



RESEARCH ARTICLE

Colony-nesting gulls restrict activity levels of a native top carnivore during the breeding season

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Keywords

Camera trapping, gulls, nesting colony, otters, predator activity, seabirds

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Funding Information

This study was funded by the Research Council of Norway (Project no: 335887), the County Municipalities of Agder (Ref. number: 22SC8392), Rogaland (Ref. number: 2022/8193) and Vestland (Ref. number: 22SC8392) as well as the County Governors of Vestland (Ref. number: 2020/1046) and Agder (Project code: FOR-2018-12-19-2172).

Editor: Marcus Rowcliffe

Associate Editor: Anthony Caravaggi

Received: 14 October 2022; Revised: 19 December 2022; Accepted: 9 January 2023

doi: 10.1002/rse2.326

Remote Sensing in Ecology and Conservation 2023; **9** (4):527–539

Introduction

Phylogenetic analysis suggests that coloniality has independently evolved in at least 20 different bird lineages (Causey & Kharitonov, 1990) and 95% of seabird species nest in colonies (Brown et al., 1990). Although the exact reasons for why birds nest in colonies has historically been a topic of debate (Causey & Kharitonov, 1990; Wittenberger, 1985), the advantages must at least be equal to the potential disadvantages for colonial nesting to be a viable reproductive strategy (Danchin & Wagner, 1997). Protection from predators through dilution effects or social mobbing has long been theorized as some of the main driving forces behind the evolution of coloniality

Abstract

Although nesting in colonies can offer substantial reproductive benefits for many seabird species, increased visibility to predators remains a significant disadvantage for most colony-breeders. To counteract this, some seabird species have evolved aggressive nest defense strategies to protect vulnerable eggs and chicks. Here, we used an experimental approach to test whether colony inhabitation by breeding gulls *Larus* spp. in western Norway impacts visitation rates of a native, mammalian predator, the Eurasian otter *Lutra lutra* during the breeding season. Camera traps were placed inside of and on the periphery of seabird colonies prior to the breeding season and left to run for one continuous year. Sighting frequency of otters on these cameras was compared to a control region free of gull nesting. We found that otter activity was significantly reduced in the colonies when gulls were incubating and rearing chicks, compared to time periods when gulls were building nests and absent from the colonies. Rhythmic activity patterns did not seem to be significantly impacted by the presence of gulls. This study provides clear evidence that certain colony-nesting species can have a direct, negative impact on visitation rates of a native carnivore. Seasonal carnivore activity patterns are likely to be highly dependent on differing nesting strategies and level of nest defense by seabirds.

(Anderson & Hodum, 1993; Causey & Kharitonov, 1990; Kruuk, 1964). Possible secondary benefits include increased access to extra-pair copulations (Danchin & Wagner, 1997; Morton et al., 1990), along with enhanced food-finding ability of colony members *via* sharing of information on available food resources (Barta & Szép, 1995; Brown, 1988). There are, however, numerous competing conceptual theories on how exactly this sharing of information takes place, if at all (Mock et al., 1988; Richner & Heeb, 1995, 1996). Despite these potential benefits, higher rates of disease and parasite transmission (Brown et al., 1990; Brown & Brown, 1996), increased antagonistic encounters with conspecifics, and heightened intraspecific competition for food and mates (Dulude

et al., 1987; Møller, 1987) remain large potential drawbacks of colony nesting. In addition, a substantial negative effect of colonialism is that such large aggregations of birds may draw unwanted attention from predators (Clode, 1993; Clode et al., 2000).

To minimize the risk of predation, seabird species tend to nest on remote islands which lay out of reach for most mammalian carnivores (Clode, 1993; Larson, 1960). However, in cases where predators can swim or fly to colonies, seabirds must rely on secondary defensive strategies to minimize predation risk on chicks. In many gull species (*Larus* spp.), the most common form of nest defense is mobbing—by which gulls collectively harass potential predators by diving at them in an effort to drive them away (Clode et al., 2000). Mobbing is usually directly related to defense of the nests and generally incurs some risk to the adults (Poiani & Yorke, 1989; Sordahl, 1990), dependent on which species is the target of the harassment (Montgomerie & Weatherhead, 1988). Clode (Clode et al., 2000) postulated that the mobbing behavior can be seen as a function of the likelihood of reproductive benefits to the adults weighed against the mortality of the adults. By this logic, mobbing intensity will be dependent on age of the adults (Pugesek, 1983) as well as the current developmental phase of the eggs and chicks. In gulls, mobbing behavior appears to increase as the breeding season progresses (Becker, 1984; Kruuk, 1964; Lemmetyinen, 1972), reaching a peak several weeks after the chicks hatch (Clode et al., 2000). By this time, a second attempt at breeding is no longer possible for most gulls (Parsons, 1976), and a large proportion of chicks are still relatively inept at seeking cover when disturbed (Evans, 1970; Smith & Diem, 1972).

From a predator's perspective, targeting gull chicks will come with its own set of risks and rewards. Predation on colony-nesting seabirds may be dependent on the caloric benefit of this seasonal surplus of prey (which may aid the predator's own reproductive efforts), weighed against potential injury, stress, and future survival brought on by mobbing and increased visibility to other predators. Theoretically, if mobbing intensity is strong enough, predators may alter activity patterns to access colonies while prey species are most vulnerable (e.g., at night) or defer to targeting easier prey items.

We aimed to determine if colony inhabitancy and associated defensive nesting behavior of gulls influenced the activity patterns of a native top predator in coastal Norwegian ecosystems, the Eurasian otter *Lutra lutra* (hereafter, "otter"). This study comes at a critical time for many gull species in western Norway, where just eight of 69 seabird reserves have breeding populations comparable to those found in 1980 (Byrkjeland, 2015). Although increased unpredictability of food sources during the

breeding season is likely the leading cause of colony abandonment, heavy predation by invasive mink is believed to have exacerbated the rate of decline (Byrkjeland, 2015). At the same time, the otter has recently managed to reestablish throughout much of western Norway after having been extirpated from almost all central and southern parts of the country due to historical national bounties and extensive overhunting (Landa & Guidos, 2020). Little is known about the ecological connections between otters and gulls in Norway, although past studies indicate that gulls can be an important food source for a closely related species, the North American river otter *Lontra canadensis* during the breeding season (Hayward et al., 1975; Verbeek & Morgan, 1978). Predation by river otters can be substantial, accounting for more than 6% of total chick deaths (Verbeek & Morgan, 1978). If Eurasian otters manage to exert a similar predation pressure in Norway, this may put additional stress on gull colonies which are already struggling.

In this study, we implemented a non-invasive, experimental design using remote sensing by camera traps to continuously monitor otter activity patterns in gull colonies over a one-year period in western Norway (Fig. 1A). We simultaneously monitored a control region (Fig. 1B) in the same area of western Norway as the gull colonies to determine what otter activity patterns look like in places free of gull activity. We hypothesized that otter sighting frequency would significantly decline during the breeding season on the colonies, as a response to increased gull aggression, while otter activity outside of gull colonies would not significantly vary. Specifically, we theorized that otter activity would be lowest towards the end of the chick-rearing period, when gulls had invested the maximum amount of total energy into raising the chicks and would therefore respond strongest to otter activity within this timeframe. Given that most gull species are diurnal and have a reduced ability to see at night (Burger, 1988; Hayes & Hayward, 2020; Indykiewicz et al., 2021; Yorio et al., 2005), we hypothesized that otters would be predominantly nocturnal during the breeding season to access colonies when gulls are most vulnerable. Lastly, we aimed to verify if distance to nearest nest had any effect on otter sightings on nearby cameras traps within and outside of the breeding season.

Materials and Methods

Study area

Gull colonies

The study focuses on four gull colonies (Colonies 1–4) and one control region in western Norway (Fig. 1). All studied colonies are located on relatively small islands

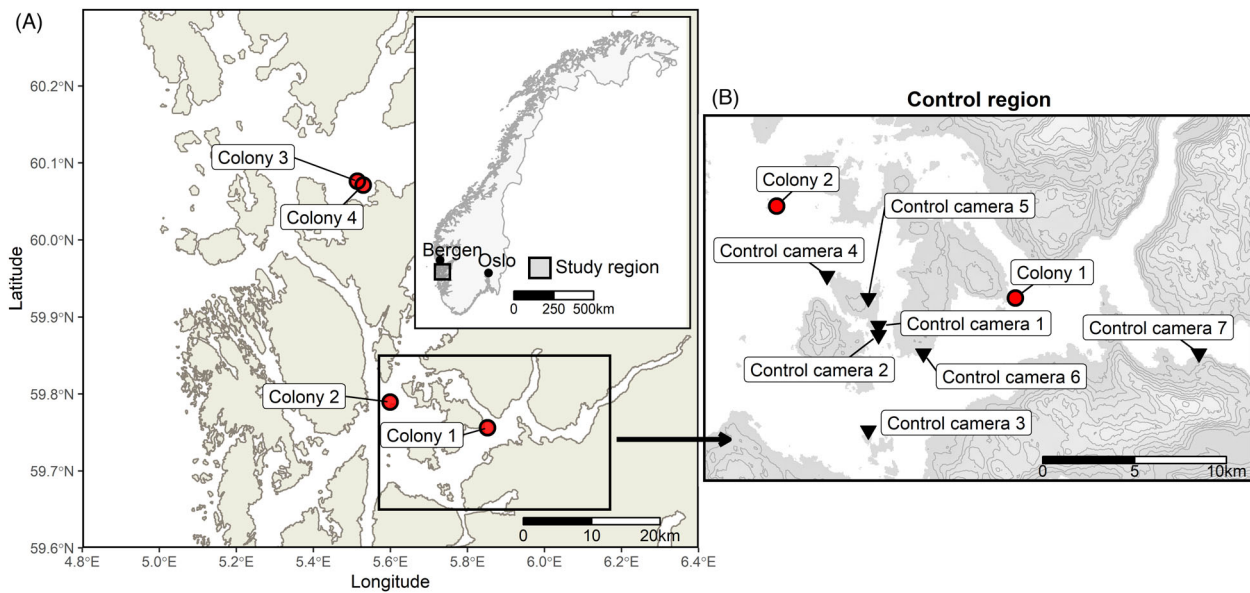


Figure 1. Locations of the study seabird colonies in western Norway (A), along with the locations of camera traps in the control region (black triangles in (B)). Elevational binwidth in the topographical map (B) was set to 100 m. Mapping data supplied by Kartverket™.

(4500–62 000 m²) within the fjord systems that characterize the region. Each colony is part of an archipelago, and distance to the nearest stretch of mainland or next suitable island for otter inhabitation was less than 472 m ($\bar{x} = 273 \pm 174$ m), which is well within the maximum swimming distance for otters (Kruuk, 2006) and should not limit access to the colonies.

Topography and vegetation on the studied colonies facilitate good breeding conditions for the gull species studied here. Tree cover is sparse except for the occasional pine, with vegetation being dominated by rushes and graminoids. Although steep rockfaces are present on some colonies, maximum elevation is only 21 m. Access to freshwater should not limit otter activity on any of the study colonies as freshwater pools are present on all islands (Kruuk & Balharry, 1990). Marine littoral vegetation fringing the colonies is dominated by fucoid macroalgal species (*Ascophyllum nodosum* and *Fucus vesiculosus*) and brown algal species (*Pelvetia canaliculata*; Husa, Kutti, et al., 2014; Husa, Steen, et al., 2014). This in turn hosts healthy fish communities within the study region and nearby fjord areas, with the most numerous clades between depths of 5 and 20 m being gadoids and labrids (Salvenes & Nordeide, 1993; Tambs-Lyche, 1987).

Nesting activity by gulls was dominated by great black-back gulls *Larus marinus*, herring gulls *Larus argentatus*, lesser black-back gulls *Larus fuscus*, and common gulls *Larus canus*. All nest locations were detected by walking pre-determined transects through colonies just prior to hatching in the third week of May 2020 and were

registered using a handheld GPS device. Species identification was carried out simultaneously by identifying nest and egg characteristics such as egg size and shape, nest materials, and location. Number of breeding pairs ranged from 3 to 334 per colony. Location and number of nests per species on each colony during the 2020 breeding season can be found in Table 1 and Figure 2. In addition to gulls, eider ducks *Somateria mollissima*, greylag geese *Anser anser*, and a large variety of passerines and waders nest on all colonies including Eurasian oystercatchers *Haematopus ostralegus*, meadow pipits *Anthus pratensis* and common blackbirds *Turdus merula*. White-tailed eagles *Haliaeetus albicilla* are abundant throughout the study region and are known to predate upon nesting gulls, along with the occasional golden eagle *Aquila chrysaetos*. No rodent species or other small mammals are found on any of the colonies.

Control region

Finding suitable islands to serve as control “colonies”, which displayed similar topography and vegetation to the experimental islands, but which lacked gull breeding activity proved a challenge. Most treeless islands and skerries in western Norway of similar size to those studied here are home to breeding seabirds in the summer months, which would negate effectiveness as control islands.

Therefore, all camera trap locations used in the control group came from an ongoing otter monitoring program by the Norwegian Institute for Nature Research (NINA)

Table 1. Information on the study colonies and the control region.

Colony	Island size (m ²)	DTNL (m)	Nesting gull species	# gull nests	Nesting density (m ² /nest)	Gull activity period			Inc.	Chick rearing	AFC	# camera traps	# otter pics.
						Nest constr.	Inc.	AFC					
1	4,560	424	<i>L. canus</i>	29	157	April 1–30, 2020	May 1–31, 2020	June 1–August 31, 2020	March 1–31, 2020 & September 1, 2020–February 28, 2021 (combined)	4	23		
2	12,530	65	<i>L. marinus</i> <i>L. argentatus</i> <i>L. fuscus</i>	1 18 5	522	March 1–April 14, 2020 & February 1–28, 2021 (combined)	April 15–May 15, 2020	May 16–August 31, 2020	September 1, 2020–January 31, 2021	5	119		
3	62,900	428	<i>L. marinus</i> <i>L. argentatus</i> <i>L. fuscus</i>	2 270 62	188	March 1–April 14, 2020 & February 1–28, 2021 (combined)	April 15–May 15, 2020	May 16–August 31, 2020	September 1, 2020–January 31, 2021	11	343		
4	17,600	117	<i>L. marinus</i>	3	5866	March 1–April 14, 2020 & February 1–28, 2021 (combined)	April 15–May 15, 2020	May 16–August 31, 2020	September 1, 2020–January 31, 2021	4	498		
Control region	NA	NA	NA	NA	NA	March 1–April 14, 2020 & February 1–28, 2021 (combined)	April 15–May 15, 2020	May 16–August 31, 2020	September 1, 2020–January 31, 2021	7	1381		

DTNL, distance to nearest landmass; Inc., Incubation; Nest constr., Nest construction; AFC, Absent from colony; pics., pictures.

in western Norway. Seven camera traps from the monitoring program were selected to serve as a control based on overlapping timeframe of data collection with the gull colonies. The control region lies in the same area as Colonies 1 & 2 (Fig. 1B) and supports the same marine fauna and flora found around the seabird colonies. However, terrestrial vegetation in the control region is dominated by large pines *Pinus* spp. and deciduous trees near the shoreline and in the surrounding fjord landscape. Terrestrial prey assemblage for otters is therefore more varied in the control region, including a variety of rodents, amphibians, and birds. Intraguild predators such as red fox *Vulpes vulpes*, pine martens *Martes martes*, and American mink are common in the control area. Despite this difference and potential biases, the control region serves as a good comparison for our purposes, where we can study a sympatric otter population with similar demographic history to those inhabiting nearby seabird colonies and gain a baseline model of what otter activity looks like in areas free of breeding gulls.

Camera trapping

To optimize the effectiveness of data collection, all colonies were searched prior to camera trap placement for signs of otter activity. Camera placement in colonies began in 2018 and was an ongoing process until the official beginning of the study in 2020. Since we only had access to a limited number of camera traps ($n = 24$ on study colonies), we preferentially chose trapping locations based on apparent use of the area by otters (field observations of the number of scats in an area and/or density of trails) and by trying to maximize the distance between camera traps. Camera traps were placed in areas that would offer the easiest route onto the islands from the ocean (i.e., ravines and gullies) and could partially protect otters from gull harassment during the gull breeding season. Field observations show that otters almost exclusively use these “passageways” to gain access to gull colonies and predate upon eggs and chicks (Verbeek & Morgan, 1978). Choice of camera trap locations in the control region followed the same guidelines as the seabird colonies. Locations were chosen based on apparent use of an area by otters, judged from the number of scats found or density of otter trails. Though cameras in the control region were not preferentially placed in areas that would offer protection from gull harassment, all locations were close to the shoreline (<5 m) and were either placed in small caves, bouldered areas, or close to the tree line. As such the camera locations would offer similar levels of cover for otters, reducing potential biases between the control and colonies.

The infrared camera traps used throughout the study were the Reconyx™ Hyperfire 2 (Reconyx Inc., Holmen,

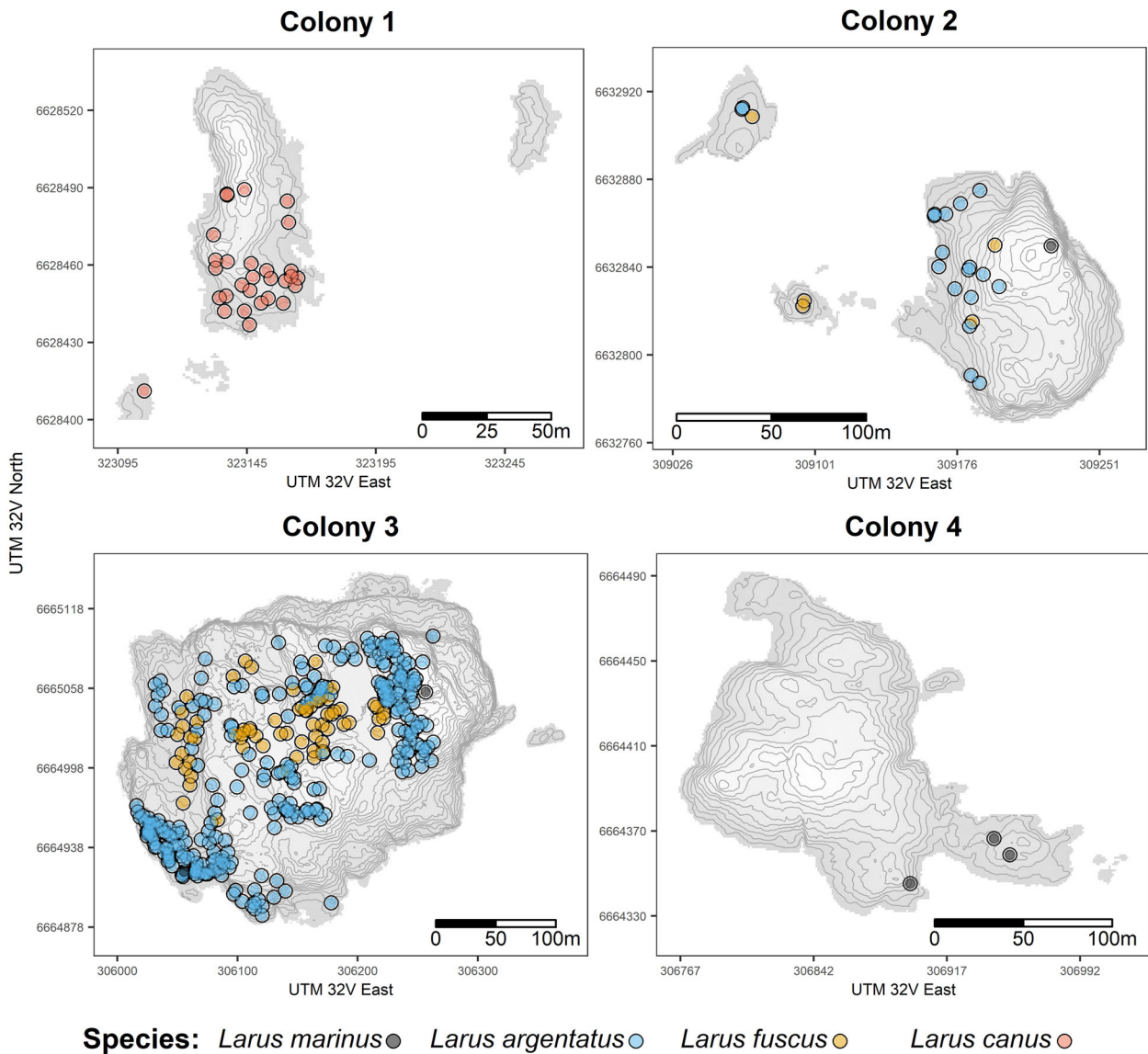


Figure 2. Topography and nesting locations of different gull species in the study colonies. Elevational binwidth is 1 m on all islands. Mapping data supplied by Kartverket™.

USA). Cameras were set to a 0.2 s trigger speed after detecting motion on “high” sensitivity and took three pictures per motion sequence separated by 1 s. We set a 3-min quiet period between motion sequences to avoid repeatedly capturing pictures of moving vegetation that would drain the batteries and fill SD cards. Cameras were placed on metal supports and bolted to exposed rock facing the direction of marking spots or trails. Trapping locations were not baited. All cameras were placed between 20 and 30 cm above the ground and *ca.* 1–2 m from the marking spot. Visitation by otters often occurred within the same day of camera placement, and we therefore assumed that neither camera placement nor routine checking had any

effect on otter activity (Findlay et al., 2017). We checked the cameras once every 3 months to replace SD cards and batteries if necessary. The studied timeframe covers 1 year of continuous camera trap monitoring over the four colonies and control region, beginning on March 1st, 2020, and ending on February 28th, 2021.

Statistics

Camera sightings were defined on an hourly basis, which is similar to or slightly more conservative than previous studies on semi-aquatic mustelids (Crego et al., 2018; Day et al., 2016; Leuchtenberger et al., 2014; Rheingantz

et al., 2016). Since Eurasian otters in general have no distinctive markings or fur color patterns, we were not able to distinguish individuals and therefore have no estimates on population levels in the study area. However, the average coastline length of studied islands was just 802 m (± 198 m), which is well under the known mean territorial length for both male and female otters in coastal environments (Heggerget, 1995; Kruuk & Moorhouse, 1991). Given spatial distribution patterns of Eurasian otters, it is therefore likely that each island lies within the territorial boundaries of at least one male and one female (Kruuk, 2006; Kruuk & Moorhouse, 1991; van Dijk et al., 2020). Eurasian otters generally do not travel in groups aside from when pups are still dependent on their mother; (Kruuk, 2006) therefore, any instances of multiple otters being captured within the same picture were treated as litter sightings.

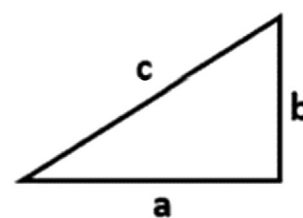
To determine how use of colonies by gulls affected the activity patterns of otters over the course of a year, otter sightings were grouped into four distinctive time periods of gull activity: (1) Nest construction, (2) Incubation, (3) Chick rearing, and (4) Absent from colony. Length of time periods varied slightly dependent on gull species. For great black-backed gulls, herring gulls, and lesser black-backed gulls, nest construction took place (and combined data) between March 1st and April 14th, 2020, and February 1 and 28th, 2021. Incubation took place between April 15th and May 15th, 2020, and chick rearing occurred between May 16th and August 31st, 2020. Gulls were absent from colonies between September 1st, 2020 and January 31st, 2021. These time periods are slightly delayed for common gulls (only on Colony 1), with nest construction happening between April 1 and 30, 2020, incubation between May 1st and 31st, 2020 and chick rearing from June 1st to August 31st, 2020. Common gulls were absent from the colony between March 1st and April 1st, 2020, and September 1st, 2020, until the study concluded on February 28th, 2021. Otter sighting frequency within these timeframes was calculated by dividing the number of sightings per time period by the total amount of days the camera was active per time period. This value was then multiplied by 100 to obtain an integer. Sighting frequency was determined on an individual basis per camera trap. Sighting frequency per gull activity period in the control region was based on those used for herring gulls and greater and lesser black-back gulls due to these species being the most commonly represented, present on all but one of the colonies.

We used linear mixed-effects models (R package “nlme”; Pinheiro et al., 2022) to determine how gull activity patterns influence sighting frequencies of otters on all studied colonies and control region. Colony number and camera location were set as random-effect factors.

Distribution of model residuals was calculated through Levene’s test for normality (R package “car”; Fox et al., 2021) and Shapiro–Wilk’s test for homogeneity. In cases where the assumptions for homogeneity and normality were not met, we used generalized linear mixed models (GLMMs), as they allow for deviations from constant variance and non-normality of data. GLMMs were modelled through the “MASS” package (Ripley, 2022) in R. We used an ANOVA to test for variance between gull activity periods, followed by a post-hoc multiple comparisons test (Tukey HSD) to determine significance between groups. This was done using the lsmeans (Lenth, 2018) and multcomp (Hothorn et al., 2022) packages in R.

Distance of camera traps to nearest gull nest was determined by taking the square root of the sum of the distance between the camera traps and nearest nest and the difference in elevation between two points (Equation 1). Distance to nearest nest is only relevant for camera traps located within the seabird colonies. Cameras in the control regions were therefore excluded from this analysis. Distribution of model residuals followed the same procedure as outlined above. The effect of distance to nearest nest on sighting frequency between gull activity periods was also modelled through GLMMs. Colonies were grouped by gull activity periods, with colony and camera locations kept as random-effect factors.

Data on otter time of activity were automatically registered when pictures were taken. We used the R package “suncalc” (Thieurmél & Elmarhraoui, 2019) to assign dusk and dawn time periods (defined as when the sun is 6° below the horizon after sunset and before sunrise, respectively) for each day of the study based on given latitude and longitude positions for each camera trap. This information was then paired to the camera trap data by day of the year so that all otter sightings were assigned a dusk and dawn time period. This made it possible to control for the changes in daylight between seasons. Rhythmic activity patterns were split into nocturnal and diurnal



$$c^2 = a^2 + b^2$$

Equation 1. Calculating nest distance to the nearest camera trap “c”, where “a” is the linear distance between the camera trap and the nest and “b” is the difference in elevation between the two points.

categories. Otters captured between dusk and dawn were considered nocturnally active, while activity falling outside of this time period was diurnal. We used Pearson's chi-squared tests to determine how otter rhythmic activity patterns varied between control and experimental colonies and between the gull activity periods.

All statistics and figures were made using the R project for statistical computing, version 3.6.1, and level of significance for all models was set to $p < 0.05$.

Results

Cameras were active on the study colonies and in the control region for 2026 trap nights during nest construction, 898 trap nights during incubation, 2826 within the chick-rearing period, and 4627 trap nights when gulls were absent from colonies. Otters were captured on camera a total of 2364 times between all locations ($n = 31$). The control region recorded the majority of otter sightings ($n = 1381$) over the studied timeframe. Colony 4 logged the highest number of sightings between colonies 1–4 ($n = 498$), followed by colonies 3 ($n = 343$), 2 ($n = 119$), and 1 ($n = 23$). Otter litters were sighted a total of 189 times between all camera trap locations. The vast majority of litter sightings ($n = 184$, 97%) were in the control region. Time periods with litter activity recorded higher mean otter sighting frequencies ($\bar{x} = 82 \pm 49$ compared to $\bar{x} = 51.3 \pm 44$), but this difference was not significant ($p = 0.60$, $df = 19$, $SE = 12.1$). Camera failure occurred relatively infrequently, though one camera died for the entirety of nest construction period on Colony 1. Inclement weather made it difficult to fix another dead camera throughout all of the chick-

rearing period in the control region. Aside from these incidences, there were no large gaps in data collection.

Temporal gull activity on otter sighting frequency

Results suggest that colony inhabitancy during two of the gull activity periods (incubation and chick rearing) had a significant, negative effect on visitation rates of otters to colonies during the breeding season (Fig. 3). Nest construction appeared to have no impact on otter activity, with sighting frequency being almost indistinguishable from when gulls were absent from the colonies ($\bar{x} = 13.8$ compared to $\bar{x} = 15.5$, respectively, $p = 0.98$, $df = 85$, $SE = 0.16$). Following nest construction, otter activity decreased significantly to a mean of $\bar{x} = 3.45$ during incubation ($p = 0.001$, $df = 85$, $SE = 0.25$). Otter activity rose slightly during the chick rearing phase to a mean sighting frequency of $\bar{x} = 6.25$, though this was not significant. Afterwards, the transition between the chick rearing phase and gull absence from colonies coincided with a significant increase in otter activity ($p < 0.001$, $df = 85$, $SE = 0.19$). In contrast to the seasonal swings in otter activity on the gull colonies, the control region recorded no significant change in sighting frequency between any of the gull activity periods (Fig. 3). Otter sighting frequency in the control region was, however, significantly higher during every gull activity period compared to the colonies ($p = 0.02$, $df = 8$, $SE = 0.74$). Opposite to the gull colonies, otter activity in the control region peaked during the incubation phase, though not significantly.

While all colonies showed a similar trend in the decrease of otter sighting frequency during the

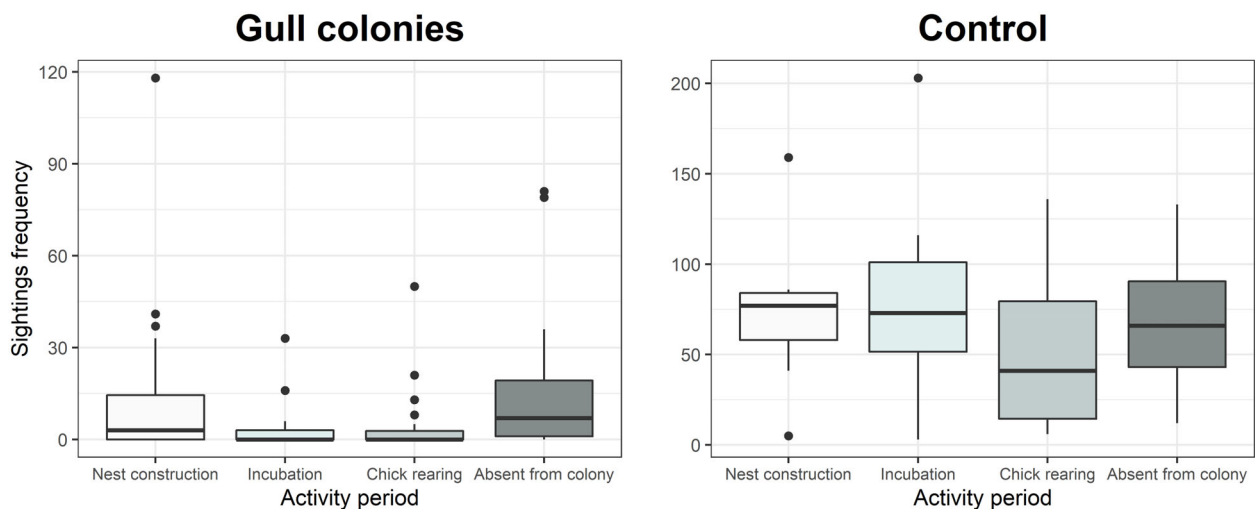


Figure 3. The change in otter sighting frequency between nest construction, incubation, chick rearing, and absence from colony in the studied gull colonies (combined) and in the control region.

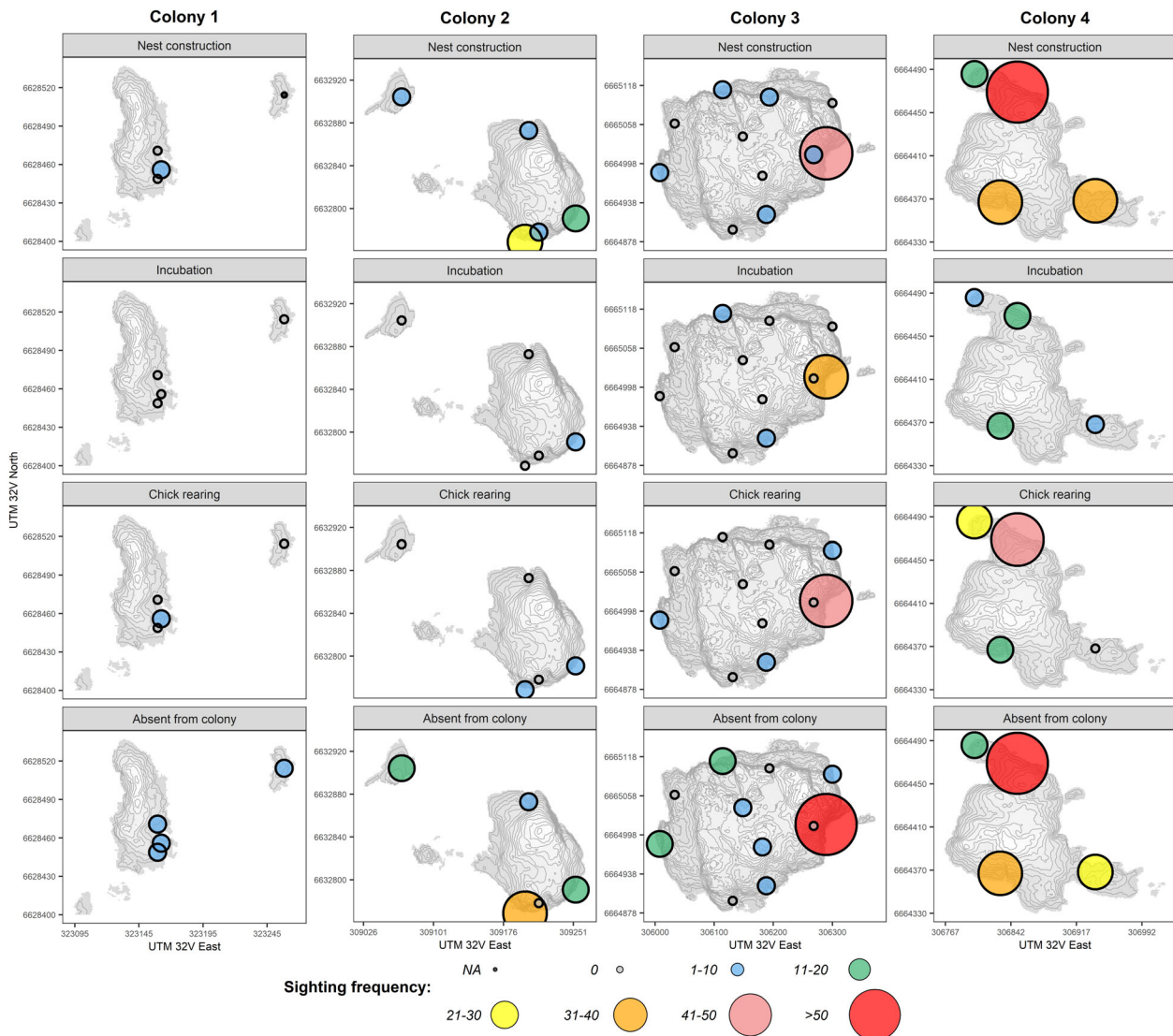


Figure 4. Sighting frequency of otters during nest construction, incubation, chick rearing, and when gulls are absent from the colonies (top to bottom) in relation to the spatial distribution of camera traps (individual points within each colony). Mapping data supplied by Kartverket™.

incubation and chick rearing periods, there was some local variation in the significance of changes in sighting frequencies between individual colonies (Figs. 4 and 5).

Effects of proximity to nesting gulls on otter sighting frequency

Otter marking spots located furthest from active nests were clearly preferred both within the breeding season and outside of it. Sighting frequency significantly increased in response to distance to nearest nest during nest construction ($p = 0.03$, $df = 17$, $SE = 1.07$), incubation ($p < 0.01$, $df = 18$, $SE = 1.5$), chick-rearing

($p < 0.001$, $df = 19$, $SE = 0.004$), and absence from colonies ($p = 0.02$, $df = 19$, $SE = 0.004$).

Rhythmic activity patterns

Otters were predominantly nocturnal on the gull colonies and within the control region, with percentage of night sightings ranging between 60 and 90% between gull activity periods. Otters showed no significant difference in rhythmic activity patterns between the control region and gull colonies during the breeding season aside from during nest construction (75% compared to 90%, respectively, $\chi^2 = 21.2$, $df = 1$, $p < 0.01$). Proportion of recorded nocturnal activity was virtually the same during

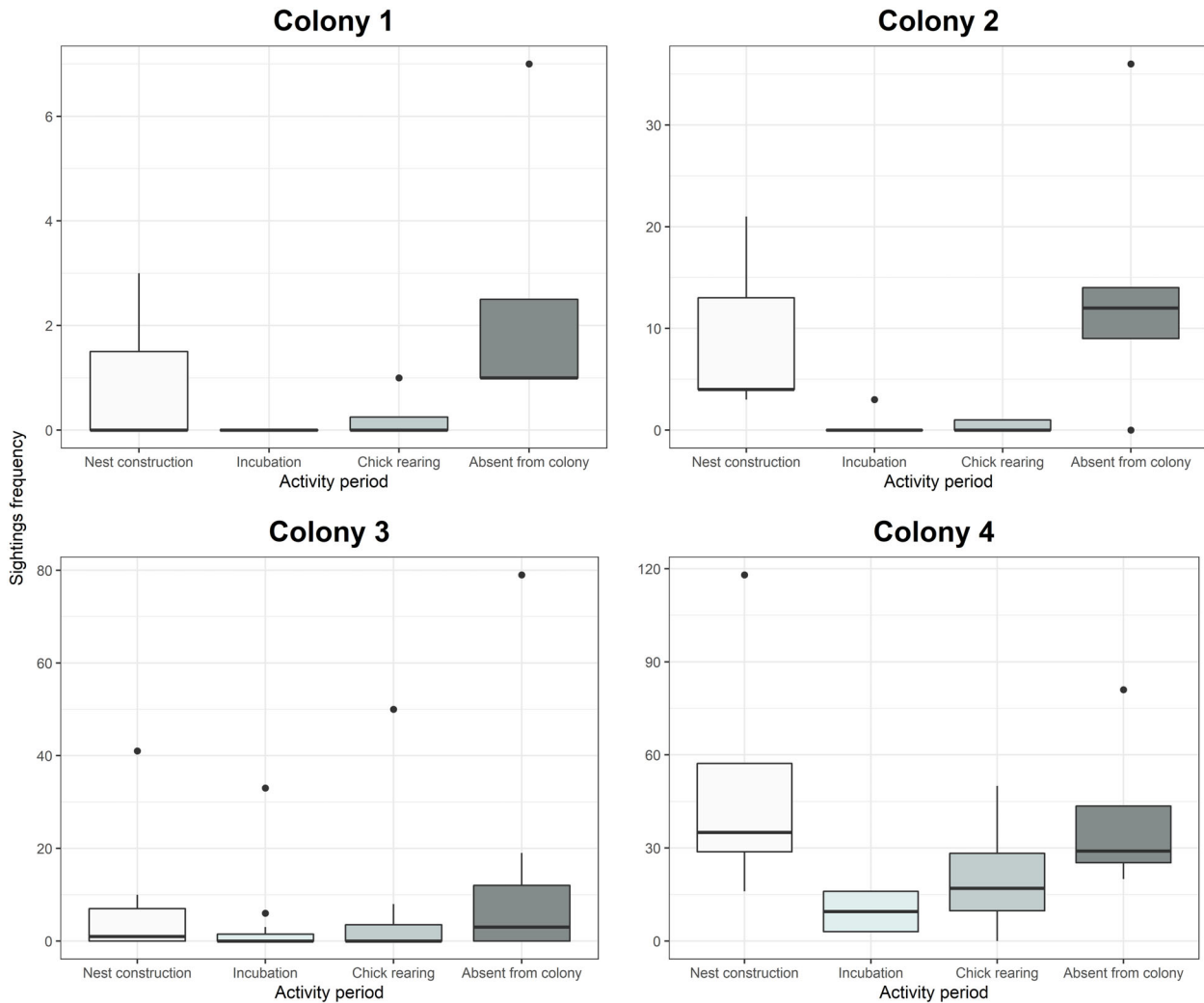


Figure 5. The change in otter sighting frequency between nest construction, incubation, chick rearing, and absence from colony in the four studied gull colonies.

the chick rearing period (77% and 78% nocturnal sightings between gull colonies and control, respectively). Percentage of nocturnal sightings in the control region during incubation was less than on the colonies (60% compared to 75%, respectively), though this was not significant ($\chi^2 = 2.2$, $df = 1$, $p = 0.14$). However, outside of the breeding season, the proportion of otter activity at night within the gull colonies was significantly greater than in the control region (88% over 82%, $\chi^2 = 7.56$, $df = 1$, $p < 0.01$). Rhythmic activity patterns were the opposite of what was predicted within the gull colonies. Nocturnal activity peaked when gulls were constructing nests (90%) and decreased significantly during the incubation phase (75%, $\chi^2 = 5.5$, $df = 1$, $p = 0.02$) and was also significantly less during chick rearing (77%, $\chi^2 = 13.0$, $df = 1$, $p < 0.01$). Nocturnal activity again

significantly increased when gulls vacated the colonies (88%, $\chi^2 = 24.4$, $df = 1$, $p < 0.01$). Similar to the colonies, nocturnal activity in the control region decreased significantly between nest construction and incubation (75% to 60%, respectively, $\chi^2 = 11.2$, $df = 1$, $p < 0.01$). Afterwards, nocturnal activity increased markedly again during chick-rearing (78%, $\chi^2 = 13.9$, $df = 1$, $p < 0.01$) and stabilized at 82% during the absence from colonies time period.

Discussion

The influence of gull activity on otter sightings

The camera traps could not provide information on the direct interactions between otters and gulls, but the

difference in seasonal otter activity patterns between the colonies and the control region provides strong evidence that otters actively avoid gull colonies during certain periods of the breeding season. Although our methods provide little information on species interactions, gulls are commonly known to be aggressive when defending eggs and chicks, and gull mobbing is a likely cause of the significant decrease in otter activity on active seabird colonies during incubation and chick rearing. These results offer a significant improvement on our current understanding of these species interactions in Northern Europe, as most previous related studies focused primarily on singular predation events or gull interactions with North American river otters (Hayward et al., 1975; Verbeek & Morgan, 1978).

Although the gull breeding season officially begins with nest construction, this activity appeared to have no impact on otter sightings within the colonies. Even though nesting territories are defended against conspecifics within this timeframe, the presence of otters would likely not elicit a strong defensive response from the gulls as there is relatively little investment in reproduction at this time, and risks associated with defensive behavior would likely provide marginal benefits to reproductive success. Following nest construction, otter activity decreases significantly during incubation. Our observation that otter sighting frequency in the colonies was lowest during incubation lends weight to previous studies which suggest that nest defense by adult gulls grows during incubation (Becker, 1984; Kruuk, 1964; Lemmetyinen, 1972), reaching a peak about 2 weeks after the eggs hatch, during which chicks have limited dispersal ability (Clode et al., 2000). Even though our grouping of activity periods did not allow for comparison of such specific timeframes, this effect was likely true, but remained hidden due to this 2-week period encompassing just 13% of the chick-rearing time period. Although the relative reproductive value of chicks increases with age (Barash, 1975) and nest defense behavior of adults is predicted to increase correspondingly (Andersson et al., 1980; Biermann & Robertson, 1981; Greig-Smith, 1980; Pugesek, 1983; Shields, 1984), the improved dispersal and hiding ability of chicks over time likely allows adults to decrease mobbing intensity (Sordahl, 1990) and thereby offset costs of reproduction as chicks approach fledging. This, combined with the fact that adults must spend more time on foraging trips as chicks mature (Pugesek, 1983), and the total number of breeding pairs within a colony decreases over time as chicks die, could result in overall lower mobbing response from adults in later stages of the breeding season. Accordingly, otter activity was high during nest construction, lowest during the incubation, increases slightly during chick-rearing, and again increases when gulls leave the colonies.

One potential contributing factor to reduced otter activity during summer months could be that female activity is restricted to areas close to denning locations before pups are old enough to leave the natal den (Kruuk, 2006). Although most of the coastal Norwegian otter population does not have a defined breeding season (Heggberget, 1993), the majority of births happen in summer and autumn (Heggberget & Christensen, 1994). This could potentially result in less otter sightings in summer months in general, as female activity is restricted to areas close to natal dens. However, considering pups were only sighted four times during autumn of 2020 on Colony 1, we believe breeding activity had an insignificant effect on our results. Opposite this, one may assume that the increased conspicuousness of family groups could inflate sighting frequencies of otters in time periods where litters are present. However, we found this assumption to be unsupported by our data. Given that litters were sighted regularly throughout the year at all camera locations in the control region, we believe it is unlikely that breeding behavior had a significant influence on sighting frequency between gull activity periods.

Distance to nearest nest

While mobbing functions to protect nests from immediate threats, time spent away from nests defending eggs and chicks leaves the nest open for thieves like hooded crows *Corvus cornix* and conspecifics (Kilpi, 1988). It is therefore probable that nest defense behavior follows a cost/benefit function by which mobbing intensity decreases as predator distance to nest increases. Our results show that otter activity does increase along with distance to nearest nest during the gull breeding season. However, the same relationship remained true even in time periods when gulls were absent. This later result could indicate that marking spots furthest from nesting locations are simply preferred regardless of time of year.

Rhythmic activity patterns

The lack of difference in nocturnal activity between the control and colonies during the incubation and chick rearing phases is a likely indicator that gulls have little impact on the rhythmic activity patterns of otters. Nocturnal activity was indeed 15% higher within the colonies during the incubation phase, though this was not significant and may have been influenced by the relatively low total number of otter sightings during this period on the colonies ($n = 28$). When examining just the colonies, otters were significantly more active during the day within the breeding season (aside from nest construction) compared to periods when gulls had left the breeding islands. Although the exact

reason for this pattern remains unclear, the comparatively low proportion of nocturnal sightings during the breeding season could be another indication that otter predation on gulls during the breeding season is relatively low. Verbeek and Morgan (Verbeek & Morgan, 1978) found that predation events on gulls by North American river otters took place exclusively between dusk and dawn. Although we cannot prove that otters did not predate upon gulls, their eggs or chicks in this study, given that the aforementioned river otters and those studied here, share much of the same dietary preferences (Kruuk, 2006), and the relatively low proportion of nocturnal activity during the breeding season is a likely indicator that gulls are not an important food source for otters in western Norway. However, given the increase in diurnal activity during the incubation phase within the control region, it is also plausible that temporal activity patterns are regulated by factors like changes in selection of prey species between seasons (Kruuk, 2006) rather than gull activity. This is, however, difficult to expand upon without data on seasonal availability of fish species around studied colonies and corresponding information on dietary composition of studied otters.

Ecological implications

For aquatic (i.e., sea otter *Enhydra lutris*) and semi-aquatic mustelid species (i.e., Mink, Eurasian otter, North American river otter), predation upon birds appears to be related to overall adeptness to life in water. Species like the sea otter only occasionally predate upon birds, while less aquatic mustelids like mink rely more heavily on avian prey during certain months (Riedman & Estes, 1988). Results suggest that the otters studied here fall closer to sea otters on this spectrum. This relationship is likely dependent on several factors. In addition to colony inhabitation by gulls, access to alternate prey types during the summer months probably has a large impact on visitation rates to colonies by otters. While coastal waters in Western Norway lack a peak biomass of the otter's main fish prey species in any single season, summer and autumn months generally support the highest densities of shallow water fish species that are most often targeted (Heggberget, 1993). In addition to the increased abundance of coastal fish, marine invertebrates, small mammals, and riparian birds are also at their highest abundances in late spring and summer. The combined effect of this could be that gull eggs and chicks are passed up in favor of easier, readily available prey items outside of colonies.

Our results lend support to the hypothesis that colony-nesting offers some protection for species like those studied here, at least from one native top predator, the otter. These findings are a piece of a complex puzzle, and there are undoubtedly many factors influencing predator

visitation rates to colonies aside from the actual presence of gulls. Swimming distance to other parts of a predator's territory, overall spatial size (territorial value) of the colonial islands, as well as nesting densities throughout the breeding season and between years will likely all play a role in predator activity patterns. Surveying four colonies over just a single year did not result in enough data for us to develop models to validate these assumptions. However, studying otter visitation patterns over several years, or between a larger number of colonies, could help shed light on these effects.

It is unlikely that all predator species would react so strongly to the presence of nesting gulls nor that otters would react the same way to other colonial nesting seabird species. Another recent camera trap study shows that black guillemots *Cephus grylle* are susceptible to predation by Eurasian otters where nests are accessible in Scotland (Johnston et al., 2020), and both juvenile and adult Atlantic puffins *Fratercula arctica* are well known to be predated upon inside their burrows in Northern Norway (Systad pers. obs.). River otter predation on burrow-nesting species like fork-tailed storm petrels *Hydrobates furcatus* can be substantial, accounting for up to 24% of adult mortality in areas accessible to otters (Quinlan, 1983). In all of these cases, it is plausible that otter activity levels would be substantially different than what we describe here, and it is likely that differing reproductive strategies between species will elicit varying responses from otters and other main predators. To better assess how risk of predation varies according to species and location, future studies should focus on how various nesting strategies, as well as other ecological factors like nesting density and swimming distances to colonies affect visitation rates by a larger range of mammalian and avian predators.

Acknowledgements

This study was funded by the Research Council of Norway (Project no: 335887), the County Municipalities of Agder (Ref. number: 22SC8392), Rogaland (Ref. number: 2022/8193) and Vestland (Ref. number: 22SC8392) as well as the County Governors of Vestland (Ref. number: 2020/1046) and Agder (Project code: FOR-2018-12-19-2172). We wish to thank Arild Breistøl for his help in the field and for providing us with the data he has collected over the last decade on the temporal nesting activity patterns of the gulls focused on here. Lastly, we wish to thank our two anonymous reviewers for their insightful, constructive feedback.

Author Contributions

AL and GS conceived the project idea and designed the study. SG and AL secured project funding and carried out

the fieldwork. SG analyzed the data, handled the statistics, and led the writing of the manuscript. JvD was heavily involved in review of the manuscript and synthesizing the project ideas. All authors contributed to draft editing and gave final consent to publish.

Data Availability Statement

All data presented within this study are available in the article's supplementary information files. All datasets are publicly available online from the Dryad Digital Repository ("<https://protect-eu.mimecast.com/s/TVJhCzXxZFM51vGCwjuHz?domain=doi.org>" <https://doi.org/10.5061/dryad.p2ngf1vtw>), or can be made available upon request.

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