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Interactions between white-tailed eagle *Haliaeetus albicilla*, seabirds and tourism;
how the breeding success of the endangered black-legged kittiwake *Rissa tridactyla* is affected

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Acknowledgements

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Abstract

In many seabird colonies along the coast of Norway, the increased population of white-tailed eagle *Haliaeetus albicilla* and the growing industry of birdwatching tourism are causing a dilemma for management decisions. Thus, this study aimed to examine the indirect effect of white-tailed eagles and tourists on the breeding success of the endangered seabird species, black legged kittiwake *Rissa tridactyla* in the bird cliffs at Hornøya Island. By investigating kittiwakes' escape response (the number of empty/abandoned nests) provoked by eagle disturbance, as an indirect top-down effect on egg survival by facilitating nest predation by crows, ravens and/or larger gulls, we examined this indirect effect by asking three questions: (1) *Is the escape response among kittiwakes stronger when white-tailed eagle is present?* (2) *Is the escape response independent of nest location or are the nests in the periphery of the study plot more frequently abandoned (testing the diluting hypothesis – safety in numbers)?* (3) *Is there a negative relationship between disturbance and egg survival?* The data used to answer these questions, were collected by Reconyx Hyper Fire time-laps cameras deployed in two test plots (plot A and B), where plot A was located in a non-disturbed sheltered area of the cliff and plot B was installed next to a tourist trail. In each plot a sample set of n=30 active kittiwake nests was made. Number of eggs were counted, in addition to number of white-tailed eagles in the area. The number of tourists were provided by the local business of birdwatching tourism with a total number of 220 tourists visiting the study area in May and June. By fitting generalised linear mixed-effect models the results showed that the escape response was stronger when white-tailed eagle was present, with a much stronger response in plot B. Moreover, it was likely a diluting effect in plot B, as the nests in the periphery were more frequently abandoned, and the distance between abandoned nests were much smaller than in plot A. Nevertheless, a trend found in the data indicates that high frequency of escape response may have a risk effect of limiting egg survival, thus affecting the breeding success of black-legged kittiwake. Lastly, we discuss potential factors causing the differences found in escape response between and within the study plots and the application of time-laps cameras as a non-intrusive tool in long-term monitoring of interactions between kittiwakes, white-tailed eagles, nest predators and tourists in a seabird colony.

Key words: escape response, indirect predatory effects, egg predation, breeding success, black-legged kittiwake, white-tailed eagle, *Rissa tridactyla*, *Haliaeetus albicilla*

Contents

Introduction

The abundance of black-legged kittiwake *Rissa tridactyla* along the Norwegian mainland has declined much (6-8% annually) from about 280 000 pairs in 1980 to 82 000 pairs in 2013 and is still causing concern (Dehnhard et al. 2021, Fauchald et al. 2015). As a result, the black-legged kittiwake (from now on only called kittiwake) is currently categorized as an endangered species (Artsdatabanken 2021). Although the declining trend is similar in nearly all kittiwake colonies, dynamic differences in yearly variation between them may indicate that their circumstances during the breeding season (and not in the shared winter-areas) is a likely important factor explaining this population decrease (CAFF 2020). The underlying mechanisms behind this decline are not well understood, yet a combination of bottom-up (resource limitation) and top-down (predation) effects are plausible explanations. It is believed that bottom-up effects are only explaining half of the decline, however the extent that may be explained by top-down effects is still not quantified (Dehnhard et al. 2021).

Top-down effects may be mediated directly or indirectly (e.g., Begon et al. 2014). Direct effects arise when predation leads to direct mortality of individuals by consumption (Begon et al. 2014). Whereas indirect predatory effects include predator-induced changes in behaviour and physiology that may negatively affect the prey's birth rate (Travers et al. 2010). The white-tailed eagle *Haliaeetus albicilla* is an example of a predator with potential to add extra pressure on the declining kittiwake population (Dehnhard et al. 2021). In terms of indirect predatory effects, white-tailed eagles may disturb incubation or chick rearing adult birds in the breeding season, causing nesting parents to abandon eggs/chicks and thus leaving them vulnerable to predation from other predators (Hipfner et al. 2012). Disturbance may provoke antipredator responses among kittiwakes such as the behaviour of escaping their nests to avoid direct predation. Consequently, a facilitation of nest predators such raven *Corvus corax*, hooded crow *Corvus cornix,* great black-backed gull *Larus marinus* and herring gull *Larus argentatus* may negatively affect the survival of eggs and chicks (Hipfner et al. 2012). Thus, it is believed that several years of disruption by white-tailed eagle is a major contributing factor, explaining the several ensuing years of unsuccessful breeding in many kittiwake colonies in Norway (Anker-Nilssen 2010; Anker-Nilssen & Aarvak 2006).

Kittiwake and seabirds in general have relatively long lifespan (up to 28 years; Coulson 2011), mature late and produce few offsprings (e.g., Begon et al. 2014). As a result, kittiwakes may drop reproduction in years of unfavourable conditions such as low food

availability and significant disturbance by predators or humans during the breeding season (Jacobsen et al. 1995). During spring and summer kittiwakes breed mostly in sub-arctic and arctic colonies on steep sea- and coastal cliffs (Coulson 2011). Coulson (2011) has suggested that a kittiwake colony is a series of small interlinking groups, where breeding kittiwakes appear to respond only to neighbouring pairs within a radius of 3-5 meters. When autumn arrives, most of the Norwegian kittiwake colonies leave their established nesting spots to forage across wintering grounds in the North-West Atlantic Ocean (CAFF 2020). Like other seagulls, kittiwakes are limited to only catch prey species within the top metre of the water surface (Coulson 2011). The kittiwake population, adjacent to the southern Barents Sea in northern Norway, feed mostly on capelin *Mallotus villosus*, but may shift to herring *Clupea harengus L.* in years when capelin is scarce (Barrett et al. 2007). Consequently, abiotic factors such as severe storms may feedback to kittiwakes' food availability by making prey species move deeper into the sea to avoid the disturbed bodies of water (Baird 1990).

The lack of breeding success and recruitment of fledglings has shown to be an important factor determining kittiwake population dynamics in the most northern bird colony in Norway (Hornøya; Reiertsen et al. 2013). The population dynamic of kittiwake may be explained by alterations in food accessibility because of local prey depletion, e.g., fisheries ripple effects of capelin stock collapses (Gjøsæter et al. 2009) and/or environmental induced fluctuations in prey availability (Oro et al. 2004). In non-breeding areas the bottom-up effect of prey density has shown to affect adult kittiwake survival (Reiertsen et al. 2014). Short-term fluctuations in prey availability are also likely to have an impact on kittiwakes' breeding conditions (Suryan et al. 2002). Another plausible mechanism behind the reduced survival of eggs, fledglings, and adults in seabird species, may be predation. The abundance of predatory birds such as the white-tailed eagle has increased much the past five decades due to conservation measures taken in 1968 (e.g., Heggøy & Øien 2014).

White-tailed eagle belongs to the opportunistic raptor family *Accipitridae* and is one of the largest bird species in Europe (weight: 4.1-6.9 kg, wingspan: 2.0-2.4 m) (Grant et al. 2011). Their distribution span from the northern Palaearctic and Scandinavia to central and southeast Europe, and central and northern Asia, in addition to some isolated populations that exist in southwest Greenland, northeast Ireland and western Scotland (Nadjafzadeh 2011). Nevertheless, the largest population in Europe are distributed across Norway (Myklebust 2020). The white-tailed eagle has a diverse diet that commonly consists of fish, birds, and mammals, including scavenging of carcasses (Sulkava et al. 1997, Sandor et al. 2015).

Due to their dietary flexibility, the population are not usually limited by food scarcity (Sandor et al. 2015). Local feeding niche may vary with availability of food, which determines the niche width at the individual level – indicating that some individuals may still specialize if a resident prey species is locally abundant, despite a broad generalist diet of the species, e.g., some eagle-individuals may be more specialised to hunt for marine birds in cliffs where they are abundant (Nadjafzadeh et al. 2016). As a result of conservation measures taken in Europe since 1934, the population of white-tailed eagle have increased in northern and central Europe is no longer under threat and is considered viable (Artsdatabanken 2021). In the period between 1970-1990 around 1 500 breeding pairs were estimated in Norway (Schimmings & Øien 2015; Gjershaug et al. 1994). By 2002 the population had grown to 1900-2200 pairs, and as the numbers continued to increase, it was estimated to 2008-4200 pairs in the years 2012-2013 (Schimmings & Øien 2015; Heggøy & Øien 2014). The population in southern Norway is still increasing, however, the abundance of eagles in northern Norway appears to have flattened out in recent years (Heggøy & Øien 2014).

The re-establishment of the white-tailed eagle population has had indirect negative effects on survival of eggs and fledgelings of several seabird species breeding along the Norwegian coast (Anker-Nilsen 2009). Yet, the current knowledge of interactions between white-tailed eagle and seabirds, and eagles' indirect effect on the breeding success of seabirds, is still inadequate to underpin future decision making. It is documented that white-tailed eagles have a negative influence on breeding seabirds in the north-eastern Pacific, the north-western Atlantic and in northern Europe (Hipfner et al. 2012). Seabirds may be directly affected by eagle predation on adults and fledglings (DeGange & Nelson 1982; Hayward & Stout 1977) and indirectly by altered behaviour caused by the apparent fear of predation attacks (antipredator responses) that also may increase the level of stress, a risk effect in which it may lead to reduced fitness and survival of individuals (Creel 2011; Creel & Christianson 2008; Harfenist & Ydenberg 1995). Risk effects are the costs of the behaviour to avoid predation, which reduce the risk of being attacked or killed as pray (Creel 2011). When for example breeding individuals of kittiwake alter their behaviour (flushing - abandoning their nest) in response to an approaching eagle, the escape responses are expected to carry costs. Despite absence of direct predation, risk effects by antipredator responses can still be large, because they may reduce reproduction rather than survival and are therefore easily mistaken for limitation by food supply (Creel & Christianson 2008). Meta-analysis on predator-prey interactions has shown that the impact of intimidation can be at least as strong as direct

consumption (Preisser et al. 2005). On top of that, the risk of egg-predation by corvids and large gulls may increase when breeding individuals flush away from their nest, leaving eggs and fledglings unprotected (Galusha & Hayward 2002; Parrish & Paine 1996).

Frequent disturbance by white-tailed eagle has the potential to bring additional costs to reproduction through antipredator responses, e.g., strong antipredator responses may influence whether breeding kittiwakes drop and delay reproduction. Antipredator responses allow animals to alter their behaviour to changing predator densities, in turn affecting the direct effect of predation (Ives & Dobson 1987). Yet, the mortality by direct predation in seabird populations is usually not high enough to affect population growth rate (Hipfner et al. 2012). On the other hand, indirect risk-effects deriving from interactions with white-tailed eagle, may negatively impact the population growth rate in case of several years of reproduction failure. Thus, as predatory, and bottom-up effects of food supply may act additive or synergistic on seabird demography and population dynamics, it is important to document these effects.

Human activities such as bird watching may also affect breeding seabirds (Ellenberg et al. 2007, Lorentsen & Follestad 2014). Birdwatching tourism is a growing business globally and as well as in Norway (e.g., Balmford et al. 2015). It is often alleged that this type of tourism provides a preventive effect to eagle disruption in bird cliffs, despite little documentation underpins these claims (e.g., Hentati-Sundberg et al. 2021). One of the theories of why kittiwakes have an increasing tendency to breed in urban areas is to avoid predation and disturbance by white-tailed eagles, which facilitates the question whether human activity may decrease the effect of white-tailed eagle (Anker- Nilssen & Aarvak 2009). However, tourism in and around seabird colonies is not without consequences for the seabirds, since disturbances by tourist traffic close to nesting seabirds (e.g., guillemot) are documented to have a negative effect on the survival of the chicks (Reiertsen et al. 2018). Although Reiertsen and colleagues (2018) did not find a negative effect on kittiwakes.

When a kittiwake pair have settled in a bird cliff to breed the predation risk may vary between nest sites, thus differences in antipredator response of the individuals in a colony may occur (Massaro et al. 2001). A Canadian study from Gull Island, Newfoundland, found that nests of black-legged kittiwake were more likely to be attacked in plots with fewer nests, compared to plots with higher nest density, and were more frequently visited by great black-backed gulls and herring gulls, with less likeliness to fledge young (Massaro et al. 2001).

Massaro and colleagues (2001) also found that the size of sub colonies and nest density affect the survival of kittiwake offsprings and that nest location relative to the cliffs' upper edges was significantly affected by the risk of gull predation.

The selfish herd theory postulates that individuals within a population attempt to reduce their predation risk by putting other conspecifics between themselves and predators (Hamilton 1971). According to the dilution effect hypothesis the individual risk of being the victim to predation attacks gets smaller by being one of many in a larger group (Foster & Treherne 1981). Thus, it is reasonable to ask whether the most beneficial nest sites may possibly be occupied by individuals of highest quality, and that there might be a diluting effect within the colony, in turn forcing individuals of lower fitness to settle in the most exposed cliffs of the seabird colony (Mooring & Hart 1992, Schmidt & Ostfeld 2001). Therefore, nesting in the centre of a colony consisting of many individuals, where the density of birds is highest, may be a way to "dilute" the risk of being attacked, as low densities are often linked to low fitness (Stokes & Boersma 2000).

Because the knowledge of the role predation plays on seabirds' antipredator responses is poor, this study aimed to document and quantify the indirect effect of white-tailed eagle presence on the breeding success of black-legged kittiwake by monitoring the escape responses of adult pairs, i.e., temporary abandonment of their nests, by the use of time-laps cameras. We investigated whether kittiwake's escape response, provoked by white-tailed eagle presence, affected egg survival by facilitating predation from ravens and large gulls, and whether the response varied within two plots (areas with and without tourism) and between the centre and edge of the study plots.

To examine this indirect effect, we asked three main questions: (1) is the escape response among kittiwakes stronger when white-tailed eagles are present, (2) is the escape response independent of nest location or are the nests in the periphery of the study plot more frequently abandoned (a test of the diluting hypothesis – safety in numbers), and finally (3) is there a negative relationship between disturbance and egg survival. During the study period we also counted the daily occurrence of white-tailed eagles in proximity to Hornøya, to provide an estimate of the size of the local population.

Material and method

Study area and species

The study was carried out between May 20th and June 11th in 2020 at Hornøya, a Norwegian island of a cliff-dominated habitat with a diverse composition of seabird species (Fig. 1). The island is located in northeastern Finnmark, adjacent to the southern Barents Sea, a rich marine ecosystem, which makes up the right conditions for several seabird species to establish colonies, such as black-legged kittiwake, common guillemot *Uria aalge*, Brünnich guillemot *Uria lomvia*, European shag *Phalacrocorax aristotelis*, razorbill *Alca torda*, and Atlantic puffin *Fratercula arctica* (Sigler et al. 2012). Additionally, the fairly large gull species herring gull and great black-backed gull occur as ground breeders in grass dominated habitat at the top and eastern side of the island. Occasionally, species of the *Corvidae* family such as raven and hooded crow are observed among the marine birds.

Figure 1. Location of the study area, Hornøya, in the eastern- and northernmost municipality of Norway, Vardø.

Due to the rich composition of seabirds, Hornøya Island has become a popular destination for birdwatching tourists and photographers. Between 1500 – 1900 birdwatching tourists visit Hornøya annually (Reiertsen et al. 2018). The island used to be dominated by kittiwakes, and in the early 1980s, 21 000 nesting couples were registered. Today the population is slightly between 3000 – 4000 nesting pairs (Reiertsen, unpubl.). In recent years, observations of large numbers of white-tailed eagles have been documented in 2012, 2018 and 2019, with numbers varying between 30 – 46 (Reiertsen, unpubl.). It has also previously been observed that seabird species breeding openly and not in underground holes, have been disturbed by eagles such that nests and other breeding spots in the cliffs get abandoned. The combination of seabird species (e.g., kittiwake), large gulls, ravens, crows, and white-tailed eagles are object to complex multispecies interactions, where the input of anthropogenic influence from tourism adds another factor which may further complicate the interactions (Fig. 2).
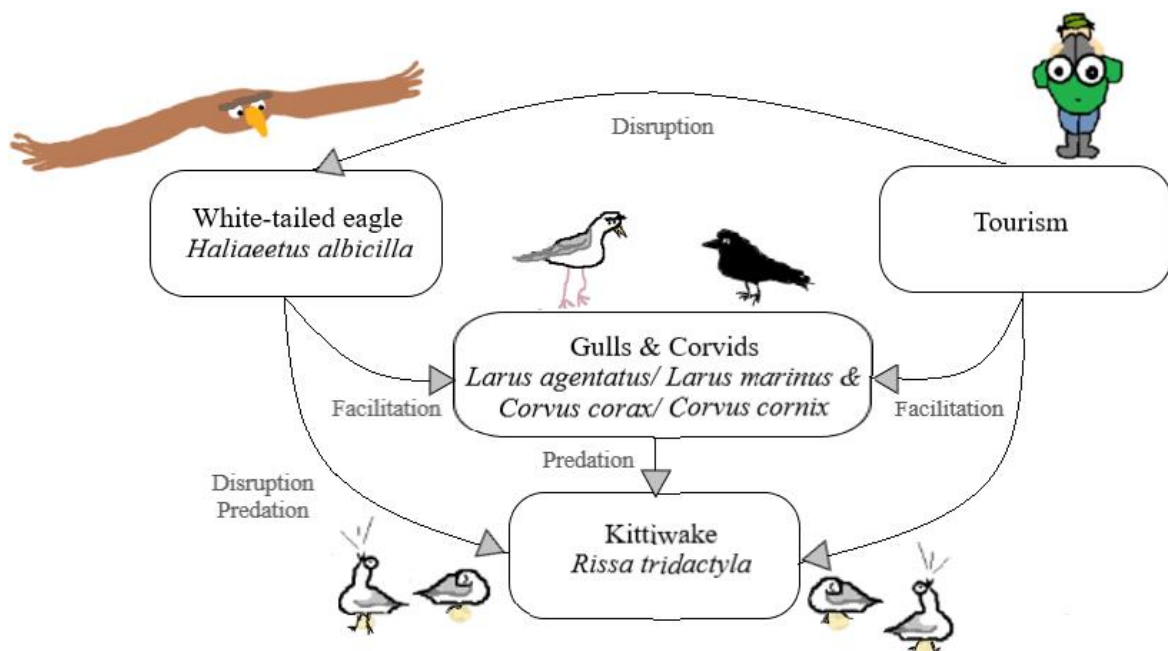

Figure 2. The conceptual model illustrating the potential effects of white-tailed eagle and tourism on black-legged kittiwake, by facilitating predation on kittiwake eggs by corvids and gulls, as well as disrupting breeding individuals of this endangered species.

Study design

This project was based on a nested design, consisting of the following hierarchical levels: area (Hornøya Island), plot (A and B – where tourism was only allowed by plot B), and sample period. Each plot had a sample size of n=30 active nests with breeding kittiwake pairs, whereas data was extracted from three sample periods (see Appendix, Fig. A1 for illustration of the study design). Altogether, four fixed time-laps cameras (Reconyx HyperFire) were applied to document the escape response (temporary abandonment of nest by both parents) of the kittiwake pairs in our sample (De Pascalis et al. 2018) (Fig. 3).

Figure 3. Deployment of the second time-laps camera for plot A prior to the data collection.

For each of the two plots, two time-laps cameras were deployed (referred to as the main- and the second time-laps camera). Whereas the main time-laps camera covered the kittiwake sample (n =30) within its picture frame and documented nest escapes (see Fig. 4), the second time-laps camera was mainly installed to capture eagle- and raven observations beyond the picture-frame of the main camera, that possibly generated perturbation (provoked kittiwakes to escape their nest) within our sample of adult kittiwake pairs. The two plots were selected with respect to topography that allowed camera installation, whereas the nests were randomly selected. The time-laps cameras were installed to take pictures every 10th second for 15 days (May 28th-June 10th). The midnight sun made it possible to take relatively good pictures 24 hours each day.
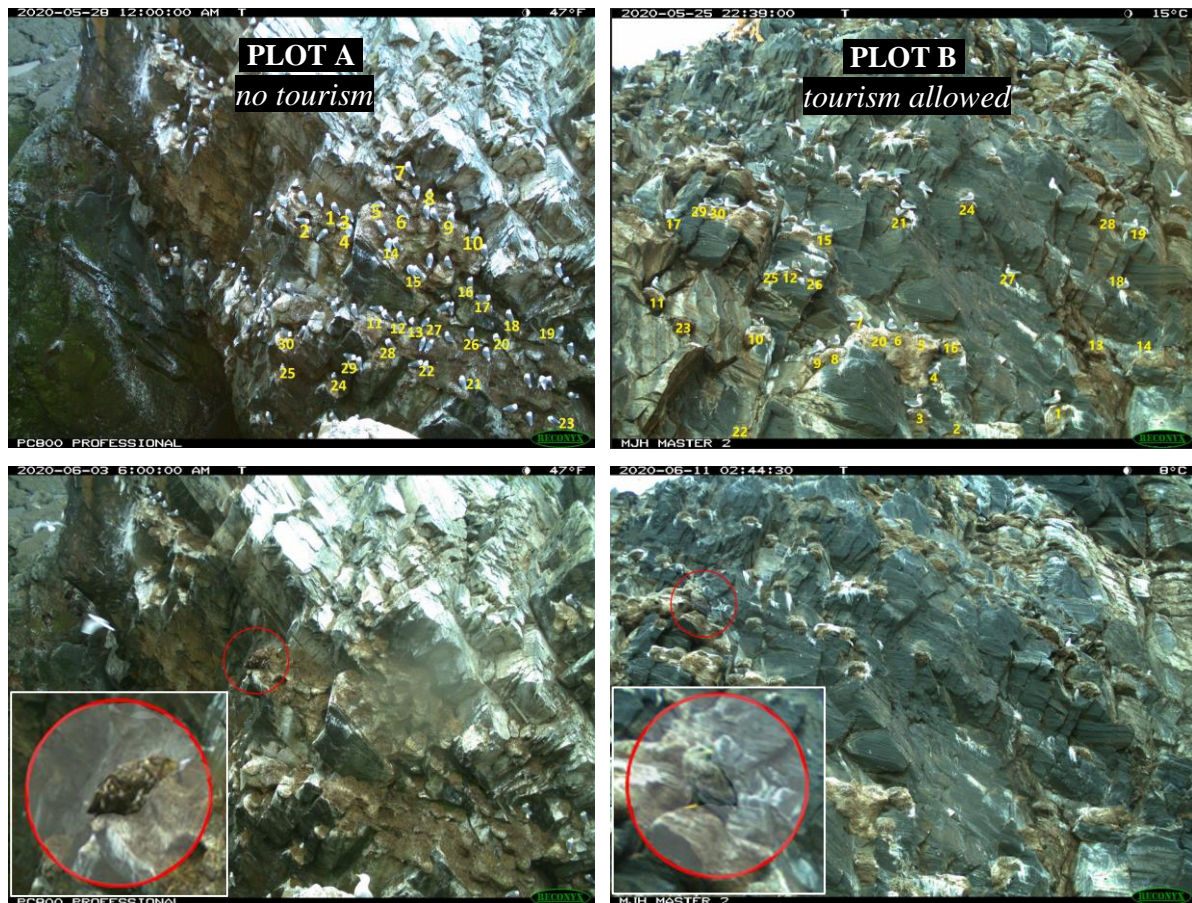
Figure 4. Pictures taken by the main time-laps camera. The upper panel shows the numeration of the sample (n=30 – active nests with breeding kittiwake pairs) at both plot A *no tourism* (left) and B *tourism allowed* (right). The lower panel illustrate a situation from each plot where white-tailed eagle is present (sitting within the red circles). Most of the numbered kittiwake pairs from the upper panel have escaped in the lower panel.

The dates May 28th, June 3rd and June 10th were randomly selected for plot A. The same dates were selected for plot B but due to camera problems June 3rd, June 4th were selected instead. The picture material from the sample periods was visually inspected when punching the raw data, containing the following parameters: date, time, plot, eagle observations, eagle activity (flying and sitting), raven observations, kittiwake absence (the proportion of abandoned nests within the sample of n=30). Counting kittiwakes, eagles and ravens in each picture is time consuming and to reduce the processing of data, I selected three random days, and every 10th picture with an interval of 1 minute and 40 seconds between each snapshot.

During the review of imagery, each of the 30 selected nests at each plot got the value 0 or 1, based on the absence or presence of the specific kittiwake pair per picture. Thus, in cases where at least one kittiwake was present at the nest, the observation got classified as present by the value 1. Observations of white-tailed eagles and ravens were also categorized as absent

or present by 0 or 1 when they were observed within the picture frame of either the main- or the second time-laps cameras. Furthermore, the eagle observations were categorized in sitting (1) or flying (2) eagles, because the escape response among kittiwakes may be different regarding the eagle activity.

Due to the time-laps cameras limitations regarding range and time, we assumed that false negative observations, i.e., observations indicating absence, despite actually presence, when no eagles nor ravens were documented by the time laps cameras, may occur in the data. First, false negatives can be explained by the limited coverage of the picture frame and angle of the time-laps cameras which excludes birds that are flying/sitting out of reach. Secondly, the coarse aggregation of pictures in time (1 min. and 40 sec.) risks concealing white-tailed eagles and ravens. Moreover, we may assume that the distance between an eagle and the kittiwakes is another important factor with potential to influence the strength of kittiwakes' escape response (Jiang & Møller 2017).

To get a measure of breeding success we planned to count the number of eggs in each nest within the sample at plot A and B once a day during the study period, with help from camera observations. Due to the topography, distance to nests and angle of camera, the eggs could not be counted by camera observations as planned. Therefore, the eggs were manually counted. To avoid disruption of breeding seabirds we limited the counting to three times at each plot, respectively 6th, 8th and 10th of June at location A and 6th, 8th and 11th of June at location B. The last visit to the study plot and last egg status were reported by June 30th.

To get an indication of the number and activity of white-tailed eagles flying or sitting in proximity to Hornøya Island, eagle individuals were manually counted four times a day (morning, noon, afternoon and evening) from an observation point at the top of the island with an overview of most of the western side, during the whole study period (May 20th-June 11th, 2020). The eagles were counted from the same viewpoints every day. We noted the location of where each eagle was observed, if they were flying or sitting, and attempted to determine their age. We counted 72 times over 23 days.

Statistical analysis

Count data, such as number of empty nests, that are collected from snapshots of short time intervals, like in this study (1 minute and 40 seconds), are typically zero-inflated and temporally autocorrelated (see Appendix, Fig. A3). To account for this, we fitted generalised linear mixed-effect models (glmm's) to the data, with time treated as AR1 (1st order autoregressive) model and sampling day as a random intercept. The general form of the fixed effect part of the model is:

$g(\mu) = \eta = \alpha + \beta1WTEagles + \beta2Plot + \beta3WTEagles*Plot + \varepsilon$

Where g(.) is the link function, which transforms the expectation of the response variable to the linear predictor, μ is the expected value of the response (number of empty nests), η is the linear predictor, α and β are parameters to be estimated, WTEagles is presence/absence of white-tailed eagles, Plot is plot (A and B) and ε is the residuals that are assumed to be independent and identically distributed $N(0,\sigma^2)$. First, a glmm poisson model was fitted to the data but due to overdispersion (OD=10), a negative binomial glmm (nb.glmm) was fitted to the data; OD for the nb.glmm was ca. 1.

Because the study lacks a fully factorial design, in which the observations of flying (n=17, only observed at location B) and sitting eagles (n=350) were not evenly distributed between the two plots, the flying eagle observations were removed from the data before fitting the models. However, prior to the removal of the "flying eagle" data, we tested if there was a difference between flying (n=17) and sitting (n=95) eagles at plot B and sitting eagles generated a significant stronger escape response than flying eagles (p < 0.05).

To examine the escape response in each plot we estimated the mean "distance to centre" (D2C) and the mean "distance to nearest neighbour" (D2NN) of the empty nests and tested if these estimates differed from random "nest departure". To test for potential differences between observed and random "nest departure" in plot A and B, we randomly draw *n* "nests" at time step *t* (total number of time steps = 2592), where *n* is the observed number of empty nests at time step *t*, and repeated this procedure 1000 times thereby allowing calculation of 1000 differences between random and observed "nest departures". If the 95% confidence intervals (95%CI) of this distribution with respect to D2C and D2NN overlapped zero, there was no difference of random "nest departure". If the 95%CI of the D2C was significantly lower (negative) than zero, the nests in the periphery were more frequently abandoned than

nests closer to the centre and vice versa. If the D2NN was significantly lower than zero, the distance to nearest neighbour was greater than if nests were abandoned randomly and vice versa. The spatial position of each nest, needed to calculate D2C and D2NN, was derived from the pictures of the upper panel in Fig. 3 for both plot A and B.

The significance level (α) of all analysis was set to 0.05. All statistical analysis and graphic visualization of data were done by using the open-source software R. The graphics were produced by using the function *ggplot* and *ggarrange* available from the R-packages *tidyverse* (Wickham et al. 2019) and *ggpubr* (Kassambara 2020). The glmm's were fitted using the glmmTMB package (Magnusson et al. 2021). The conceptual models (Fig. 2 and Fig. A1) were illustrated in the Microsoft software, *Paint 3D*.

Results

Data material extracted from the time-laps cameras

We extracted a total of 5184 observations from 2592 pictures per plot A and B, hence 864 pictures per sample period (day). The data material was summarized by date and plot, showing the number of present kittiwake pairs (total/percentage), the number of present white-tailed eagles (total), the number of eggs (total), and the number of tourists (total per month) provided by the local business engaged with bird watching tourism in Vardø (Tab. 1).

Table 1. Summary statistics of data collected in plots A and B in May-June 2020. NA implies no data was collected.

Date	Plot	#Total kittiwake pairs present (%)	#White-tailed eagles	#Egg	#Tourists (per month)
28.may	A	25 158 (97,06%)	0	NA	0
03.jun	A	25 238 (97,37%)	20	NA	0
06.jun	A	NA	NA	23	0
08.jun	A	NA	NA	20	0
10.jun	A	24 057 (92,81%)	235	19	0
11.jun	A	NA	NA	NA	0
30.jun	A	NA	NA	0	0
28.may	B	20 868 (80,51%)	35	NA	32
04.jun	B	22 477 (86,72%)	55	NA	188
06.jun	B	NA	NA	25	188
08.jun	B	NA	NA	38	188
10.jun	B	24 795 (95,66%)	22	NA	188
11.jun	B	NA	NA	40	188
30.jun	B	NA	NA	0	188

The data material has more observations of white-tailed eagles in plot A, than plot B, with respectively 255 (all sitting) and 112 (95 sitting/ 17 flying) (Tab. 2).

Table 2. The table shows the total number of absent (no) and present (yes) white-tailed eagle observations in plot A and B, and whether the eagles were flying or sitting.

Plot	A		B	
Eagle	No	Yes	No	Yes
#observations	2337	255 (all sitting)	2480	112 (17 flying)

Furthermore, the data were used to visualize diurnal variation in escape response of kittiwake pairs (number of empty nests) in plot A and B (left y-axis, blue/orange lines) in relation to observations of sitting white-tailed eagles (right y-axis, black lines), over the course of the three sample periods (Fig. 5). Moreover, there were too few or no observations of raven and larger gulls in the study plots, to include these species in the analysis.
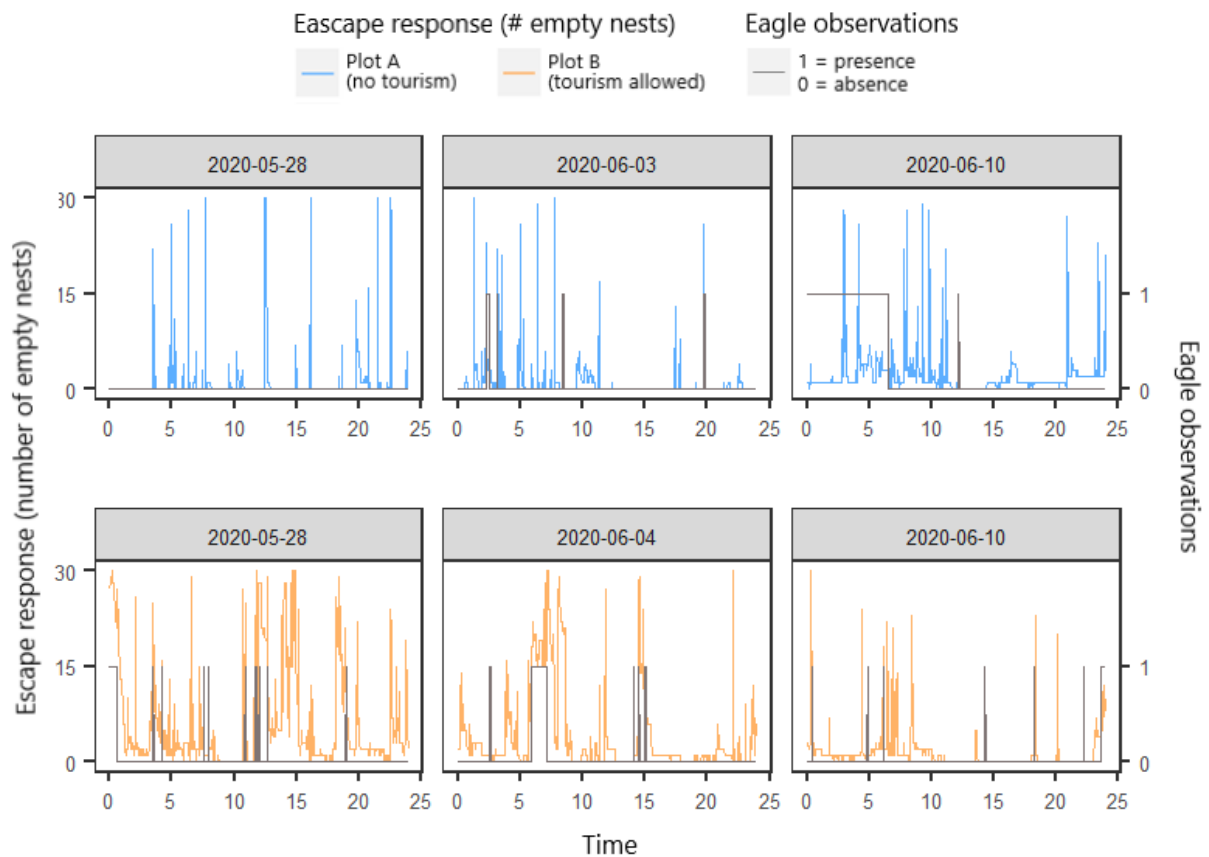

Figure 5. Diurnal variation in number of empty nests (left y-axis) in the two plots, A (blue lines) and B (orange lines), during the three sample periods (May 28th, June 3rd /4th, and 10th) at Hornøya Island in 2020. The dark lines (right y-axis, 0 = absence or 1 = presence) illustrate when sitting white-tailed eagle was observed. The observations have a time resolution of 100 seconds.

The distribution of the escape response frequency was skewed and were illustrated by histograms showing the differences between the plots (see Appendix, Fig. A2).

(1) Is the escape response among kittiwakes stronger when white-tailed eagle is present?

The escape response among kittiwakes differed significantly, indicating that it was stronger when white-tailed eagle was present (p < 0.001), compared to observations when eagles were absent (see Fig. 6 and Tab. 6).
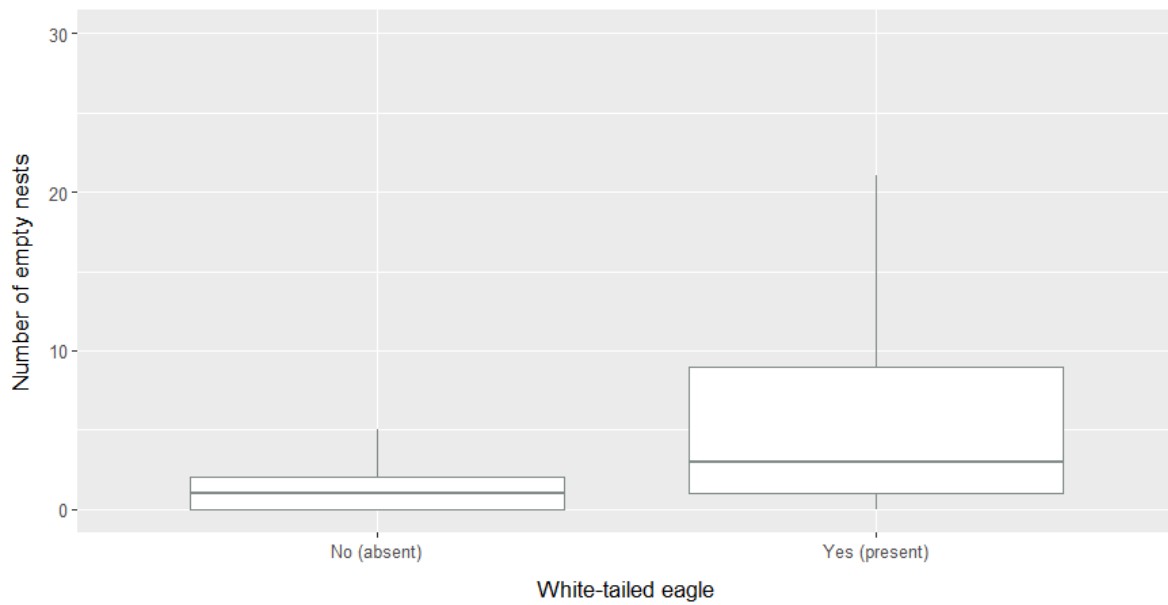

Figure 6. Escape response of kittiwakes, in terms of number of empty nests, as a function of absence and presence of white-tailed eagles. The boxplot illustrates the median and interquartile range.

Also, the response was significantly stronger in plot B compared to plot A (p<0.001) (Tab. 3).

Table 3. The model summary shows the estimate, standard error, z-value and p-value of the parameters, Plot and WTEagles, and includes only significant results.

Parameter	Estimate	Std. Error	Z value	Pr(>|z|)
Intercept	-0.5805	0.1991	-2.916	**
Plot B	1.0855	0.0495	21.928	***
WTEagles	1.4667	0.1242	11.811	***
Plot B * WTEagles	0.2346	0.2292	1.024	

Significance levels: "***" = p < 0.001, "**" = p < 0.01, "*" = p < 0.05, "." = p < 0.1

The model residuals in sampling time declined relatively fast and was relatively uncorrelated after 5 minutes with a lag of 1 minute and 40 seconds (See Appendix, Fig. A3).

(2) Is the escape response independent of nest location or are the nests in the periphery of the study plot more frequently abandoned? (a test of the diluting hypothesis – safety in numbers)

The result of testing for differences in escape responses between individuals nesting in the centre or in the periphery of the study plots, shows a large difference between plot A and B. A significant difference was found between observed and random escape response in mean D2C in plot B (lower left panel) and mean D2NN in plot A (upper right panel), whereas no difference was found in mean D2C in plot A (upper left panel) and in mean D2NN in plot B (lower right panel) (Fig. 7). In plot B, the escape response was significantly higher in the peripheral nests than those in the center of the sample, and the mean distance between the abandoned nests were not significantly larger than random escape response. In plot A, the escape response seemed to be smaller in the peripheral nests than the nests close to the centre, although this was not a significant result. However, the distance between abandoned nest in plot A were significantly larger than random escape response.
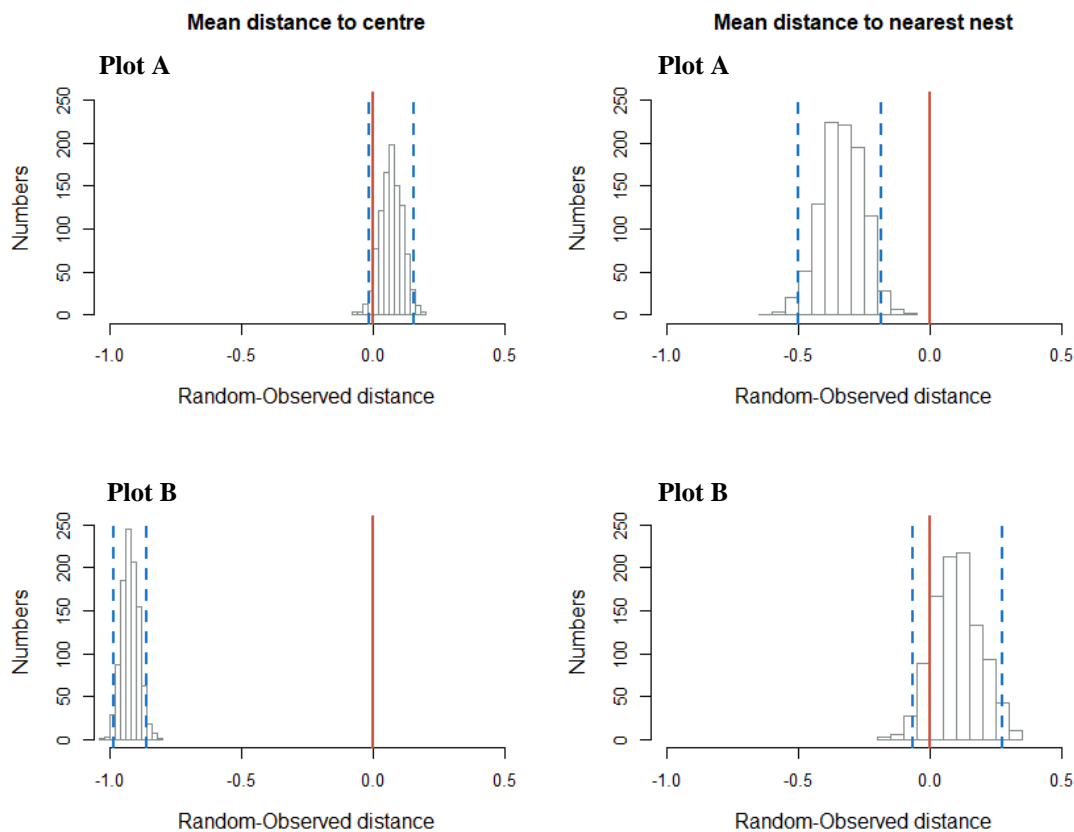

Figure 7. Difference in mean distance to centre (D2C) and distance to nearest neighbor in plot A (upper panels) and B (lower panels) between random and observed nest escapement. The red line illustrates no difference, and the blue dotted lines represent the 95% confidence interval (CI) of the differences estimated by 1000 bootstrapping replicates of nest escapements (see methods for details).

(3) Is there a negative relationship between disturbance and egg survival?

The graphic visualizations (Fig. 8) display that there might be a negative relationship between disturbance and egg survival, as the number of eggs decreased when the mean escape response increased in plot A, and contrary in plot B where the number of eggs increased when the mean escape response decreased. Rregardless of eagle observations, the mean escape response, varied both over time and between the two plots (Fig. 8, left panel). The mean escape response was stronger in plot B (tourism allowed) and decreased over time in contradiction to plot A, where the mean escape response was weaker but had an increasing trend. Moreover, the number of eggs per sampling day increased over time in plot A, while it decreased in plot B (Fig. 8, right panel). The result was the same in both plots with an egg loss of 100% by June 30th.
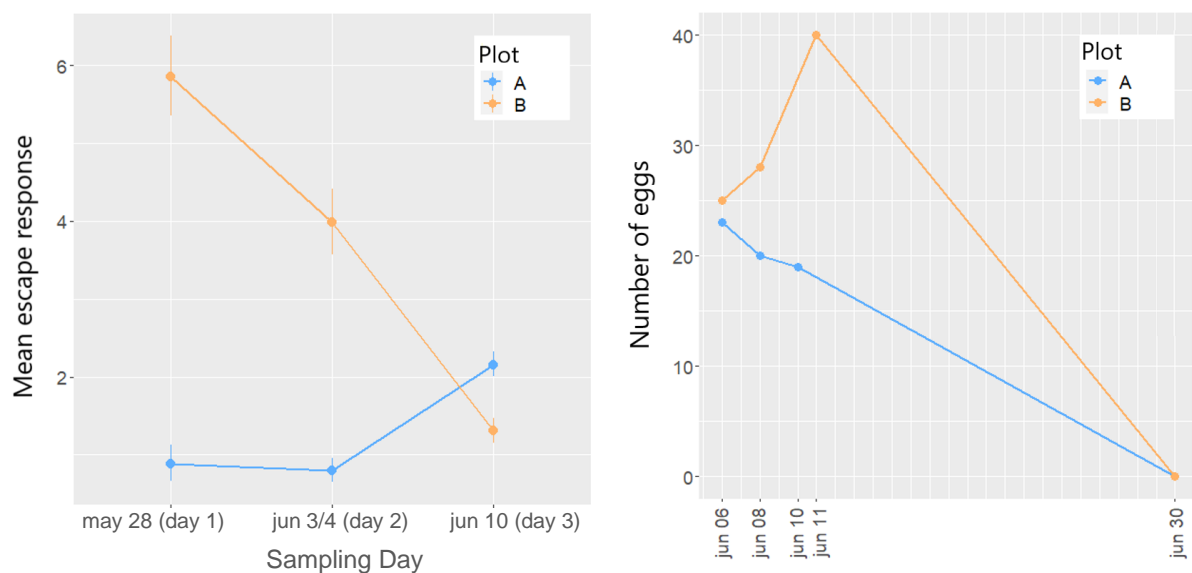

Figure 8. The left plot illustrates the mean of nest escapes per sampling day, and the plot to the right visualize the breeding success by number of eggs in the sample for each plot A (blue line) and B (orange line).

The result of fitting the negative binomial model for testing the effect of day in each plot, and comparing the response between the three days, showed that there was a significant response in day 1 ($p < 0.001$) and day 3 ($p < 0.001$) in plot A. Whereas the response was only significant at Day 3 ($p < 0.01$) in plot B (Tab. 4).

Table 4. Model summary of each plot A (upper panel) and plot B (lower panel), showing the response when accounting for the parameter Day, providing estimate, standard error, z-value and p-value for only significant results.

Plot A

Parameter	Estimate	Std. Error	Z value	Pr(>|z|)
Intercept	-3.2809	0.4818	-6.810	***
Day 2	0.2333	0.6525	0.358	
Day 3	3.1919	0.6403	4.985	***
Number of observations: 2592				

Plot B

Parameter	Estimate	Std. Error	Z value	Pr(>|z|)
Intercept	0.9128	0.6095	1.498	
Day 2	-0.6906	0.8617	-0.801	
Day 3	-2.1910	0.8691	-2.521	*
Number of observations: 2575				

Significance levels: "***" = p < 0.001, "**" = p < 0.01, "*" = p < 0.05, "." = p < 0.1

Estimate of the local white-tailed eagle population during the study period at Hornøya

The daily counting of eagles in the area indicates that the local eagle population near Hornøya consists of at least 30 individuals (see Appendix, Tab. A1). On average the eagles are more often observed sitting than flying (see Appendix, Tab. A2). In the end of the study period, we were left with the impression that most of the white-tailed eagle population consisted of immatures and that one or two couples were adults. No nests were detected in the area. The majority of the observed eagle individuals were determined as immatures (4 years or younger), and it was never observed more than two individuals older than 6 years during one counting event, although the total count of eagles of 6 years or older were 12 (see Appendix, Tab. A3).

Discussion

The results show that the escape response among kittiwakes were stronger when white-tailed eagle was present, with a much stronger response in plot B, where tourism was allowed, than in plot A. The plots had also different internal differences, when comparing the escape response between nests in the periphery and nests closer to the centre. There was also found a trend in plot A which indicates that eagle disturbance may be negatively linked to egg survival. Nevertheless, the breeding failed in both plots.

During the study period there were ca. 30 white-tailed eagles observed in the study area each day. Apparently, this abundance was high enough to have an indirect predatory effect on kittiwakes breeding success by generating high frequency of escape responses. When a white-tailed eagle approaches a seabird colony and provoke intimidation, it is likely to generate perturbation of the colony in shape of an altered behavioural response. In scenarios of high predator abundance, potential prey must balance between the risk of being eaten and the risk of losing fitness due to loss of eggs by egg predation (Creel 2011). When kittiwakes get disrupted by an eagle, and respond by abandoning their nest, eggs will be left without any protection and nest predators such as crows, ravens and large gulls, will get free access to predate (Massaro et al. 2001, Anker-Nilsen 2009, Hipfner et al. 2012). As previous studies have suggested such escape responses has in turn potential consequences for the breeding success if frequently displayed (Hipfner et al. 2012). Although we did not directly observe ravens predate on kittiwake eggs, a few ravens (ca. 4-6) were sporadically observed during the study period. According to the local Norwegian Nature Inspectorate in Vardø, the raven population near Hornøya was hunted during the past winter (conversation during fieldwork in June 2020). Compared to the previous season prior to the study season (in 2019) the raven population were allegedly estimated to about 30 individuals.

Since the escape response was stronger in plot B compared to plot A, local conditions, and heterogeneity between different areas in the bird cliff are likely to affect the results. The difference in response between the two plots may be related to differences in topography; plot A lays in a canyon, whereas plot B was more exposed. The bird cliff in plot A was facing another ca. 5 meter away and differed from the bird cliff in plot B as this cliff was easier accessible and faced the tourist trail by the shore. Such variations in bird cliff formation may affect the eagles manoeuvring possibilities differently. With a wingspan of ca. two meters,

white-tailed eagles are likely to have difficulties with quick manoeuvring between narrow cliff formations (Grant et al. 2011).

In plot B the kittiwake pairs nesting by in the periphery responded significantly stronger than those nesting closer to the centre of the study plot. Although no significant difference was found in plot A, the response was slightly stronger among the kittiwake pairs in the centre in this plot. One explanation may be that the kittiwake pairs in the periphery in plot A were less exposed compared to those nesting in the periphery in plot B. In plot B the distance between the abandoned nests were smaller than random, whereas it was significantly larger in plot A. The larger distance between neighbouring kittiwake pairs, the less connected may the escape response be (Coulson 2011). Thus, the relatively small distance (higher connectedness) between the abandoned nests in plot B may also explain why the escape response were stronger here.

Why kittiwakes in a colony do not respond equally to predators, may be due to different predation risk regarding their spatial nest position within the colony, as one of the strategies to reduce predation-risk, according to the selfish herd theory, is to keep other conspecifics between themselves and predators (Hamilton 1971). Thus, as previous studies have shown that nests close to the edges of a kittiwake colony are more exposed to nest predation by corvids and gulls with implications for survival of recruits (e.g., Massaro et al. 2001), it is likely that nest sites closer to the centre of the colony are more beneficial for breeding success. Differences in escape response might also be an indication of individual differences in kittiwakes' fitness, since one explanation may be that low quality individuals or younger individuals may be forced to nest in less quality areas (Schmidt & Ostfeld 2001). The kittiwake's predation risk may not be the same for all individuals and may be reflected as differences in how often escape responses were displayed.

Although aggregative behaviour in marine birds is commonly attributed avoiding predation pressure, other studies (e.g., Clode 1993) suggest that colonial nesting might rather be a result of utilisation of dispersed and unpredictable prey species, than ensuring safety in numbers. Clode (1993) argued that such aggregation leads to increased vulnerability to predation, rather than being a strategy adopted to combat it. Like for other marine predators, search time in food acquisition have often high energetic costs for kittiwakes (Williams et al. 2004, Enstipp et al. 2007, Stephens & Krebs 1986). Therefore, settlement at locations close to rich resources, e.g., the Barents Sea, where prey concentrations persist throughout the spring and

summer is commonly regarded as beneficial for marine birds (Sigler et al. 2012). However, because individuals of colonial birds that establish nests in the edges of the colony are likely to be less connected to neighbouring pairs and possibly more exposed, there is a chance that when disrupted, the escape response may be different between individuals nesting in the middle of a colony compared to individuals nesting by the edges (Coulson 2011).

Besides topography and nest location, disruption by tourists passing by plot B may also be a possible explanation of why the escape response was higher in this plot. However, in a recent study it is discussed that tourists may limit the presence of white-tailed eagle by human presence near seabird colonies (e.g., Hentati-Sundberg et al. 2021), but this was on another seabird species (common guillemot). An interesting field observation to mention was that we unintentionally caused short term behavioural cascading effects by disrupting white-tailed eagles when moving around the bird cliffs; by encountering eagles sitting in the cliffs, in turn making them fly away, which lead to big flushings of kittiwakes. If tourists encounter eagles sitting close to a seabird colony, we might expect a similar cascading effect, whereas the presence of tourists may lead to increased frequency of escape responses because the eagles are forced to fly more frequently between places to sit. Despite the suggestion of Hentati-Sundberg and colleagues (2021), that tourism has a preventive effect on breeding failure of common guillemots by reducing disturbance of white-tailed eagles, the risk of tourisms' negative effects on seabirds breeding success consists.

Weather the white-tailed eagles were sitting or flying, is also likely to affect the data, in which the kittiwakes display escape responses or not. A significant difference between the response to sitting or flying eagles was found in plot B, where the kittiwakes responded stronger to sitting than flying eagles. Thus, it is likely to think there might be a difference in plot A as well, although the response to sitting and flying eagles might not necessary be the same as for plot B. Our results also indicated that the distance between eagles and the kittiwakes may influence the behaviour of kittiwakes. Because most animals keep a safe distance to potential predators, trade-offs are usually forced between foraging and other critical behaviours against flight with potential negative consequences for population trends if energy budgets are consistently negative (e.g., Jiang & Møller 2017).

It's not surprising that increased escape response, due to disturbance by white-tailed eagle, is negatively linked to egg survival; a more recent study showed that kittiwakes' nest escapement gives access to nest predators (De Pascalis et al. 2018). Given the strong escape response during the study period, it is likely that the disturbance by white-tailed eagles may be an important factor explaining the breeding failure of the kittiwakes in both plots. Such disturbances that provoke kittiwakes to leave their nests are likely to result in high rates of nest predation. One of the time-laps cameras documented a sequence of an egg stealing raven jumping from nest to nest after the kittiwakes had been disturbed. This event of nest predation by raven was discovered during review of imagery and highlights the possibility that egg predation by raven is a likely important link in eagles' indirect effect on kittiwakes breeding success. Yet the hunting measures the previous season causing the low numbers of ravens, did not seem to affect the breeding success of the kittiwakes in any of our plots, since the last visit to the study plots reported that none of the eggs in the sample had survived. However, large gulls were likely to be an important egg predator contributing to the kittiwakes' breeding failure this study season, as several factors indicating poor food availability were reported this year (e.g., diet-samples from kittiwakes showed a dominance of krill *Euphausiacea* – an indication of capelin scarcity which are shown to be an important food source for successful recruitment of kittiwakes and the other large gull species (Reiertsen, unpubl.)).

Ideally, the number of eggs should have been counted at least once a day to get a better measure of breeding success. However, the eggs were only counted three times, because of the kittiwakes' late egg laying, this study's shortage in time, and with respect to limiting our own disturbance of the birds. Anyways, the fact that the kittiwakes started to breed late this season is a factor difficult to plan for. Therefore, the proportion of eggs taken by corvids and larger gulls during the study period where not possible to quantify. Nevertheless, because we observed the raven predate on eggs, the possibility that this may have occurred later in the season cannot be ruled out.

Time-laps cameras have proven to be a useful tool in seabird monitoring day and night, despite of certain limitations when it comes to examining multispecies interactions (De Pascalis et al. 2018). Treatment of false negatives regarding the issue with time-laps cameras limited range, may be solved by a wide-angle lens, whereas the issue of concealed white-tailed eagles and ravens due to the coarse interval of pictures in time, could be solved by a higher time resolution, i.e., finer than 1 minute and 40 seconds (100s). Since the time-laps cameras were installed to take pictures every 10th second, we were able to correct some false

negative observations regards the eagle parameter. If the finer resolution of 10 seconds in between the "100s" observations had documented an eagle, the eagle parameter was corrected from *absent* to *present*.

An interesting observation was that the white-tailed eagles that were sitting a certain distance away from the sample seemed to provoke less escape responses among the kittiwakes (Fig. 5, plot A 10 June); the second time laps camera captured an eagle sitting still for 6,5 hours from midnight till early morning. This single sitting eagle represents 41 of the total number of eagle observations at plot A. We did not explore the consequence of this event in the results, which comprise 27% (234 out of 864) of the observations in plot A 10 June, and it is difficult to say how this event may have biased the results. However, it's likely the eagle-effect is underestimated due to the high presence of eagles (ca. 30 individuals, Tab. 3). One way to explore this is by Jackknife resampling of data (e.g., Nisbet et al. 2018) implying that one randomly select one observation (each 100s) in the 6.5 h period and run the glmm, and then repeat this n-1 (i.e., 234-1) times. In other cases, as documented in Fig. 4, white-tailed eagle provoked escape response by sitting among the sample or sitting next to but staying within the kittiwakes' field of vision. Thus, we argue that distance to eagle and its activity should be accounted for in further studies on escape responses of seabirds.

During the study period we experienced that the eagles flying above us did not always move away when we were present, which indicate that the interaction links between white-tailed eagle, human presence and seabirds are intricate and that eagles may adapt to human presence. It is a possibility that eagles may adapt to human presence and learn that people are not a threat. Such adaptations may have implications for future management, in which tourist traffic as a mean to safeguard seabirds breeding success may not work if the eagles learn how to coexist with human presence. Nevertheless, there is also a possibility that kittiwakes may adapt to changes in eagle abundance, by e.g., altering breeding site and move into more sheltered areas of the cliff.

Although, our results indicated that presence of white-tailed eagles has a significant effect on the escape response of kittiwakes, they also indicated that there might be a diluting effect in plot B. Several years of high disturbance by white-tailed eagles that indirectly effects kittiwake recruitment by facilitating nest predation, may add extra pressure on the population and maintain the population decrease. Consequently, a continued population decrease is likely to weakening the diluting effect in the colony by reducing the safety in numbers and possibly

make the remaining kittiwake pairs more targeted by nest predators (Stokes & Boersma 2000). Despite the same result of breeding failure among the kittiwakes in both plots, the escape response was very different between the two plots. To get a good estimate of escape response and egg survival at population level, future study design should include more plots. A consequence of only including two plots, is the possibility that kittiwake pairs which nested at other bird cliffs in the study area, may have had a different breeding success than those within the sample of this study. A challenge for future studies using time-laps cameras in long-term monitoring, is to develop more effective methods of data extraction from comprehensive sequences of imagery, so that more plots can be included in the study design. Moreover, the effect of the temporal aggregation from 10s to 100s on the result were not further explored, and it is difficult to know how this effected the results.

To sum up, the issues related to white-tailed eagle, tourism and seabirds are causing a dilemma for management and decision-makers and are underlining the need for further studies to provide adequate knowledge that can be applied when implementing measures to protect endangered species such as the kittiwake from extinction.

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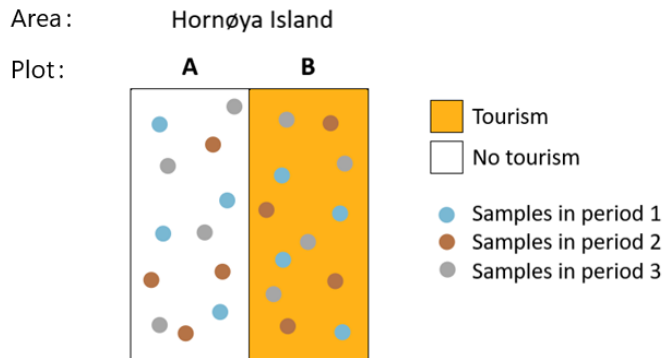
Appendix

Figure A1. The figure illustrates the nested design of this study, comprising of the hierarchal levels, *area*, *plot*, and *sample period.*
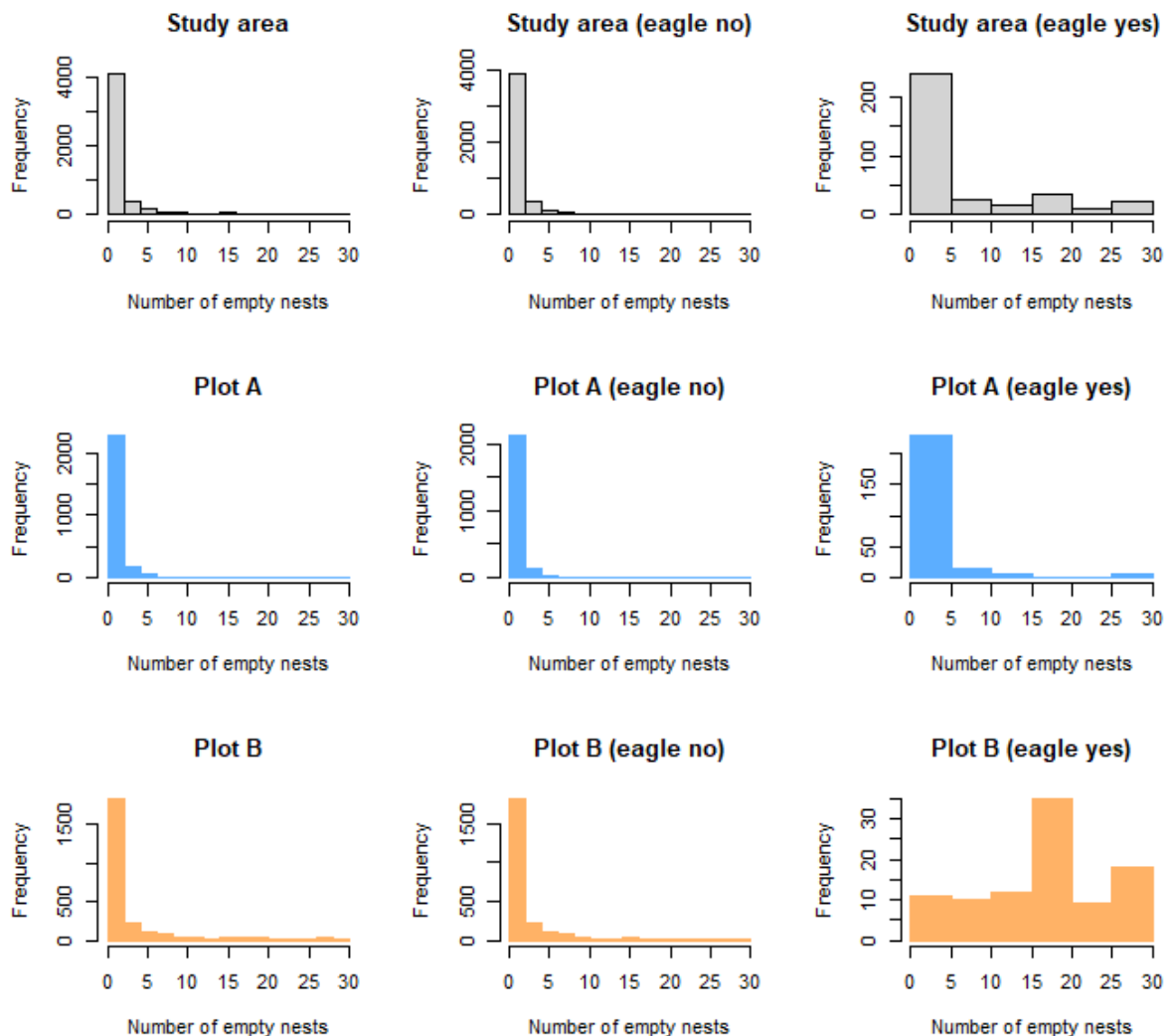

Figure A2. The histograms to the left display the frequency distributions (regardless of eagle observations) of the complete data of the study area and data of plot A and B. The histograms in the middle show the distribution when eagle was absent, whereas the histograms to the right show the distribution with presence of eagle.
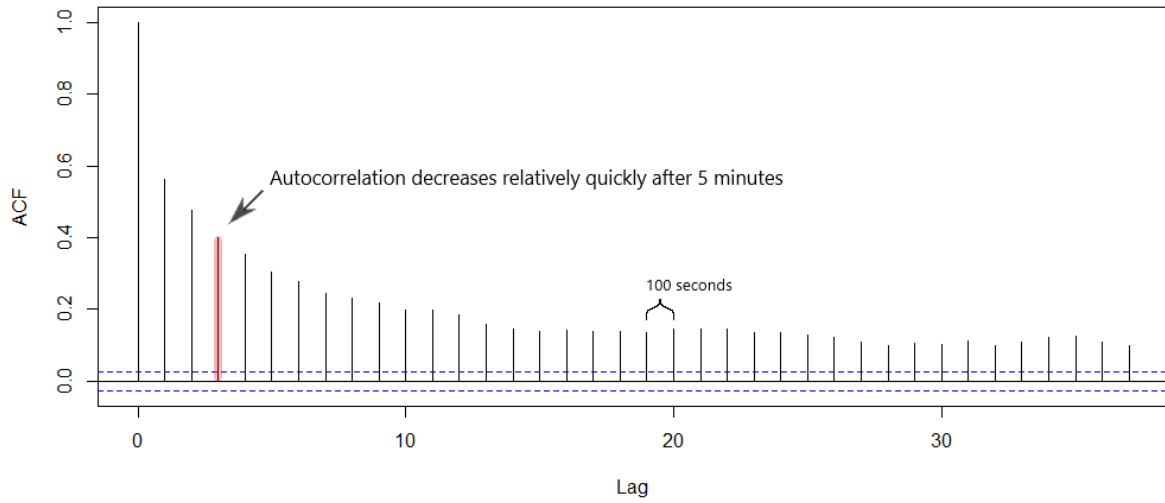
Figure A3. The figure shows the temporal autocorrelation of model residuals in sampling time.

Table A1. Minimum, maximum, and mean number of the overall eagle observations with respect to the time of the day.

Eagle observations between May 20th and June 11th				
Statistics	Morning	Noon	Afternoon	Evening
Min	5	2	8	3
Max	29	30	30	27
Mean	15	14	19	15

Table A2. The overall eagle activity with respect to the time of the day.

Eagle activity percentage distribution of all eagle observations (%)				
Activity	Morning	Noon	Afternoon	Evening
Sitting	79	81	89	85
Flying	21	19	11	15

Table A3. The number of age determined eagles per age class.

Sum of eagle observations where age class was noted						
Age class	1k	2k	3k	4k	5k	6k
Total count	2	13	2	2	2	12