* 2004, Mallory 2016) or Germany (Becker 1995, González-Solís *et al.* 2004, Braasch *et al.* 2009), while few studies on Arctic Terns have examined colonies in Northern latitudes such as Greenland or Svalbard (Syrová *et al.* 2020). To date there are relatively few papers investigating breeding success of terns in the Nordic countries such as Finland. We aimed to answer the following research questions: 1) What is the breeding (hatching and fledging) success of Arctic and Common Terns in a Natura 2000 site in West Finland, 2) is there a difference in breeding success and nest-site selection between the two tern species, 3) what are the factors influencing the breeding success of both species in relation to nest-site selection, and 4) how much does predation account for breeding failure?

2. Material and methods

2.1. Study site and species

This study was conducted during June 2023 on Hällgrund and Lillberget islands, Finland (thereafter Hällgrund islands, N 63° 38' 38" E 22° 25' 9"). This area supports 37 species that are protected under Natura 2000 (Natura 2000 ID: FI0800133), including 35 bird species and 2 mammals. The surface of the islands is 0.03 km² and covered by short vegetation and a small forest patch at the northern end. The weather during the study period was fairly stable (sea water level, air pressure) and no hard wind (<20m/s, average

4–7m/s), cold spells or heavy rain were recorded during the chick rearing period. Mean temperature in May 2023 was 7.0 °C (minimum –1.0 °C and maximum 19.3 °C) and in June 12.9 °C (minimum 1.5 °C and maximum 22.6 °C). The islands have been used by fishermen and hunters since the 18th century. Hällgrund and the surrounding archipelago belong to the Natura 2000 network and are protected according to the National Conservation Act (Anon 1993). The islands have been kept free of mink and raccoon dogs by local hunters since the 1990s (Wistbacka *et al.* 2006). An important predator on terns is the European Herring Gull (*Larus argentatus*, Burger & Lesser 1978, Hario 1994, Guillemette & Brousseau 2001). Predatory Herring Gulls are regularly expelled with a one-year delay by shooting them after detection of rings from predated tern chicks (Hario 1994) and have also selectively been culled in our study area to improve, *inter alia*, the breeding success of Lesser Black-Backed Gull (*Larus fuscus*; Wistbacka *et al.* 2022). During our study period there were 4 tern colonies on the two islands: 2 of them were mixed with both species present, one colony exclusively consisted of Common Terns (CT), and the other with only Arctic Terns (AT; Fig. 1). Both CT and AT are ground-nesting birds. Generally, the CT clutch size is 3 eggs (range of 1–4 eggs; Syrová *et al.* 2020) and 2 eggs for AT (1–3 with rare cases of 4; Syrová *et al.* 2020).

2.2. Nest location mapping and monitoring

An initial search and marking of tern nests with rocks and numbered wooden plates took place at the beginning of the field work (09. June 2023). We also recorded the GPS coordinates and several nest-site characteristics for each nest. Those included the total area covered by the colony (measured as the Minimum Convex Polygon (MCP) of all nest locations per colony), the distance to the colony center from each nest (measured as MCP centroid), the nest density per colony (*i.e.* number of nests/colony area), and the distance to predator nest sites (see section 3.4; see Table 1).

For the nest-site selection analysis we recorded the following habitat variables within 1 m² around the nest: percentage cover of

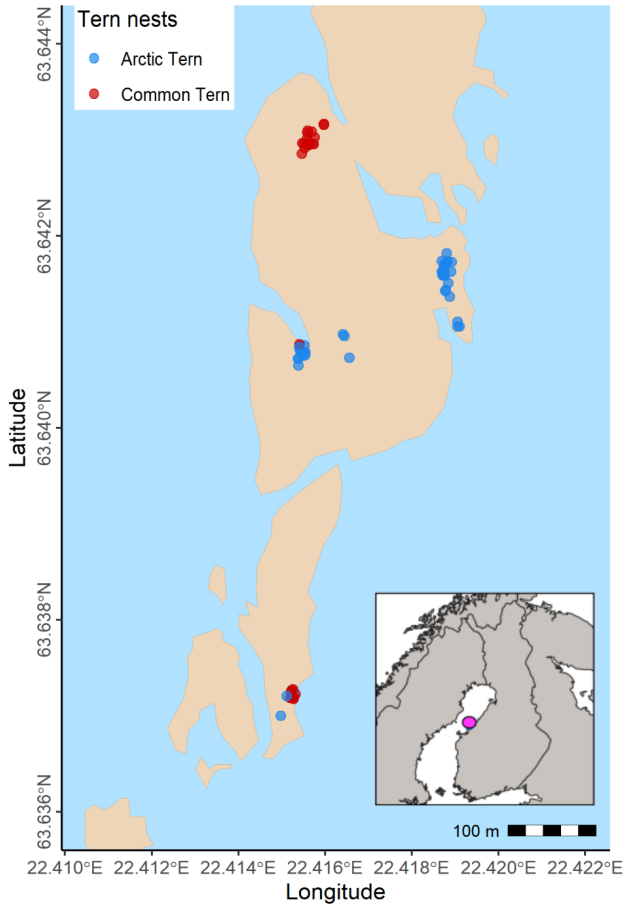


Fig. 1. Study area with Arctic and Common Tern nests. Hällgrund (North) and Lillberget (South) islands showing the 4 tern colonies with a purely Common Tern colony in the North (N=16 nests), a mixed colony in the South (N=15) and West (N=16; although dominated by Arctic Terns) and a purely Arctic Tern colony in the East (N=25). The small inset map shows the location of the study area (pink dot) on the West coast of Finland.

vegetation type (factor with 5 classes: no vegetation, bushes, forbs, grass, or moss and lichen), percentage cover of i) vegetation (regardless of the type), ii) rocks (larger than 10 cm), iii) pebbles (smaller than 10 cm and larger than sand), and iv) sand (Table 1). Those measurements were taken during the first nest visit. The vegetation around nests did not significantly change throughout the field season.

After the initial nest search and marking, every second day, the nests were visited to monitor different nest parameters: number of eggs; egg stage (*i.e.* visible cracks before hatching, cold eggs indicating egg failure); number of hatchlings. At the end of the field season, we then calculated per nest the hatching success (as the proportion of eggs that hatched), and fledgling success (as the number of chicks that reached the fledgling stage).

2.3. Predators and predation events

All colonies were observed from a distance every 1 to 3 days by 1 or 2 observers, during sessions of 30 minutes for the first week and then 120-minute observation sessions from 19 June to 30 June (survey effort was lower at the beginning as more time was needed for nest-site mapping and chick ringing activities). The observers were situated approximately 100 m from the colonies to minimize disruptions as advised by Mallory (2016). Using binoculars and scopes, we recorded the number of attempted or successful predation events per colony, visible defense attempts by adult terns, as well as other disturbances or activities in the colonies. A predation attack was marked as successful if the predator was seen flying off with an egg or chick. For the analysis we calculated the predation event rate (hereafter

Table 1. Nest site and nest position characteristics of monitored Arctic (*Sterna paradisaea*) and Common Tern (*S. hirundo*) nests at 4 colonies in western Finland, 2023. Mean and standard deviation (SD) are given for all 4 colonies together and separately (colonies North, East, West, South; see Fig. 1).

Variable	Mean \pm SD Total	Mean \pm SD North	Mean \pm SD East	Mean \pm SD West	Mean \pm SD South
Local nest-site habitat (1 m ² around nests)					
Vegetation %	48.75 \pm 25.49	50.00 \pm 22.51	51.80 \pm 22.86	25.00 \pm 18.97	67.67 \pm 20.6
Rocks %	48.54 \pm 28.53	50.00 \pm 22.51	48.20 \pm 22.86	75.00 \pm 18.97	19.33 \pm 24.19
Pebbles %	2.71 \pm 8.18	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	13.00 \pm 13.99
*Moss/lichen %	36.53 \pm 24.03	48.44 \pm 17.29	45.00 \pm 24.02	30.00 \pm 23.31	16.67 \pm 16.55
*Forbs %	28.89 \pm 23.26	15.00 \pm 10.80	22.20 \pm 21.70	46.25 \pm 26.55	36.33 \pm 18.75
*Grass %	30.21 \pm 21.57	31.88 \pm 20.16	24.80 \pm 21.33	20.31 \pm 16.78	48.00 \pm 18.30
*Bush %	4.86 \pm 11.29	5.94 \pm 11.86	8.00 \pm 14.65	3.44 \pm 8.70	0.00 \pm 0.00
Nest position in relation to colony and predatory gulls					
Distance center (m)	17.87 \pm 10.77	10.79 \pm 5.71	22.15 \pm 11.95	26.88 \pm 3.8	8.66 \pm 4.47
Nest density (nr/m ²)	0.044 \pm 0.03	0.05 \pm 0	0.04 \pm 0	0.01 \pm 0	0.09 \pm 0
Colony area (m ²)	682.78 \pm 466.97	354.33 \pm 0	707.89 \pm 0	1460.27 \pm 0	161.97 \pm 0
Distance predator (m)	106.67 \pm 51.44	51.19 \pm 10.26	173.25 \pm 9.94	75.30 \pm 14.20	88.34 \pm 2.34

* as proportion of the area that was covered by vegetation

predation rate) based on each predation event (*i.e.* successful and attempted predation). No predation events were recorded on eggs by avian predators. However, Otters (*Lutra lutra*), which can be potential egg predators, were observed on the islands but their impact could not be quantified. As part of the island gull monitoring, the location of nesting Herring Gulls—known to be the main predator of tern nests (Donehower *et al.* 2007; also R. Wistbacka, E. Degot & K. Kaasalainen 2023 unpubl.)—were mapped. From this we then calculated the distance to predatory gull nests from each tern nest.

2.4. Statistical analyses

All analyses were performed in R studio (R version 4.2.0, R Core Team 2022) with packages performance (version 0.10.2; Lüdecke *et al.* 2021), MASS (version 7.3.56; Venables and Ripley 2002), ggplot2 (version 3.4.2; Wickham 2016), and jtools (version 2.2.0; Long 2022).

We analyzed the hatching and fledging success for both AT and CT nests together. To answer our first research question, we calculated the hatching success as the number of eggs hatched divided by the total number of eggs per nest, while for the fledging success we used the number of fledged chicks per nest. To answer our second research question, we compared breeding success, and nest-site selection variables between the two species using generalized linear models (glm) with species as explanatory variable and hatching success, number of fledglings and the nest-site variables (Table 1) as dependent variables respectively.

To answer our third research question, we analysed the 2 response variables: hatching success and number of fledglings. To model the hatching success, we ran glm with a quasibinomial error structure. For modeling the number of fledglings, we fitted negative binomial models to account for excess zeros in the data (R function ‘glm.nb’ from package MASS). For both response variables, a global model was created that

contained predictors related to either the nest-site characteristics around the nest (Table 1A), or data on the nest's position within the colony (Table 1B). Prior to fitting the global models, we checked for collinearity between continuous explanatory variables and in case of Pearson correlation >0.5 we kept the variable with smaller p-value in a single predictor model (see Supplementary Material Fig. S1 and List S1). From the global models (*i.e.* after removing collinear variables), we performed a stepwise backward model selection by removing the variable with highest p-value at a time, until only (near-) significant terms were left in the models (*i.e.* $p < 0.1$ for $\alpha = 0.05$; see Supplementary Material List S2 for global models). We checked the model fit with regards to normality of residuals, outliers, overdispersion and homogeneity of variance (if applicable to the model type) and calculated the R^2 as a Goodness-of-Fit metric for each global as well as best model. For the quasibinomial models (hatching success), we calculated Tjur's R^2 (Tjur 2009) and for the negative binomial models (number of fledglings) we calculated Nagelkerke's R^2 (Nagelkerke 1991).

To answer our fourth research question, we calculated the expected number of predated tern chicks. We extrapolated predation rates to the entire chick rearing period using observed colony-specific and literature-based species-specific values. We used the following equation (Eq. 1) to perform the extrapolation:

$$\begin{aligned} \text{predated chicks} &= \text{hourly attack rate} & (1) \\ &\times \text{daily foraging hours} \times \text{chick period} \times \\ &\text{success rate} \end{aligned}$$

We calculated the expected average as well as minimum and maximum number of predated chicks per colony (as well as an average across the 4 colonies) using the following values for the terms in Eq. 1:

1. The hourly attack rate was based on our colony-specific observations (see results 3.4 and Supplementary Material Table S3)
2. Active foraging hours per day were based on the literature on European Herring Gulls (Van Donk *et al.* 2020) with an average of 18 hours per day. To allow for variation or uncertainty in those averages, we also used the minimum and maximum values on active hours with 12 and 24 hours per day respectively.
3. For the chick period we used an average period of 25 days across the two species (average CT: 25.5 days, AT: 24.5 days) with a minimum and maximum of 20.5 and 29.5 days respectively (Robinson 2005)
4. The success rate (*i.e.* calculated as the number of successful predations divided by the number of predation events) was based on our colony-specific observations (see results in section 3.4, and Supplementary Material Table S3).

Table 2. Breeding success of Common and Arctic Terns in Western Finland, 2023. Total number (#) of nests, average number of eggs per nest, total number of eggs, number of hatchlings, hatchling success (HS) and fledgling success (FS) rates per colony. CT = Common Tern, AT = Arctic Tern.

Colony	Species	# nests	Mean # eggs	Total # eggs	# hatched	HS %	FS %
North	CT	16	2.9	46	32	70	0
East	AT	25	1.8	45	35	78	0
West	AT + CT	16	1.9	30	14	47	0
South	CT + AT	15	2.6	39	30	77	47
	Total	72	2.3	160	111	69	12

3. Results

3.1. Breeding success and species differences

In total, we found and monitored 72 CT and AT nests during June and July 2023. There were 4 colonies in total: 3 on Hällgrund and 1 on Lillberget (Fig. 1). The average number of nests per colony was 18, with the Eastern colony being the largest with 25 nests. The average (mean \pm SD) number of eggs per nest was 2.3 ± 0.6 (CT: 2.8 ± 0.42 ; AT: 1.9 ± 0.46), of which on average 1.5 ± 1.01 (CT: 2 ± 1.1 ; AT: 1.3 ± 0.8) per nest hatched, resulting in an overall hatching success of 69% (Table 2). CT had significantly more eggs per nest than AT (glm poisson, $b = 0.402 \pm 0.158$

SE, $z = 2.542$, $p = 0.011$; Supplementary Material Fig. S2), while the hatching success did not differ between the species (glm quasibinomial, $b = 0.183 \pm 0.446$ SE, $t = 0.409$, $p = 0.684$). Only 14 chicks reached fledgling stage, while the other 97 hatched chicks did not survive (overall fledgling success: 12%). Since most of those fledglings were CT, the number of fledglings differed significantly between species (glm.nb, $b = 1.751 \pm 0.756$, $z = 2.318$, $p = 0.0205$; Supplementary Material Fig. S2). All 14 fledglings were from the Southern colony, while the other 3 colonies did not produce any fledglings (Table 2). More detailed descriptions of the breeding monitoring by colony can be found in the Supplementary Material (Section S2).

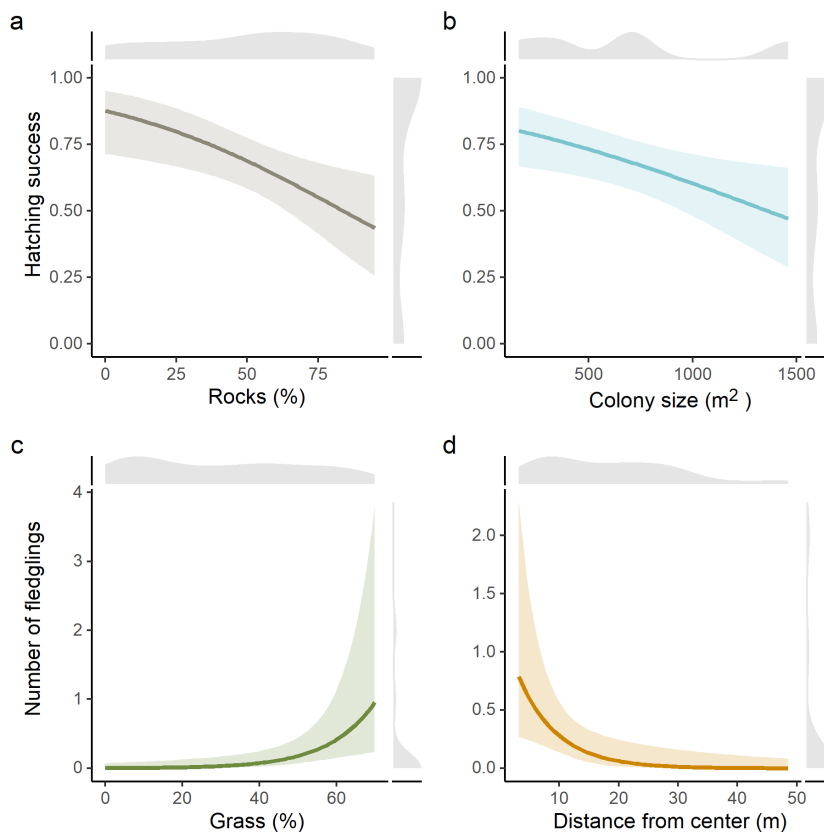


Fig. 2. Model-based regressions between the breeding success (proportion of hatched eggs per nest in a & b, and number of fledglings in c & d) and a) the percentage of rock cover within 1 m² around the nests, b) the colony area in m² measured as the MCP of all nest locations per colony, c) the percentage of grass around the nests, and d) the mean distance from the colony center to each nest. Solid lines are the model estimates, shaded areas the 95% CI and the gray shaded areas at the top and right sides of the plots are the density distributions of the raw data.

3.2. Hatching success

After removing collinear variables (Supplementary Material Fig. S1, List S1), the best model for the small-scale nest-site habitat variables included only percentage of rocks, which had a significant negative influence on the hatching success ($b = -0.666 \pm 0.243$ SE, $t = -2.735$, $p = 0.008$; Tjur's $R^2 = 14.6$; Fig. 2a). In other words, a 1 standard deviation (SD) increase in rock cover was related to a reduction in hatching success by approximately 0.7. The other variables had non-significant effects (see Supplementary Material Table S1A for the global model output). Note that rock and vegetation cover were highly negatively collinear (Pearson coefficient = -0.96), meaning that vegetation cover has an equally strong but positive effect on hatching success.

After dropping collinear variables, the best model for the nest position variables included only the colony area, which had a significant negative effect (estimate \pm SE = -0.544 ± 0.216 , $t = -2.513$; $p = 0.014$; Tjur's $R^2 = 3.0$; Fig. 2b). Colony area is strongly negatively collinear with nest density (Pearson coefficient = -0.87), so that colonies with smaller area and higher nest densities had a higher hatching success per nest. Other variables had non-significant effects in the global model (Supplementary Material Table S1B).

3.3. Number of fledglings

The best model for the small-scale nest-site habitat variables included percentages of grass, forbs and rock cover, where grass and forb cover had a significant positive effect (grass: $b = 1.818 \pm 0.658$ SE, $t = 2.763$, $p = 0.006$; Fig. 2c; forbs: $b = 1.149 \pm 0.556$ SE, $t = 2.067$, $p = 0.039$) and rocks a significant negative influence ($b = -0.700 \pm 0.352$ SE, $t = -1.991$, $p = 0.046$) on the number of fledglings per nest (Nagelkerke's $R^2 = 62.6$). Those effects suggest that a 1 SD increase in grass or forb cover is associated with an increase of approximately 1.8 or 1.1 fledglings respectively, whereas 1 SD increase in rock cover, reduces the number of fledglings by approximately 0.7. Again, note that rock and vegetation cover were highly negatively collinear (Pearson

coefficient = -0.96), meaning that vegetation cover has an equally strong but opposite effect on fledgling success. Note that the percentage of bushes was dropped from the global model due to bad model performance related to generally low percentages of this variable in our data. See global model results in Supplementary Material Table S2A.

The best model for the nest position variables included only the distance from the colony center, which had a significant negative effect ($b = -1.631 \pm 0.636$ SE, $t = -2.562$; $p = 0.010$; Fig. 2d; Nagelkerke's $R^2 = 31.9$), indicating that nests located closer to the colony center had a higher fledgling success (Supplementary Material Table S2B). Note that colony area was dropped from the global model due to bad model performance of this variable.

3.4. Predation rate

In total 65 predation attempts (*i.e.* attempted and successful attacks) were recorded during an observation time of 43.35 hours resulting in an overall attack rate of 1.4 attacks per hour (colony North: 30 predation events, 1.85 attacks/h; colony East: 3 predation events, 0.4/h; colony West: 17 predation events, 1.47/h; colony South: 15 predation events, 1.88/h). Of the total 65 attacks only 6 (9.2%) were successful (2 in colony North, 1 in colony East, 3 in colony West and 0 in colony South; Fig. 3a; Table S3). Adult terns defended against 52% of the attacks (34 in total; 15 in colony North, 1 in colony East, 9 in colony West and 9 in colony South), which was in proportion to the rate of attacks (Pearson correlation attack and defense rate = 0.98; Fig. 3a; Table S3). European Herring Gulls enacted 88% of the attacks, with only 8 attacks potentially from other species (Mew Gull *Larus canus*, Lesser Black-backed Gull, Parasitic Jaeger *Stercorarius parasiticus*, and Ruddy Turnstone *Arenaria interpres*). All successful predations were done by European Herring Gulls and were observed on chicks only, *i.e.* no direct predation on eggs were observed. However, in total 5 eggs disappeared and 1 was found broken during our field season.

From the extrapolation calculations, we found that across the 4 colonies, the number of expected

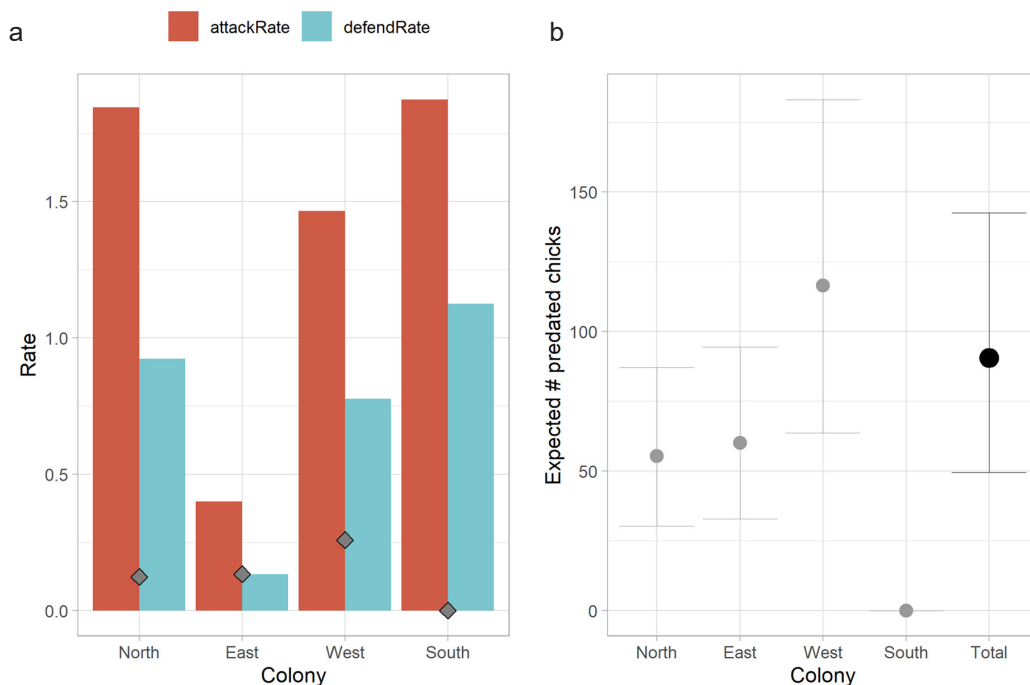


Fig. 3. a) Rates of attacks by predators (red bars) and defensive behavior by terns (blue) calculated as absolute numbers observed per hour for each colony. The gray squares indicate the rate of successful predations (number of observed successful predations per hour). b) Extrapolated expected numbers of predated tern chicks during the hatchling stage per colony and in total (*i.e.* across the 4 colonies). Points indicate average expected numbers while error bars present minimum to maximum value ranges.

predated tern chicks across the entire chick period (*i.e.* before fledging) was on average 91, *i.e.* 81% of the total 111 counted chicks (colony North: 55, *i.e.* >100%, East: 60, *i.e.* >100%, West: 116; *i.e.* >100%, South: 0; *i.e.* 0%) with a minimum of 50 (North: 30, East: 33, West: 64, South: 0) and a maximum of 143 (North: 87, East: 94, West: 183, South: 0; see Fig. 3b).

4. Discussion

In this study, we investigated the breeding success of Arctic and Common Tern colonies breeding on a Natura 2000 island in West Finland and investigated the biotic and abiotic factors influencing the breeding success. We found that the hatching success was fairly high while all except 1 colony showed a total loss during the chick stage. In terms of nest-site variables, the percentage of rock cover as well as the type of vegetation played a

significant role in explaining varying hatching or fledging success, while colonies with lower nest density (*i.e.* larger colony area) and nests farther from the colony center experienced lower breeding success. Predation played a major role during the chick stage with European Herring Gulls being the main predator.

On average, the tern nests had 2.2 eggs/nest which was expected from the literature describing clutch sizes of 1–3 (AT) or 1–4 (CT) eggs per nest (Syróvá *et al.* 2020). Mean hatching rate was only 1.5 eggs/nest resulting in a hatching success of 69%, which is in line with earlier findings too (Nisbet & Welton 1984, Monaghan *et al.* 1989). Worryingly, the 3 colonies located on Hällgrund experienced a total failure in fledging success while only the Southern colony recruited 14 chicks, resulting in an overall fledging success of 12% (fledged chicks per hatched egg) or 0.19 fledglings per breeding pair for the 4 colonies. This is substantially lower than figures from

the earlier literature (~ 0.94 for AT; Monaghan *et al.* 1989 or ~ 1.2 for CT; Nisbet & Welton 1984) and slightly lower compared to earlier years of tern colony monitoring on Hällgrund islands (mean fledglings/pair in earlier years: 0.23, Supplementary Material Table S4 and Fig. S3). The fact that only the colony in the South produced fledglings leading to a fledging success of 47% is striking and can be related to several factors. First, this was the smallest colony in terms of occupied colony area, with a concomitant highest nest density and thus shortest distance to the colony center from the nests (Table 1). With regards to nest-site habitat, nests in the Southern colony generally had more grass and thus less rocks (Table 1) and based on field observations, the terrain of this colony's location was flatter with less cliffs and slopes as compared to the other 3 colonies. Although the predator attack rate was not different from other colonies, the number of times terns successfully defended their nests was highest and hence, no successful predations were observed (see further below). Taken together, it seems apparent that a colony with higher nest density, higher nest centrality, more vegetation and a better defense rate leads to higher breeding success (Becker 1995, Whittam 1997, Buehler *et al.* 2017).

In terms of species differences, CT recruited 11 fledglings while only 3 chicks survived to fledgling stage in AT. This can be due to differing nest-site characteristics and thus potential lower predation pressure or increased nest defense in CT (see below). Earlier studies did not find a difference in breeding success (*e.g.* Chapdelaine *et al.* 1985) or nest defense behavior (Lemmettyinen 1971) between the two tern species and thus, our reported differences might be more related to nest-site and colony conditions rather than species differences. Indeed, colonies dominated by CT (*i.e.* colony North and South) generally had nests with higher centrality (shorter distance to colony center), higher nest density and smaller colony areas than AT colonies (*i.e.* colony East and West; Table 1)—all related to higher breeding success (Austin 1940, Becker 1995). In relation to earlier reports of tern breeding success on Hällgrund islands (see Supplementary Material Table S4 and Fig. S3), AT did not seem to have lower fledgling success compared CT (Fig. S3b),

and sometimes even fared better than CT or mixed tern colonies. Most of those years where AT had a higher number of fledglings recruited per pair, no predatory European Herring Gull was found in the vicinity of the AT colony which likely explains the higher breeding success (Supplementary Material Table S4).

Nest-sites were generally characterized by a mix of rocks and vegetation (Whittam & Leonard 1999), where CT nests were surrounded by higher proportions of grass and forbs and thus fewer rocks than AT nests—a pattern that has similarly been evidenced before (Robinson *et al.* 2001). Indeed, several studies discussed the preference for nest-sites with less vegetation cover by AT compared to other tern species (Hawksley 1957) and that this preference might be related to wing and tarsus length limiting the ability to move in dense vegetation (Hawksley 1957, Courtney & Blokpoel 1983). We show that nests surrounded by higher vegetation cover had up to 50% higher hatching success and nests with more grass or forbs recruited more fledglings, which can be explained by increased nest-concealment against predators (Buehler *et al.* 2017) or improved microclimatic conditions (Kim & Monaghan 2005). We also found a correlation between the colony area, nest density, and nest distance to colony center, with over 50% lower breeding (hatching and fledging) success for nests in colonies with lower nest density (and thus larger colony area) and those located closer to the colony periphery than the center. This corresponds to earlier descriptions of tern colonies, where smaller colonies (with a higher nest density) were more resilient against depredation (Austin 1940). This finding is also reflected in the Southern colony of our study, which produced fledglings and had the highest nest density and smallest colony area. A higher nest density creates more protection for nests closer to the center, at the expense of those at the periphery (Becker 1995).

We observed a fairly high number of predation events during the chick stage ($N=65$), although the number of successful predations was relatively small ($N=6$) and no predation on eggs were observed. Earlier results also suggest that chicks are predated more often than eggs (Becker 1995), which could partly be explained by a lower nest attendance by parents after hatching (Becker

1995, Robinson & Hamer 1998), especially so for AT (Robinson *et al.* 2001) which, as shown here, had a lower breeding success than CT. Since nests surrounded by more vegetation (especially grass and forbs) recruited more fledglings, we could infer that those nests were better protected from predators as has also been suggested earlier (Burger & Lesser 1978) and could partly explain the successful production of fledglings in the Southern colony. We did observe a significant difference in vegetation around the nests between the two species: CT preferred greater grass coverage around the nests than AT which is in line with earlier findings (*e.g.* Langham 1968).

European Herring Gulls were the main predator, as already observed previously (Becker 1995, Guillemette & Brousseau 2001). However, Sea Eagles (*Haliaeetus albicilla*) and Otters (*Lutra lutra*) were also seen on the island and could play a potential role as tern nest predators even if no observations were made. Only predation events of Sea Eagles on Herring Gulls were observed. Sea Eagles could theoretically attack terns, although such occurrences are quite rare (Sulkava *et al.* 1997), and predation by Otters on Arctic terns were also recorded earlier (Shannon & Thurgate 2014). In addition, neighboring smaller gull colonies such as Black-Headed Gulls (*Chroicocephalus ridibundus*) or Mew Gulls, or even Lesser Black-Backed Gulls, could attract predatory Gulls such as European Herring Gulls in the vicinity of tern colonies and make them secondary prey targets. Notably, many fewer Black-Headed and Mew Gulls were found around the successful Southern colony as compared to the other tern colonies, further supporting this assumption.

In total, 97 out of 111 tern chicks died, while our extrapolation of expected number of chicks predated during the entire chick period was 50–143 (average 91). This implies that, given that our assumed numbers for the terms in Eq. 1 are realistic, almost all chick losses were due to predation. But given that in our extrapolation we assumed a constant predation pressure throughout the chick period (*i.e.* no increase or decrease due to *e.g.* higher or lower food demand for nesting gulls), it might well be that less than the predicted 91 chicks were lost due to predation but also to other causes. Certainly, our extrapolated number of predated chicks are rather rough and limited

to several assumptions and should thus be interpreted with this caveat in mind. There were some dead chicks found in the nests that died due to infestation by ants (N=6), or due to unknown reasons. Furthermore, in the Northern colony a case of intraspecific killing was observed, where an incubating tern attacked and presumably killed a chick from a neighboring nest that had strayed too close. Other factors affecting chick survival can be lack or shortage of food provided by the parents (Monaghan *et al.* 1989), or adverse weather conditions (Scopel & Diamond 2018). The latter factor might not have been influential in this particular breeding season as the weather was mostly stable without rain, storms, or heavy sea level fluctuations.

Assuming that predation accounts for ~94% of chick mortality, reducing the impact of predation would likely increase the breeding success of Common, and especially Arctic Terns significantly—which has been shown in other parts of the world too (Scopel & Diamond 2017). AT seem to struggle more in repelling predatory Herring Gulls (Scopel & Diamond 2017) and given that this is the main predator in this area, predator control would likely benefit this species particularly. In addition, Arctic Terns are regionally threatened (RT) in 4 different zones (Hyvärinen *et al.* 2019), indicating that the species requires special attention in Fennoscandia in order to maintain stable populations. One solution to do so is to control the gull population on the islands as has been done successfully in the South of Finland with the American Mink (Nordström *et al.* 2003). Archipelago areas in Finland that are within Natura 2000 areas and are not affected by introduced predators (mink, raccoon dog) ought to be hot spots for breeding archipelago birds. However, on Hällgrund predatory European Herring Gulls hinder this for many species. Apart from our study species the Lesser Black-backed Gull (EN), Mew Gull (LC), Black-Headed Gull (VU), Ruddy Turnstone (EN), Common Redshank (*Tringa totanus*, NT) and the Tufted Duck (*Aythya Fuligula*, EN) are all seriously affected by Herring Gull predation (Red List status from Hyvärinen *et al.* 2019). Thus, targeted culling of predatory Herring Gulls is a method for enhancing populations of archipelago birds without affecting the population of

the also vulnerable European Herring Gull (VU). Selective removal of predators has been shown to be an efficient way of reducing predation on regionally endangered Lesser Black-Backed Gull (Hyvärinen *et al.* 2019) chicks in Southern Finland (Hario 1994; Hario & Rintala 2016) and to be equally effective as large-scale random culling of European Herring Gulls (Hario *et al.* 2009). Thus, selective removal of predators would be preferable both in terms of money and effort required and also for the conservation of European Herring Gulls, which are classified as Vulnerable in Finland due to long-term population decline (Ministry of the Environment & Finnish Environment Institute 2019), although the local population in the study area has been increasing (Wistbacka 2024 unpubl.).

In conclusion, our study demonstrates that one of the most important factors impacting the breeding success of tern colonies in a Natura 2000 site is predation by European Herring Gulls. Nest-site selection and colony factors also influence hatching and fledging success and are probably indirect responses to predation pressure. To enhance the breeding success in tern populations, regulation of predators (Nordström *et al.* 2003, Scopel & Diamond 2018) or creating wood shelters around nests (Burness & Morris 1992) can be potential solutions.

Effekter av predationstryck och boplatsval på häckningsframgången hos tärnor i en finländsk skärgård

Att studera och kvantifiera arters reproduktionsframgång kan bidra till att förstå populationstrender och ge vägledning för bevarandet. Här studerade vi häckningsframgången hos silvertärna (*Sterna paradisaea*) och fisktärna (*Sterna hirundo*) i kolonier på ett Natura 2000-område i Västra Finlands skärgård för att förstå vilka faktorer relaterade till boplatsval och predationstryck som bäst förklarar häckningsframgång. Vi övervakade 72 tärnbon i 4 kolonier och observerade dem under standardiserade övervakningssessioner för att registrera predatorangrepp på tärnbon. Vi körde generaliserade linjära modeller för att bestämma vilka faktorer som påverkar häckningsframgång (antal

kläckta och flygga ungar). Kläckningsframgången var hög i alla 4 kolonier med 69% av äggen som kläcktes, medan framgången för flygga ungar var låg, där endast 1 koloni producerade 14 flygfärdiga ungar medan alla andra kolonier hade noll överlevande ungar (totalt 12% blev flygga). När det gäller boplatsval visar våra resultat att en större andel vegetationsskydd ökar häckningsframgången, troligen genom bättre bo-kamouflage mot rovdjur. Bon i mindre kolonier med högre botäthet och belägna närmare kolonicentrum producerade också fler kläckta ungar och flygga ungar. De flesta predatorangrepp skedde troligtvis under ungstadiet, medan vår extrapolering förutspådde att predation står för minst 94% av alla ungförluster, vilket tyder på att rovdjurskontroll skulle kunna förbättra häckningsframgången hos tärnkolonier i Västra Finland avsevärt.

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Online supplementary material

Supplementary material available in the online version of the article includes extended data analysis description, detailed description of colony monitoring, and extended results with Figures S1–S3, Lists S1–S2, and Tables S1–S4