

The influence of re-establishing Eurasian otter (*Lutra lutra*) on the activity of invasive American mink (*Neovison vison*) on the southwest coast of Norway

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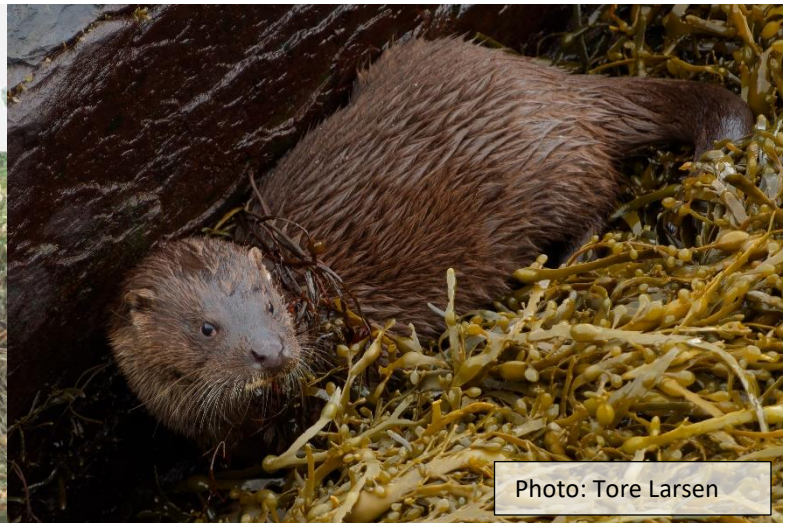
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Abstract

Invasive species are one of the most impactful sources of biodiversity loss worldwide. Generalist predators may be especially damaging, as they can reduce survival and fecundity in native species and can compete with native predators for resources. In groups of related species, competition can be a major evolutionary driving force, leading to changes in distribution and behaviour of the competing species. One such pair of related competing species is the invasive American mink (*Neovison vison*), who was introduced to Norway whilst the competing native species Eurasian otter (*Lutra lutra*) was absent in many areas due to excessive hunting. In recent years, however, the otter has returned to large parts of its historical range but is still missing in the southernmost part of the country. This provides a natural control area and allows an insight into the difference in mink activity when otters are present and absent. I used camera traps placed in common marking sites to study sighting frequency and circadian activity patterns of otter and mink in an area without otters and an area that otters returned to a decade ago. I found that activity of mink in the presence of otter remained stable at a relatively low level over seven years, indicating that otters can suppress mink populations in the area, but are not able to completely remove mink, at least not in the short term. Furthermore, the activity patterns of mink differed in the presence of otters, although the impact was opposite of what was expected. The generally nocturnal mink was more diurnal in the absence of otters, but this could be due to diet choice. This study supports previous findings that otters suppress mink and can change their behaviour, although long term effects are uncertain. Still, the suppression of mink will likely positively impact its vulnerable native prey species.

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1. Introduction

Invasive species are currently one of the main causes of species extinction and biodiversity loss worldwide (Sodhi, Brook and Bradshaw, 2009; Linders *et al.*, 2019). Most invasion events are associated with human activity (Mack *et al.*, 2000). As people move about the world, plants and animals are, accidentally or intentionally, also spread frequently and over great distances (Mack *et al.*, 2000; Smith and Smith, 2015). Outside their natural distribution range, species are free from the constraints of their usual competitors, parasites and predators, and may successfully establish themselves and spread (Smith and Smith, 2015). Many invasive species share common traits such as fast reproduction and growth, wide ecological tolerance, and a generalist diet, which often aid their ability to quickly spread in a new environment (Meyer *et al.*, 2021). Invasive generalist predators may be especially damaging to native community assemblages due to altering food webs, reducing reproduction and survival in native species, as well as competing with native predators for resources (Doherty *et al.*, 2016; Ritger *et al.*, 2020).

Competition is viewed as a major evolutionary driving force in groups of related and morphologically similar species, which can ultimately lead to changes in the distribution and behaviour of the competing species (Bonesi and MacDonald, 2004c). Whereas in some cases invasive and native species may outcompete each other through resource competition (Mooney and Cleland, 2001; Li *et al.*, 2022), in other cases, competition avoidance through niche differentiation may allow coexistence (Griffen, Guy and Buck, 2008). Niche differentiation reduces the niche overlap, and thereby competition, between two species by either niche shift (occupying a different niche space) or niche contraction (reducing niche breadth by restricting the use of shared resources) (Carvalho and Cardoso, 2020). Given the opportunity, a species may also expand its niche, for example if competition is reduced (Lister, 1976). Anthropogenic disturbances, such as hunting and trapping, can encourage the establishment of invasive species by reducing competition from native species (Tilman, 2004). This may have been the case for two semi-aquatic mustelid species: the invasive American mink (*Neovison vison*), which spread throughout Norway whilst the native competitor, the Eurasian otter (*Lutra lutra*) was absent in most of Norway due to overhunting (Heggberget, 1996).

American mink was first introduced to Norway in 1927 for use in fur farming (Bevanger and Henriksen, 1995). Escapees quickly managed to spread, and within 35 years had colonized 80-85% of the Norwegian mainland, which parallels observations from Sweden, Iceland and

Finland (Bevanger and Henriksen, 1995). By 1993 the entire Norwegian mainland was colonized, with only a few mink-free island areas (Bevanger and Henriksen, 1995). Several factors play into the success of the invasive American Mink in Norway. Mink is a generalist predator with high reproductive capacity, allowing for rapid population growth (Dunstone, 1993). Wild populations also likely maintain a high degree of genetic variability considering at least 6-7 mink varieties have been used as progenitors in the fur farming industry since it started (Bevanger and Henriksen, 1995). Norwegian coastal areas are favourable habitats for the semi-aquatic mink, with a variety of food items like fish and crustaceans available throughout the year (Bevanger and Henriksen, 1995). Moreover, the mink was able to occupy this unexploited food niche whilst the Eurasian otter was scarce or absent.

When the American mink was introduced to Norway, the Eurasian otter population was low due to excessive hunting during the 20th century, with only some remnant populations in the counties Nordland and Hedmark in Northern and Eastern Norway, respectively (Heggberget, 1996; Landa and Guidos, 2020). After receiving its protective status in 1982, the otter has been able to re-establish large parts of its historical range along the Norwegian coastline (Heggberget, 1998). However, there is still not a well-established otter population south of Boknafjorden in Rogaland county (Eldegard *et al.* 2021b), north of which fish pots and traps are common, and drowning in fishing equipment is the most common cause of death for otters (van Dijk *et al.*, 2021). Nevertheless, some few and fragmented otters have been observed in southern Rogaland and Agder, indicating continued expansion southwards (Figure 1.1) (Artsdatabanken, 2023).

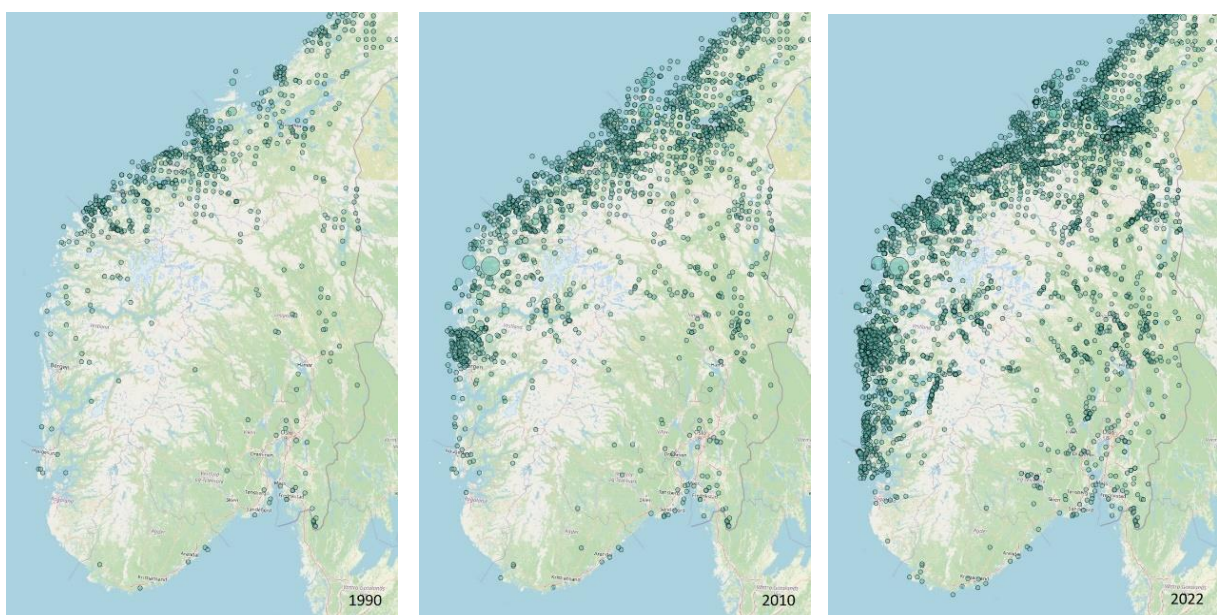


Figure 1.1 Distribution of otters in the southern part of Norway in 1990 (left), 2010 (middle) and 2022 (right). Data from Artskart.no.

Eurasian otters are the main competitors of American mink in western Europe, and in areas where otter populations were in good condition when mink arrived, the mink expansion rate was lower (Ruiz-Olmo *et al.*, 1997). Otter and mink occupy similar habitats, have overlapping diets, and are generally nocturnal (Harrington *et al.*, 2009). Otter is the dominant competitor due to their larger size (6-10kg, versus the mink at ~1kg), and are known to steal from, as well as kill mink in aggressive interactions (Bonesi and MacDonald, 2004a; Harrington *et al.*, 2009). In an experiment where otters were released into a mink-populated riverine area in England, the mink site-occupation decreased from 77% to 23% within one year (Bonesi and MacDonald, 2004c). However, in areas where otter re-establish naturally, the researchers expected mink populations to decline more slowly (Bonesi and MacDonald, 2004c). Several studies in Europe indicate a decrease in mink presence, which may be attributed to the simultaneous increase in the native otter population (Bonesi, Strachan and Macdonald, 2006; McDonald, O'Hara and Morrish, 2007). Field observations, local contact reports and trapping records give a similar impression in Norway (Heggberget, 2007). If otters are indeed able to suppress mink, then encouragement of re-establishing otters could be a practical way to reduce mink populations, which in turn could lessen the mink's negative impacts on vulnerable native species (Harrington *et al.*, 2009; Landa and Guidos, 2020).

American mink is reported to be one of the most impactful invasive mammal in Europe, affecting at least 47 native species, of which six are considered threatened (Genovesi *et al.*, 2012). Studies of the mink's impact on native species show that mink can have a significant effect on other mustelids, rodents, amphibians and ground-nesting birds (Bonesi and Palazón, 2007). The decline of native European mink (*Mustela lutreola*), as well as failed recovery attempts, is thought to be in part caused by competition with American mink (Põdra, Gómez and Palazón, 2013). Predation by mink has played a big role in the decline of the highly endangered water vole (*Arvicola amphibius*) in Britain (Bonesi, Strachan and Macdonald, 2006). Dense ground-nesting seabird colonies are especially vulnerable to mink predation, as mink will surplus-kill both chicks and adults (Clode and Macdonald, 2002). This problem has been highlighted in Norway, where mink is seen as one of the main causes of decline in several Norwegian seabird colonies, amongst other factors (The Norwegian Directorate for Nature Management, 2011). Some mink removal projects in Europe have led to positive effects on native fauna (Bonesi and Palazón, 2007), but the most effective removal projects in the long-term were carried out on small islands (Nordström *et al.*, 2002). Re-establishing otter may present less of a threat to some of the vulnerable species that mink prey on, as it

specializes on aquatic prey, and will only to a lesser extent prey on mammals, amphibians, and birds (McDonald, O'Hara and Morrish, 2007; Romero and Guitián, 2017). Among the semi-aquatic mustelids there is a tendency for the more aquatic mustelids to eat less birds, so although otters also may hunt in seabird colonies, the less aquatic mink is more likely to rely on birds in their diet (Harrington *et al.*, 2009; Riedman and Estes, 2011).

Otters are much better adapted to exploit aquatic food sources than mink and have been observed to exclude mink from their preferred habitat, as well as decrease the proportion of aquatic prey in the mink's diet (Bonesi and MacDonald, 2004a). The American mink in Europe shows a primary preference for fish, but its generalist diet makes it able to rely on alternative food sources like birds and mammals in the presence of otters (Romero and Guitián, 2017). Coexistence with otters may therefore be possible when alternative food sources are abundant (Bonesi and MacDonald, 2004c). Several European studies have observed niche differentiation in mink when otters are present: higher densities of otters led to a higher proportion of terrestrial prey in the mink's diet, and shifts in activity patterns from nocturnal to diurnal (Bonesi, Chanin and Macdonald, 2004; Harrington *et al.*, 2009). In areas where alternative prey was scarce, mink coexisted with otter for shorter times compared to areas with abundant terrestrial prey (Bonesi and MacDonald, 2004a). The isoleg theory predicts that coexistence is favoured between competing species when the dominant species is a specialist, the sub-ordinate species is a generalist, and the area has diverse enough habitats to allow the sub-ordinate generalist to segregate from the dominant specialist (Bonesi and MacDonald, 2004a). In its native habitat, the American mink does coexist with the North American river otter (*Lontra canadensis*), where diverse habitats allow for differential habitat use and foraging strategies (Harrington *et al.*, 2009).

In a status report about American mink in Great Britain it was argued that earlier findings of mink declining in response to re-establishing otter is misleading because they were based on scat surveys (Harrington *et al.*, 2020). In general, identifying field signs like scats can be problematic. DNA analysis of scats found in the Northern highlands of Scotland showed that even experienced surveyors were not able to accurately identify mink scats in the presence of other mustelids or small carnivores (Harrington *et al.*, 2010). Moreover, abundance and distribution of scats do not only depend on the abundance of the animal, but also on marking behaviour (Harrington *et al.*, 2010). Both otter and mink show seasonal variation in the amount of scats they deposit (Bonesi and MacDonald, 2004b; Kruuk, 2006). Mink has also been suggested to change its marking behaviour in the presence of otters, which makes any

inference about mink population changes based on scat findings potentially flawed (Harrington and Macdonald, 2015). Moreover, mink generally deposits scats much less frequently than otters, which makes scat surveys not ideal when comparing otter and mink abundance (Bonesi and MacDonald, 2004b). Additionally, scat surveys cannot provide information about the time of day an animal is active. Monitoring populations of mink, otter and other cryptic carnivores have often been based on detecting field signs rather than the animal itself, as more direct monitoring methods such as radio-tracking, marking and trapping are more costly and intrusive (Bonesi and MacDonald, 2004b; Harrington *et al.*, 2010). However, another direct monitoring tool, camera traps, is perceived as accessible and non-intrusive, and has also been found to more accurately detect otter activity at marking sites than scat surveys (Day *et al.*, 2016; Findlay *et al.*, 2017). Camera trap studies have become increasingly popular in recent years, and they are generally seen as a reliable monitoring tool (Delisle *et al.*, 2021).

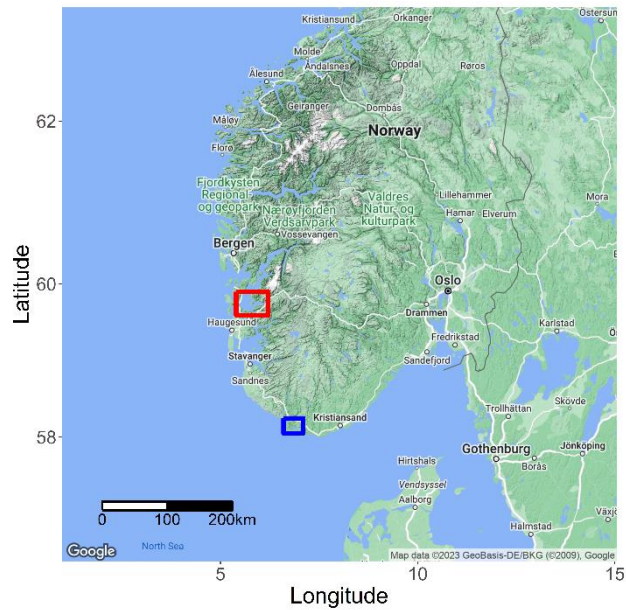
In this study I used camera traps to evaluate whether re-establishing Eurasian otters reduce or alter American mink activity in a fjord system on the southwest coast of Norway. I assessed changes in sighting frequency and circadian activity patterns of mink and otter over almost seven years within an area that otters returned to a decade ago. I compared the sighting frequency and circadian activity patterns of mink in the presence of otters with mink in an area where otters were not re-established yet. Because earlier studies have found that otters suppress mink and alter their activity patterns, I predicted that mink would have a lower sighting frequency and be more diurnal in the presence of otters. At the same time, I predicted that otter sighting frequency would increase over time, and that their activity patterns would not change.

2. Materials and Methods

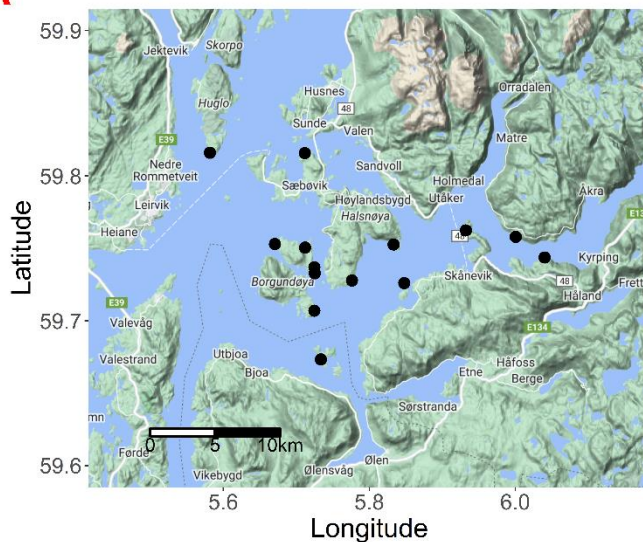
2.1 Study area

This study compared presence of mink and otter in Vestland, where otter populations are re-established, with mink presence in Agder, where otters are yet to re-establish. The impact region (with otters) is located on the southwest coast of Norway around Halsnøy, Vestland (59° 42' 0" N, 5° 47' 60" E), and consisted of 14 camera locations (Figure 2.1A). The control region (without otters) is located on the southern coast of Norway in Farsund, Agder (58° 8' 60" N, 6° 50' 60" E), and consisted of 13 camera locations (Figure 2.1B).

Both regions are fjord systems with narrow inlets surrounded by steep, mountainous terrain, and contains several islands. Most cameras were located by the shoreline and were surrounded rocky cliffs that slope into the water. Although the impact region in Vestland is sheltered by some islands to the west, both regions can be described as coastal, with dense macroalgae growth running along the coastline (Miljødirektoratet, 2023). Some of the most common fish families in the impact area are Gadidae and Labridae (Salvanes and Nordeide, 1993), which are also common in the control area along with Clupeidae (Brudeseth and Evensen, 2002; Fiskeri- og Kystdepartementet, 2013). Besides fish and other marine food sources, otter and mink also have access to several terrestrial prey such as rodents, amphibians, and birds. In addition to each other, some potential competitors in the regions are red fox (*Vulpes vulpes*), pine martens (*Martes martes*) and stoats (*Mustela erminea*).



A



B

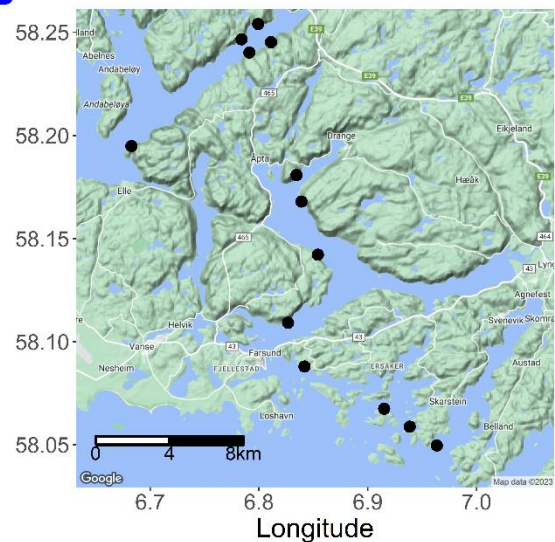


Figure 2.1 Locations of camera traps used to study mink and otter activity in the impact region (with otters) in Vestland (A) and in the control region (without otters) in Agder (B). Maps made with the ggmap package in R.

2.2 Study design and data collection process

Studies using camera traps have increased substantially: from less than 50 research papers per year between 1993 and 2003 to more than 200 per year in the following decade (Sharma *et al.*, 2020). The reliability of camera trap data has been debated, but while earlier studies did not recommend using camera traps due to commonly occurring camera malfunctions, newer studies have found camera traps to be a highly effective wildlife monitoring tool (Day *et al.*, 2016). Modern digital camera traps may provide more accurate and reliable data than indirect methods such as scat surveys, and will likely further improve with advancing technology (Day *et al.*, 2016). Camera traps can monitor continuously for months at a time and require

little maintenance, but have some limitations like the relatively high up-front costs, and the relatively small area they can monitor (Wearn and Glover-Kapfer, 2019). In a meta-analysis of 104 research papers from 1990 to 2017 comparing camera trap effectiveness to other sampling methods, digital camera traps were 65% more effective than alternative methods across a range of metrics (for example number of species detected and detection rate) (Wearn and Glover-Kapfer, 2019). Most camera traps use passive infrared motion detectors, which are thought to be effective for any endothermic species larger than 100g (Wearn and Glover-Kapfer, 2019). For examples of species caught on camera, see figure II in the appendix.

Since otter and mink use the same habitats and marking sites (Dunstone, 1993), the use of camera-traps in these areas allows for tracking population changes related to site occupancy over time for both species. In this study marking spots were located based on tips from locals, field observations of trails in vegetation and presence of scats. Each location needed to be accessible for both species, and also relatively easily accessible for camera maintenance and field survey. All cameras were therefore placed within at most ~15 metres of the shoreline, with similar substrate and vegetation, and with access to the ocean as well as freshwater puddles.

The camera-traps used were mainly the Reconyx™ HyperFire 2 (Reconyx Inc., Holmen, Wisconsin, USA). However, in 2016, 2017 and 2018, the Cuddeback™ E2 (Nontypical Inc., Green Bay, Wisconsin, USA) was also used. Both camera types use passive infrared motion detectors. The cameras were set to a 0.2 second trigger speed after detecting motion, and would capture three images per motion sequence, where each image is separated by 1 second. There was no pause between the sets of pictures. The cameras were placed facing the marking spot, 1-2 metres away and 20-30 cm above ground on metal supports bolted to exposed bedrock or larger rocks (Figure I, Appendix). Camera SD cards were collected, and batteries were replaced, if necessary, every 3 months. It was assumed that neither camera instalment nor routine checks had any effect on otter or mink activity as they were both often spotted within the same day of instalment/inspection.

The first cameras were placed in the impact region in Vestland in 2016, four years after the otter was first spotted returning to the area (Arild Landa, personal communication). More cameras were added throughout the years, and since 2020 there were 14 cameras in total. Cameras were placed in the control region in Agder in early 2021. When looking at differences in mink sighting frequency across the two regions, the studied timeframe is one year, from July 1st, 2021, to June 30th, 2022. When looking at the changes in mink and otter

sighting frequency over time, I used the impact region dataset which spans from February 11th, 2016, to August 12th, 2022. This same dataset will be used to look at changes in mink and otter rhythmic activity patterns over time. The mink rhythmic activity patterns in the impact region will then be compared to the one-year dataset from the control region.

2.3 Statistical analyses

Each animal sighting was defined on an hourly basis, meaning that observations of the same species were considered independent if there was an hour or more between their sightings. Similar to other comparable studies, this is done to reduce pseudoreplicates and keep data points independent (Wagnon and Serfass, 2016; Gil-Sánchez and Antorán-Pilar, 2020). Both Eurasian otter and American mink are solitary animals, which means sightings of more than one individual will usually be mother and pups (Thom *et al.*, 2004; Kruuk, 2006). Any sighting of multiple animals in the same image was therefore considered as one sighting, but with a litter present. The number of pups was not quantified because it was unlikely that all the pups would be present at the same time in one image, and they were usually large enough to make it difficult to tell them apart from the mother.

All statistical analyses were performed using R 4.1.1 (R Core Team 2021), and the statistical significance level for all models was set to $p < 0.05$.

2.3.1 Sighting frequency

Sighting frequency was based on the number of total monthly sightings, similar to Guidos *et al.* (2023.) For each camera, the sighting frequency was calculated by dividing the number of sightings per month by the number of days in the month the camera was active, and then multiplying by 100 to obtain an integer. This was done to account for the differing number of days in the different months, as well as camera failure.

To test for normality and homogeneity, I used Shapiro-Wilk's test and Levene's test (from R package "car": Fox and Weisberg, 2019) respectively. If the assumptions for normality and homogeneity were not met, a generalised linear mixed effects model (GLMM) was chosen. Ben Bolker's overdispersion test (Bolker *et al.*, 2022) was used to check for overdispersion, and if it was present, a negative binomial GLMM was used.

2.3.1.1 Sighting frequency across regions

To compare total mink activity in the impact and control region, I used a negative binomial GLMM (from R package “glmmTMB”: Brooks *et al.*, 2017), with region as predictor and mink sighting frequency as response, with camera location and month as random effects.

To compare how mink activity varies between the regions during the different months of the year, I used a negative binomial GLMM, with mink sighting frequency as the response, month and region as predictors, and location as a random effect. To determine if there is a significant difference between months, I used a Tukey HSD post-hoc multiple comparisons test (from R package “lsmeans”: Lenth, 2016).

2.3.1.2 Sighting frequency over time

To look at changes in mink and otter sighting frequency over time in the impact region, I used a negative binomial GLMM, with time as predictor and sighting frequency as response, with location and month as random effects.

2.3.2 Rhythmic activity patterns

Based on latitude and longitude for each camera trap, I assigned dusk and dawn time periods for each date in the dataset, using the R package “suncalc”: Thieurmel and Elmarhraoui, 2022). Every sighting got assigned the dusk and dawn time period for that date, as well as a “Light” or “Dark” category based on if the sighting was after dawn and before dusk, or after dusk and before dawn, respectively. This was done to control for the varying amount of daylight throughout the year.

To look at changes in otter and mink rhythmic activity patterns over time in the impact region, as well as compare mink rhythmic activity between the impact and control region, I used Pearson’s chi-squared test. For mink and otter in the impact region, I compared the proportion of nocturnal activity between the different years in the dataset. The one-year dataset from the control region was compared to each year in the impact region for mink.

3. Results

3.1 Camera registrations

Cameras were active in the impact region in Vestland for a total of 34877 days between all camera locations ($n = 14$) throughout the study period between February 2016 and August 2022. In total, otter was caught on camera 8946 times, and mink was caught on camera 2271 times. Otter litters were sighted 824 times, at all times of the year, but were least common during summer months, and mink litters were sighted 8 times, all in summer and autumn (Figure 3.1A).

Cameras were active in the control region in Agder for a total of 4259 days between all camera locations ($n = 13$) throughout the study period between July 2021 to June 2022. In total, mink was sighted 1433 times, and otter was sighted 52 times. 31 of the otter sightings were in one camera location, whilst the rest were divided between six other camera locations. Mink litters were caught on camera 12 times, mainly during summer (Figure 3.1B). No otter litters were sighted in the control region.

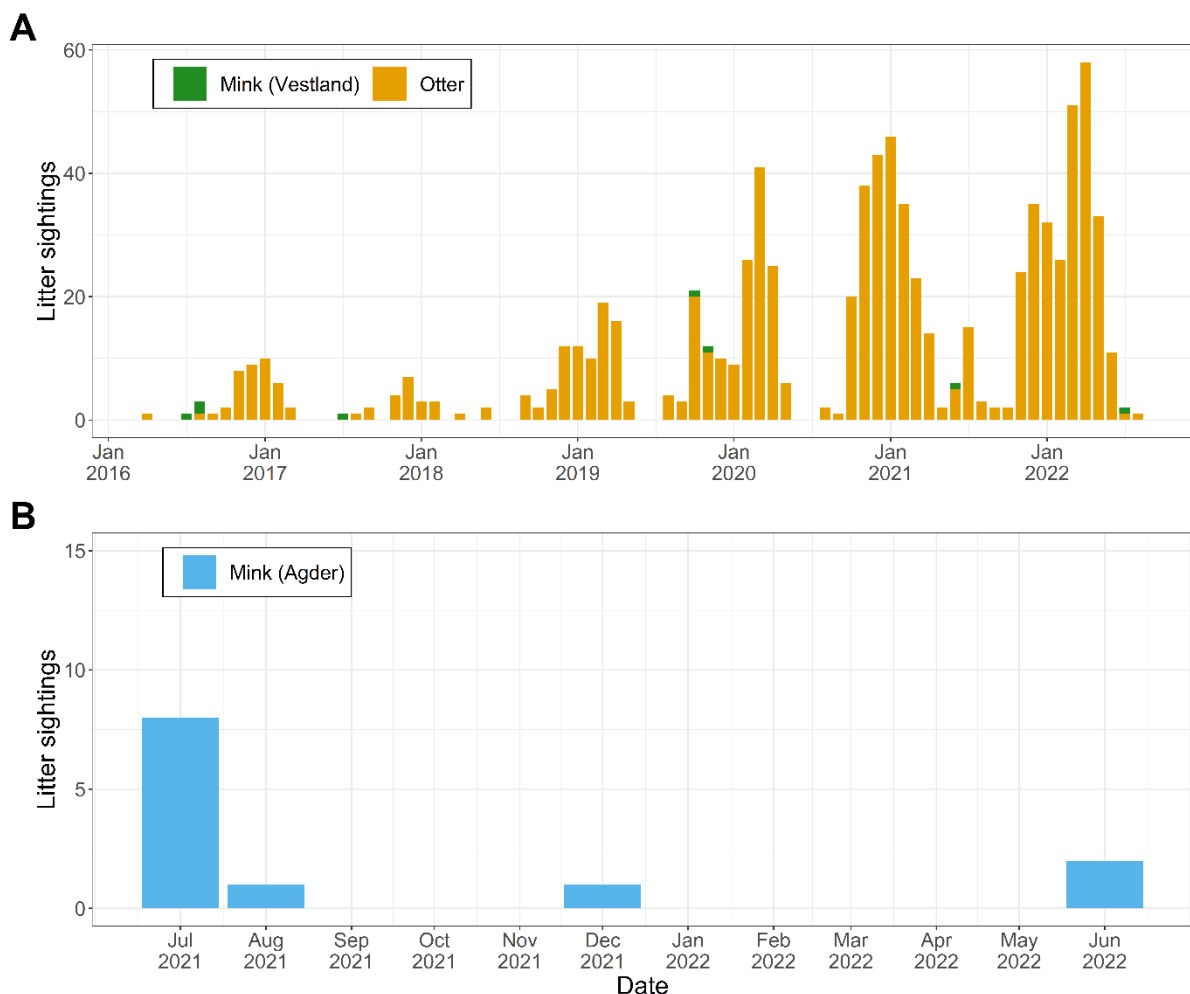


Figure 3.1 Number of otter and mink litter sightings per month over an almost seven-year period in the impact region in Vestland (A). Number of monthly mink litter sightings over one year in the control region in Agder (B).

3.2 Sighting frequency across regions

The mean total sighting frequency of mink from July 2021 to June 2022 was lower in Vestland (with otters) than in Agder (without otters) ($\bar{x} = 14.9 \pm 19.8$ and $\bar{x} = 26.9 \pm 30.9$, respectively) (Figure 3.2). However, the difference in overall sighting frequency was not statistically significant (negative binomial GLMM, $p = 0.104$, $SE = 0.41$).

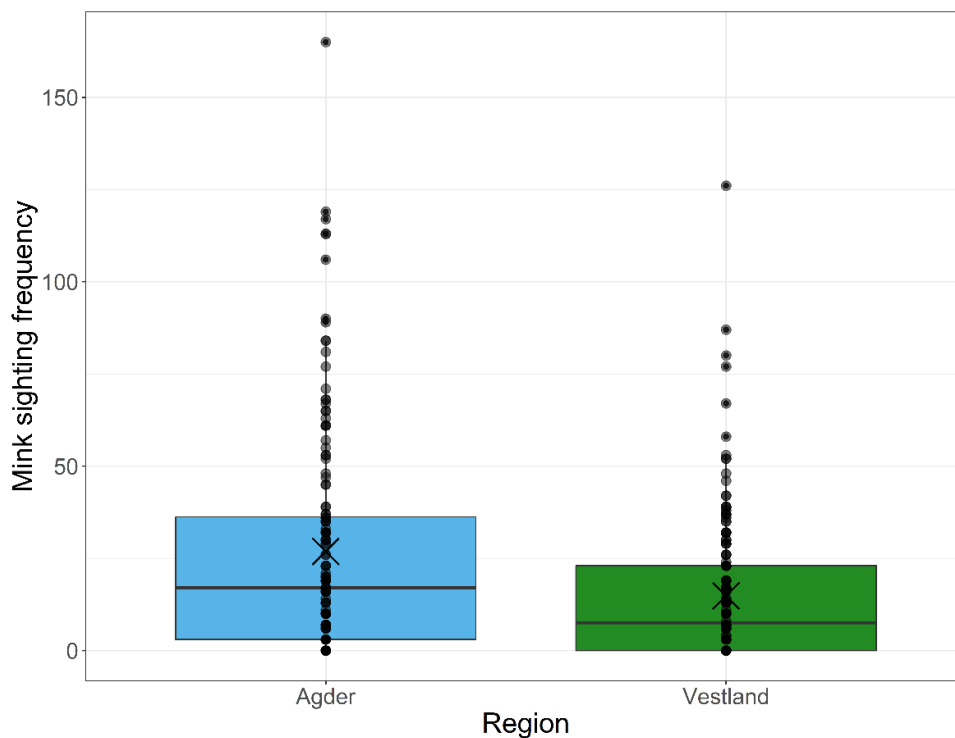


Figure 3.2 Comparison of total mink sighting frequency in the control region (Agder, without otters) and the impact region (Vestland, with otters) for one year. Each point represents the mink sighting frequency of one month in one camera location. The “X” marks the mean sighting frequency for the entire region for the whole year.

On a monthly basis, mean sighting frequency of mink was higher in Agder compared to Vestland for all months except November (Figure 3.3A). Nevertheless, the difference in overall mink sighting frequency between the regions was not statistically significant for any of the months. Within both regions the mean sighting frequency was highest in March and had decreased significantly in May in both regions (Tukey HSD, Agder: $p = 0.03$, $SE = 0.28$, Vestland: $p = 0.04$, $SE = 0.343$), as well as in June in Vestland (Tukey HSD, $p = 0.045$, $SE = 0.329$). The overall pattern in both regions show a peak in sighting frequency in March, but in Agder there is also a smaller peak in August-September which is absent in Vestland (Figure 3.3A). The mean sighting frequency of otters in Vestland was also highest in March (Figure 3.3B) and was significantly higher than the previous months July (Tukey HSD, $p = 0.003$,

SE = 0.200), August (Tukey HSD, $p = 0.008$, SE = 0.222), and September (Tukey HSD, $p = 0.018$, SE = 0.239), as well as the following month June (Tukey HSD, $p = 0.01$, SE = 0.179).

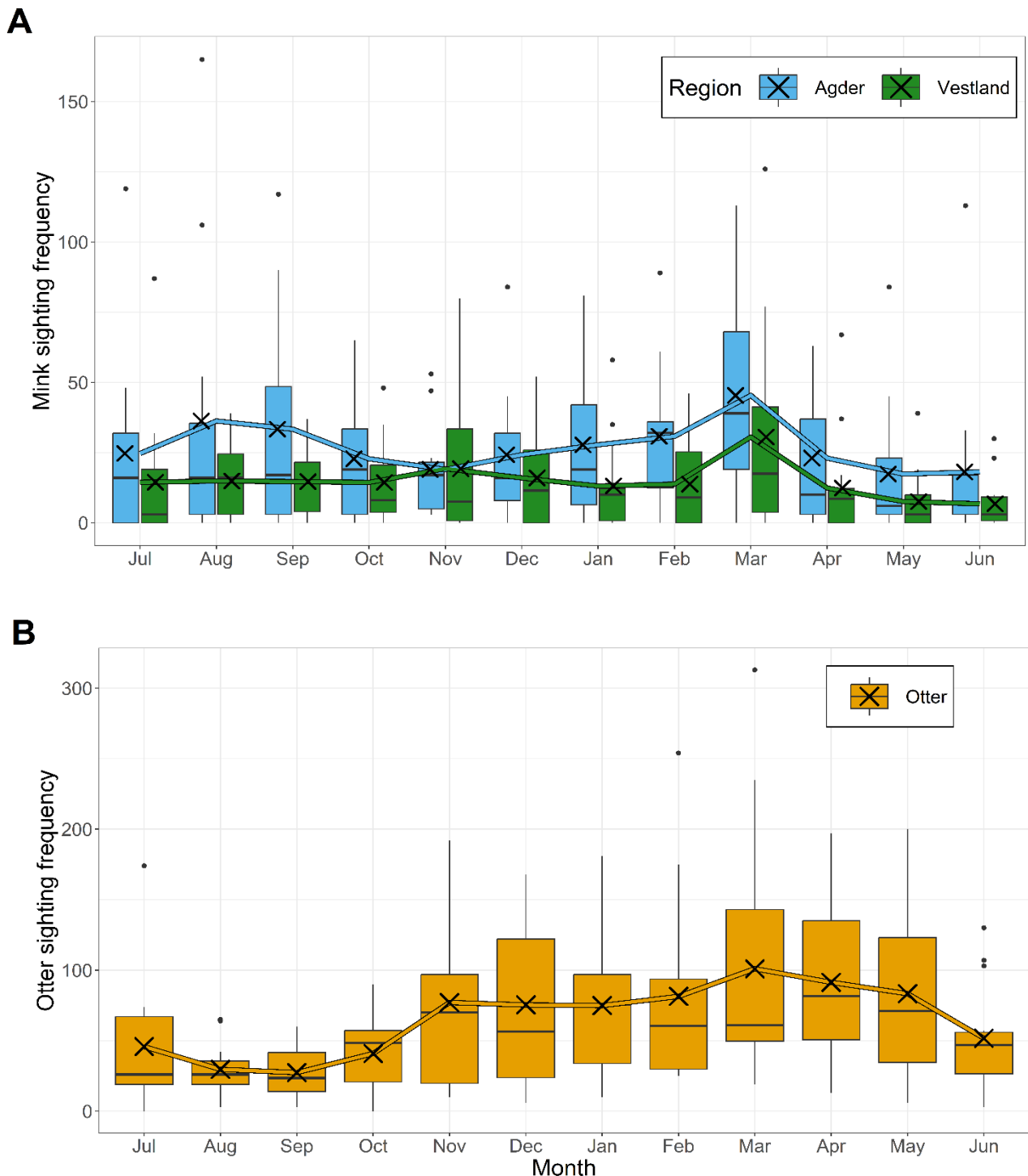


Figure 3.3 Comparison of mink sighting frequency on a monthly basis in the control region (Agder, without otters) and the impact region (Vestland, with otters) for one year (A). Otter sighting frequency on a monthly basis in Vestland for one year (B). “X” marks the mean sighting frequency of all camera locations in the respective regions for each month. Lines between mean values illustrate the overall pattern.

3.3 Sighting frequency over time

From February 2016 to August 2022 in Vestland, the mean sighting frequency of otter increased from $\bar{x} = 20.0 \pm 18.5$ in 2016, to $\bar{x} = 72.7 \pm 58.1$ in 2022 (Figure 3.4). The overall otter sighting frequency in Vestland increased significantly over the almost 80-month study period (negative binomial GLMM, $p < 0.001$, $SE = 0.0014$).

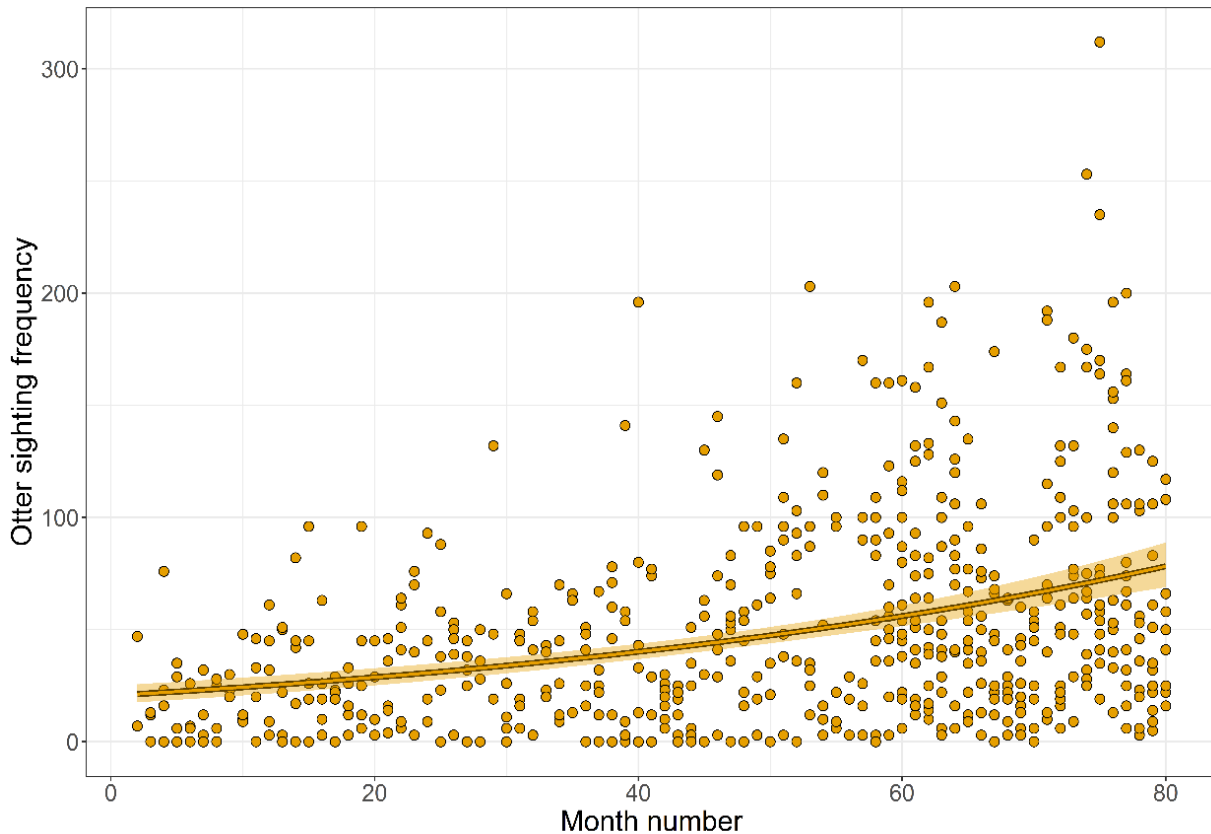


Figure 3.4 Changes in otter sighting frequency over an 80-month period in the impact region (Vestland).

Sighting frequency of mink in the impact region in Vestland did not appear to noticeably change over the 80-month study period (Figure 3.5), decreasing slightly from $\bar{x} = 16.3 \pm 12.4$ in 2016, to $\bar{x} = 12.4 \pm 18.6$ in 2022. Moreover, there was no significant change in the overall mink sighting frequency over the almost seven-year study period (negative binomial GLMM, $p = 0.33$, $SE = 0.002$).

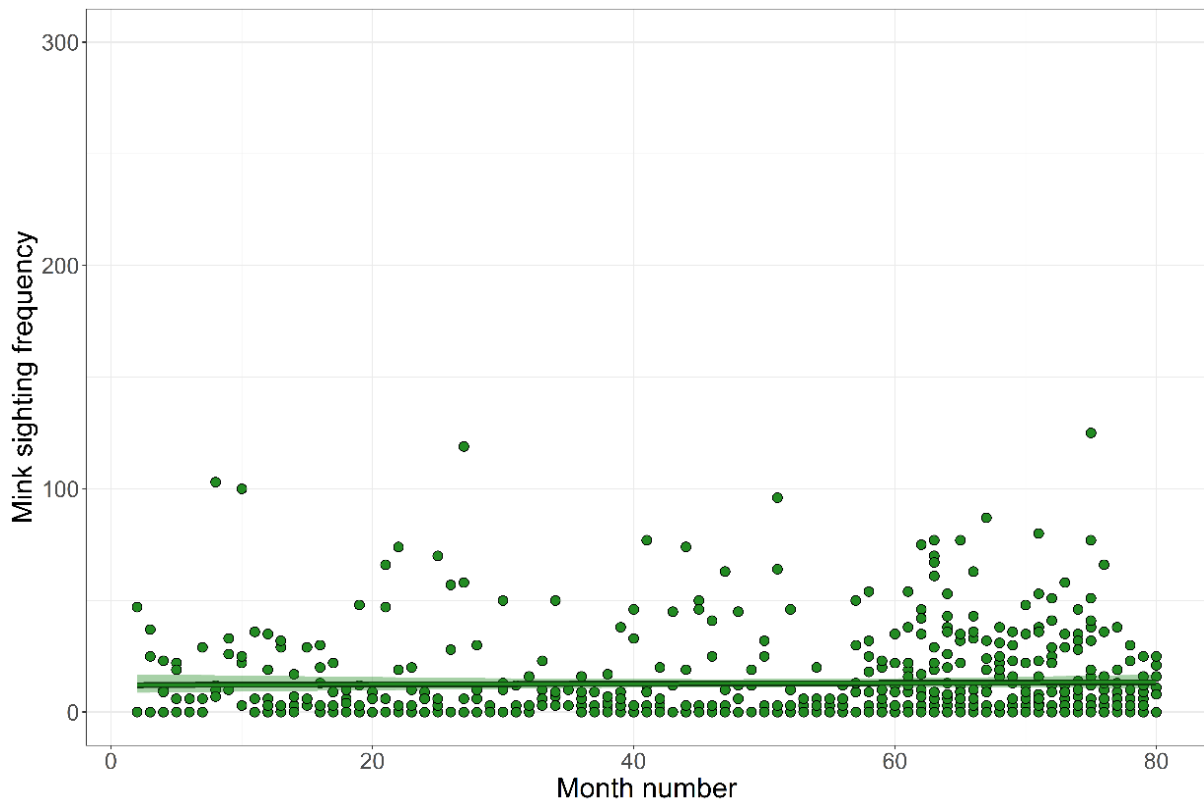


Figure 3.5 Changes in mink sighting frequency over an 80-month period in the impact region (Vestland), where otters are present.

3.4 Rhythmic activity patterns

Otters in the impact region were predominantly nocturnal throughout the almost seven-year study period (Figure 3.6), with proportion of nocturnal sightings in each year ranging from 69% to 82%. The mean proportion of nocturnal activity for the whole study period was $\bar{x} = 77.7\% \pm 4.4\%$. The proportion of nocturnal activity in otter remained relatively stable between the years, but decreased slightly in later years. Between 2019 and 2020 the nocturnal activity decreased from 81% to 77%, respectively ($\chi^2 = 4.5$, $p = 0.03$). Between 2021 and 2022 the nocturnal activity decreased from 76% to 69%, respectively ($\chi^2 = 22.5$, $p < 0.001$). However, 2022 does not include data from the whole year, as the dataset ended August 12th.

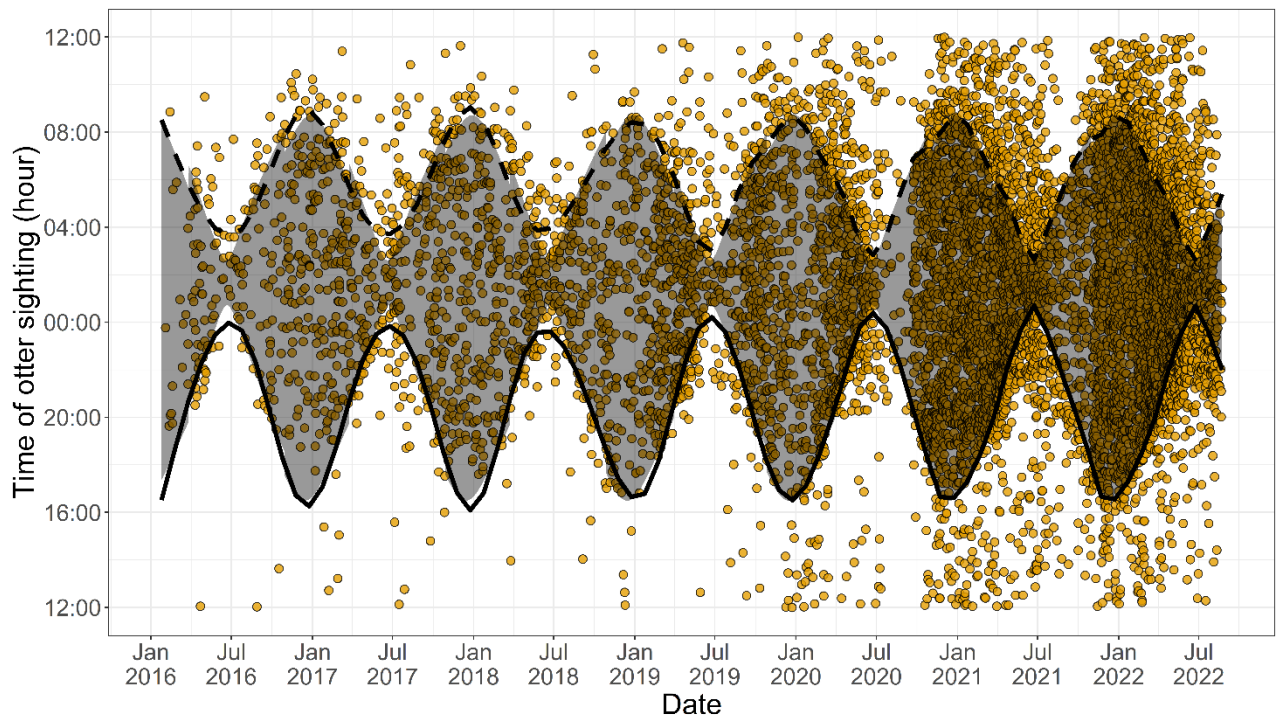


Figure 3.6 Time of day when otters were sighted in the impact region (Vestland) throughout an almost seven-year period. Each point is an otter sighting. Lines show how the time of dusk and dawn varies throughout the year. The dashed black line represents dawn, the solid black line represents dusk. The shaded area between dawn and dusk represents the time of day when it is dark out, and any sighting within this area is nocturnal.

Activity of mink in the impact region was more spread out throughout the day compared to the otters (Figure 3.7). The proportion of nocturnal sightings in each year ranged from 44% to 66%, and the mean proportion of nocturnal activity for the whole study period was lower than for otters with $\bar{x} = 56.6\% \pm 6.8\%$. The lowest proportion of nocturnal activity (44%) was in 2016, the first year of the study period, which increased significantly in the following year to 60% ($\chi^2 = 5.2, p = 0.02$). From 2018 to 2019 the proportion of nocturnal activity decreased significantly from 66% to 54% ($\chi^2 = 4.0, p = 0.046$). Otherwise, there were no significant changes between the years, and the proportion of nocturnal activity in mink remained relatively stable.

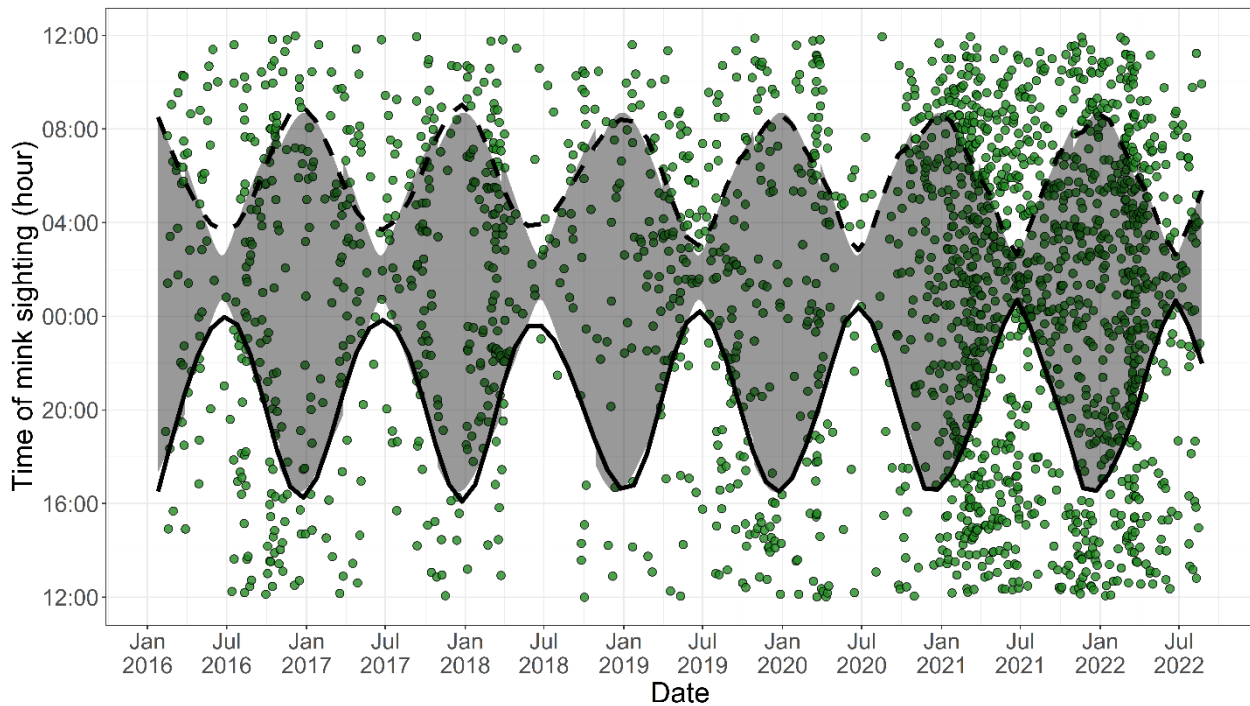


Figure 3.7 Time of day when minks were sighted in the impact region (Vestland) throughout an almost seven-year period. Each point is a mink sighting. Lines show how the time of dusk and dawn varies throughout the year. The dashed black line represents dawn, the solid black line represents dusk. The shaded area between dawn and dusk represents the time of day when it is dark out, and any sighting within this area is nocturnal.

The study period of mink activity in the control region spanned one year, from July 2021 to June 2022. Compared to the impact region in Vestland, mink activity was more diurnal in the control region in Agder (Figure 3.8). The proportion of nocturnal activity for mink in the control region was 34%. The first year of the study period of Vestland, 2016, with 44% nocturnal activity was not significantly different from the one-year period in the control region ($\chi^2 = 2.8$, $p = 0.09$). However, all the other years from the impact region had significantly higher proportions of nocturnal activity than the one-year period in the control region: 2017 with 60% nocturnal activity ($\chi^2 = 22.7$, $p < 0.001$), 2018 with 66% ($\chi^2 = 38.9$, $p < 0.001$), 2019 with 54% ($\chi^2 = 17.2$, $p < 0.001$), 2020 with 55% ($\chi^2 = 17.2$, $p < 0.001$), 2021 with 57% ($\chi^2 = 42.3$, $p < 0.001$), and 2022 with 60% ($\chi^2 = 39.0$, $p < 0.001$).

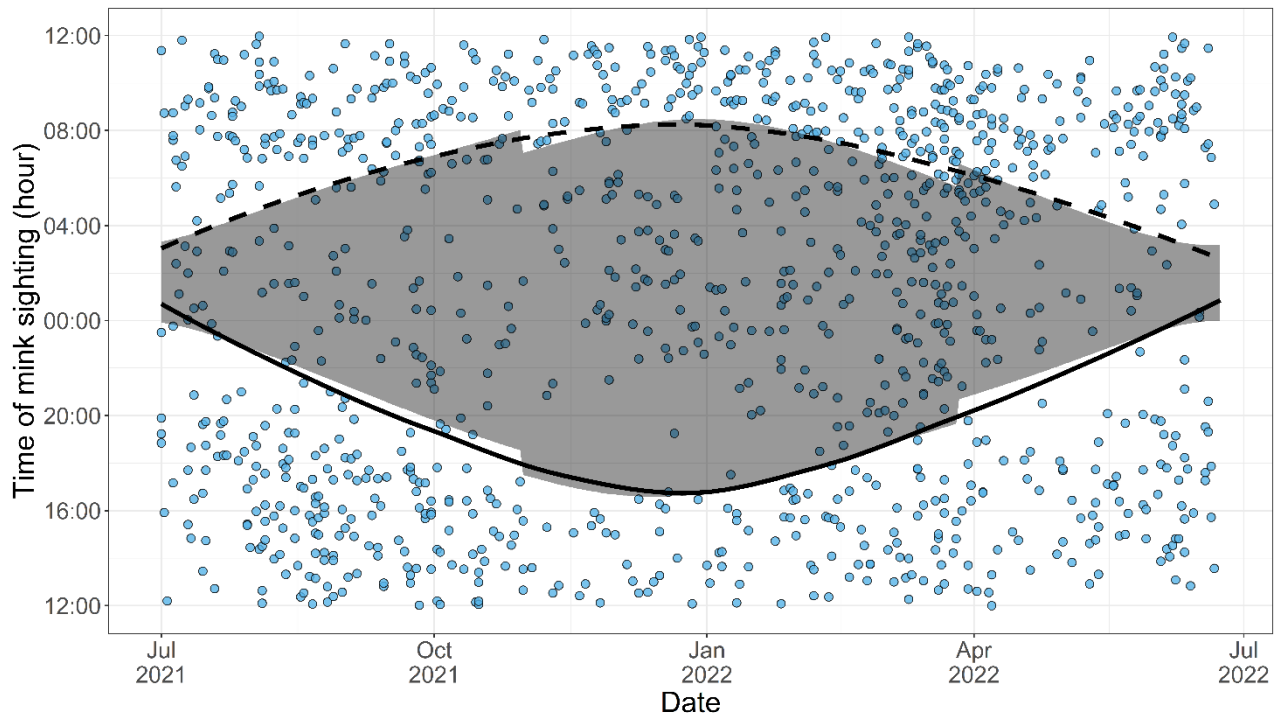


Figure 3.8 Time of day when minks were sighted in the control region (Agder, without otters) throughout a one-year study period. Each point is a mink sighting. Lines show how the time of dusk and dawn varies throughout the year. The dashed black line represents dawn, the solid black line represents dusk. The shaded area between dawn and dusk represents the time of day when it is dark out, and any sighting within this area is nocturnal.

4. Discussion

4.1 Camera registrations

When considering how much longer cameras were active in Vestland compared to Agder (almost seven years, compared to one year, respectively), there were not that many more mink caught on camera in Vestland (2271, versus 1433 in Agder). Although there were fewer cameras in the beginning of the study period in Vestland, the total number of active camera days in Vestland and Agder (34877 and 4259, respectively) shows the marked difference in monitoring times. The small difference in mink sightings could therefore indicate a more active mink population in the control area.

In Vestland mink litters were most common during the summer and autumn months and were also most common during summer in Agder. The breeding season of mink in northern Europe is in March, followed by the birth season in May, and the dispersal of pups usually starts in August (Dunstone, 1993). Consequently, it is reasonable that mink litters were mainly caught on camera during summer or early autumn. An interesting finding is that more mink litters were sighted in Agder in one year than during the almost seven-year study period in Vestland (12 compared to 8, respectively). This could indicate that minks have fewer litters in Vestland, or that mothers avoid bringing their pups to the common marking sites where the cameras are placed. (Harrington *et al.*, 2009) found that mink in the presence of otters have decreased body condition, possibly due to stress, which can lead to higher rates of reproductive failure, and thus population declines in the long-term. It is also noteworthy that mink pups seemed harder to catch on camera than otter pups. The minks moved very fast, which made the cameras less likely to capture more than one individual in the same frame. However, the difference in mink litter sightings between the impact and control regions is still likely ecological as the same camera models and settings were used in all locations, which means this bias would exist across both regions.

Otter litters were sighted at all times of the year but were least common in summer. Otters have a more flexible timing of reproduction than mink, and can have pups year-round (Heggberget and Christensen, 1994). However, Heggberget and Christensen (1994) found that on the coast of Norway, the main birth peak occurred during summer and autumn, due to seasonality in prey availability. The fewer litter sightings during summer are therefore likely because the mother and new-born pups are restricted to dens. Figure 3.1A shows an increasing number of litters sighted over time, which is affected by fewer cameras in the beginning. However, since 2020 no more cameras were added, and there still seems to be an

increase in the following years, which could mean otters are becoming more abundant in the impact area of this study. On the other hand, most otter sightings in the control area were on the same camera, which indicates that otters are not yet common in the area but are starting to return.

4.2 Sighting frequency across regions

The mean sighting frequency of mink in total and on a monthly basis was higher in Agder compared to in Vestland, but the difference was not significant. Still, it could indicate higher mink activity in the control area. The high variability in sighting frequencies could make effects more difficult to detect (Altman and Krzywinski, 2015), which could be improved by using more camera locations, and thus more data (Moore, McCabe and Craig, 2017). The highest mean sighting frequency in both regions was in March, and in Vestland there was also a smaller peak in August-September. These peaks coincide with the breeding season and the dispersal season, respectively. The drop in activity from March to May-June likely represents decreased female activity due to birth, where mother and pups are restricted to dens (Dunstone, 1993). However, the dispersal season peak was absent in Vestland, which could suggest that mink have fewer pups in the presence of otter, or that fewer pups make it to the dispersal season. Few mink litters were caught on camera in Vestland.

The highest mean sighting frequency for otters was also in March, but otter activity was more steadily high from November to May, compared to mink. The lower activity in summer and early autumn coincides with the fewer litter sightings in figure 3.1A, which further supports that mother and new-born pups could be restricted to dens during this time period.

4.3 Sighting frequency over time

The sighting frequency of otters in Vestland became significantly higher over almost seven years. Although there were fewer cameras, and thus less data in the beginning, the overall pattern indicates increasing otter activity over time. The difference between the years was considered in the statistical model, and since the data points represent sighting frequency on a monthly basis, it is likely that even with more data in the beginning, the points would not necessarily have higher values, unless several highly active locations were missing. Overall, in accordance with the increasing litter sightings in figure 3.1A, it is likely that that otters are becoming more active or abundant in the impact area in Vestland.

There was no significant change in the sighting frequency of mink over almost seven years in Vestland. Moreover, the line looks straight, although the mean sighting frequency is slightly lower at the end compared to the beginning. There is the same problem as with the otters with fewer data points at the start of the study period, which means there could have been higher sighting numbers in the beginning. However, this is questionable since, as previously explained, additional data points would likely not have higher values unless several highly active locations were missing. Previous studies found that mink activity decreases in the presence of otters (Bonesi, Strachan and Macdonald, 2006; McDonald, O'Hara and Morrish, 2007), but the results of this study do not support this finding. However, the results support that mink is suppressed and not increasing in activity in the impact area. The low activity during dispersal season further supports that there is likely little recruitment to newer generations of the mink population in Vestland. Bonesi and MacDonald (2004c) found that mink populations decreased most dramatically during the first year after otters were intentionally introduced, and later stabilized at a lower level than before otters were introduced. No such dramatic decrease is visible in this study's data, but since otters reportedly arrived in the impact area four years before the study started, it is possible that the mink population already experienced its most dramatic decrease.

It is also possible that mink populations did not decrease in the presence of otters, but rather were displaced from the coastal area. However, Bonesi and Macdonald (2004a) argues that even in the presence of otters, mink do not become exclusively terrestrial, and are still tied to the water. Mink would therefore likely not completely abandon the coastal environment. Additionally, inland habitats are inhabited by other potential competitors like red fox, pine martens and stoats, which would likely compete for the same terrestrial resources as mink. For example, Carlsson *et al.*, (2009) found that mink populations in Sweden increased when red fox populations were struggling, and then subsequently decreased when the fox populations recovered.

4.4 Rhythmic activity patterns

Otters in Vestland were mainly nocturnal, with around 80% of activity happening whilst it was dark, similar to (Findlay *et al.*, 2017). The proportion of nocturnal activity remained relatively stable throughout the study period, but a noticeable decrease occurred between 2021 and 2022 (76% to 69%, respectively). It is possible that a larger and thus denser population leads to resource partitioning with more variation in activity patterns (Findlay *et al.*, 2017).

However, the dataset from 2022 ended August 12th, and it is possible that there could have been more nocturnal activity later that year that would bring the nocturnal activity back up to the same level as previous years. The previous year (2021) displayed this seasonality, with 71% and 81% nocturnal activity in the first and second half of the year, respectively. The larger amount of data in later years in figure 3.6 also makes it look like there is more diurnal activity, but the proportion of nocturnal activity is still comparable to previous years and is relatively stable at around 80%. Additionally, Eurasian otters are predominantly nocturnal in most of their range (Harrington *et al.*, 2009), with some exceptions like in the Scottish Isles (Kruuk, 2006).

The activity of mink in Vestland was spread more throughout the day compared to otters, with around 55-60% nocturnal activity. This could indicate that otters displace mink from nocturnal activity, as is seen in another study (Harrington *et al.*, 2009). However, the lowest proportion of nocturnal activity (44%) was observed during the first year of the study period, which is closest to when otters first arrived in the area. This could mean that when otters first arrived, minks were more drastically displaced, and that this mellowed out a bit later, as the proportion of nocturnal activity became more stable in the following years. Another possibility is that otters were not able to permanently displace the activity patterns in mink, or that additional pressures like diurnal predators prevent mink from switching to predominantly diurnal activity. One such apex predator is the white-tailed eagle (*Haliaeetus albicilla*), which is one of few natural predators of mink in the coastal region of Norway (Fylkesmannen i Aust- og Vest-Agder, 2017), and its population has increased substantially in the last 40 years, with a stronghold in western Norway (Heggøy and Øyen 2014). An example of altered activity patterns in the face of diurnal predators, is the Island fox (*Urocyon littoralis*), which increased nocturnal activity in the presence of golden eagles (*Aquila chrysaetos*), and reverted to diurnal activity after eagle removals (Hudgens and Garcelon, 2011).

The mink in Agder was more diurnal compared to the mink in Vestland, with 34% nocturnal activity, which was surprising since mink was expected to be more nocturnal when not competing with otter. Minks are often reported as mainly nocturnal, but diurnal activity has also been recorded, particularly in females (Dunstone, 1993; Wellman and Haynes, 2009). Dunstone (1993) pointed out that the activity patterns of an opportunistic forager like mink can be variable and complex, as they often depend on the activity patterns of prey. Small mammals like mice and rabbits are mostly active at night, or are crepuscular, and birds are mainly diurnal, but can still be predated at night (Dunstone, 1993). Aquatic prey, however, is

easier to hunt during the day because the visual capacity of mink is limited under water (Dunstone, 1993; Harrington *et al.*, 2012). The American mink in Europe shows a primary preference for fish (Romero and Guitián, 2017), and it is possible that in a coastal region absent of otters, minks are more likely to rely on fish rather than small mammals like mice. Similar inferences were made by Poláčková *et al.* (2022). Mink in Agder were several times caught on camera carrying fish, which indicates that fish is an important food source in this area and could explain why mink is more diurnal in Agder.

All years of the study period in Vestland except the first (2016) had significantly higher proportions of nocturnal activity than the one-year period in Agder. 2016 was not significantly different to the control region and was only four years after otters reportedly came back to the area. It is therefore possible that the mink activity in 2016 most closely resembles mink activity before otters arrived. This could indicate that minks were originally more diurnal in Vestland, like they are in Agder, as one could assume fish is an important food source there as well, and that mink in Vestland currently eats more nocturnal prey to avoid competing for fish with otters. Similarly, the European green crab (*Carcinus maenas*) consumes fewer mussels, its preferred prey, around the dominant competitor Asian shore crab (*Hemigrapsus sanguineus*) (Griffen, Guy and Buck 2008). There is, however, no data on mink activity in the impact region from before otters arrived, so it cannot be verified whether the low proportion in 2016 was a pattern or just variation in the data. It is also only 2016 that has a relatively low proportion of nocturnal activity (44%), and this increases substantially already the next year (to 60%), before it stabilizes around that level for the rest of the study period.

4. 5 Limitations of the study

It has been suggested that the infrared camera traps used in this study could struggle to detect semi-aquatic animals like otter and mink when their fur is soaked with cold water (Findlay *et al.*, 2017). However, several otters and mink were captured on camera exiting water, even in winter, throughout this study.

There were fewer cameras, as well as more camera malfunctions in the beginning of the study period in Vestland. There were also some camera malfunctions in the one-year study period (July 2021 to June 2022), but only in Vestland. Four out of the 14 camera traps in Vestland experienced malfunctions where 2-4 months of recordings were missing, and these were all in

the same months (July-October). The missing data coincides with the dip in otter and mink sighting frequency in figure 3.3. However, camera malfunctions were considered when calculating sighting frequency, and the dips make sense ecologically, as discussed in sections 4.1 and 4.3.

Although the minks in Agder seem more active than in Vestland, there was no significant difference in the registered sighting frequency between the two regions. It is possible however, that with high variability in sighting frequencies there was too little data, and that the study period was too short to see a significant difference. More camera locations and data may be needed to discover the difference in mink activity between the regions.

The rhythmic activity of mink in Vestland may be influenced by the confounding effect of the diurnal apex predator white-tailed eagle. Whilst otters could push mink towards more diurnal activity, white-tailed eagles may push towards more nocturnal activity. Moreover, there is a larger recorded breeding population of white-tailed eagles in Vestland, compared to Agder (Heggøy and Øyen 2014). However, there is no data available for the impact region that could control for effects of white-tailed eagles on the activity patterns of mink. There is also no data that could control for effects of potential competitors like red fox, pine martens and stoats on mink abundance and activity patterns. However, these competitors would likely have similar effects in both regions as there is no indication of differing distribution and population sizes between Vestland and Agder (Eldegard *et al.* 2021a, Eldegard *et al.* 2021c, Eldegard *et al.* 2021d).

4.6 Implications of the study

When American mink was introduced to Norway, the otter population was low, which could have provided a niche expansion for mink, as mink would likely not have become as numerous if otter had been present at the time of introduction (Ruiz-Olmo *et al.*, 1997).

Crego, Jiménez and Rozzi (2018) found that on a remote island free of predators, mink was more diurnal (owing to diurnal prey) and was active in a larger area compared to in its native habitat. Similarly in Norway, the absence of otter in Agder could have allowed the mink to preferentially prey on fish, which likely explains the diurnal activity. Otters are expected to re-establish in the south of Norway eventually, and the few observations of otters in Agder, indicates that they are starting to return. However, the frequent drowning of otters in fishing equipment in southwestern Norway (van Dijk *et al.*, 2021) could continue to act as a

competitive release for mink in both regions, allowing the mink to coexist with otter for a longer time period. However, despite a high number of deaths in fishing gear, the otter population seems to be increasing in the impact area.

Whilst some studies have found that re-establishing otters suppress mink in Europe, other studies found that mink are still abundant and have instead changed their behaviour, thus facilitating coexistence (Harrington *et al.*, 2009; Harrington and Macdonald, 2015). This study supports both arguments, as mink populations in Vestland are not increasing, and minks have differing activity periods in the impact and control area. In its native habitat, the American mink does coexist with the North American river otter, which is attributed to diverse habitats which permit differential habitat use and foraging strategies (Harrington *et al.*, 2009), in accordance with the isoleg theory (Bonesi and MacDonald, 2004a). Coastal areas are diverse and productive ecosystems, which is likely to enhance coexistence between otter and mink in Norway (Bonesi, Dunstone and O'Connell, 2000). Additionally, rodents were often caught on camera, and although they were not monitored using standard methodology, the frequent mice activity registered in both regions indicates a considerable alternative food source for mink.

Christensen (1995) found that in the presence of otters, minks show a preference for agricultural land, but shows no preference between wild or developed habitat in the absence of otters. This indicates that otters can exclude mink from their preferred habitat, which has also been found in a previous study (Erlinge, 1972). However, this study was based on scat surveys, and changes in scat frequency may be due to changes in marking behaviour rather than changes in the population. Furthermore, Bonesi and MacDonald (2004a) argue that even in the presence of otters, mink do not become exclusively terrestrial, and are still connected to the water. Still, human settlements could provide a refuge for mink from the competition of otters.

The case of otter and mink in Europe is the opposite of what is normally associated with invasions. Whilst the invasive mink is established, the native otter is returning to its natural habitat, and it is also the native otter that affects the activity of mink, whilst presence of mink has little effect on otter activity (Harrington *et al.*, 2009). However, there are other examples of invasive species who became established whilst a native predator was absent and were subsequently impacted by recovering native predators. The North American grey squirrel (*Sciurus carolinensis*) was introduced to Britain around the year 1900 whilst the pine marten (*Martes martes*) was largely absent (Slade *et al.*, 2023). The grey squirrel population

increased substantially, thus replacing the native Eurasian red squirrels (*Sciurus vulgaris*) (Twining *et al.*, 2022). After the pine marten received its protective status in the 1970s, the red squirrel population decline was reversed (Twining *et al.*, 2022). A lack of anti-predatory behaviours and refuges for the invasive grey squirrels led to pine martens preying upon grey squirrels at a greater frequency compared to native red squirrels (Slade *et al.*, 2023). Similarly, the re-establishment of otters on the coast of Norway could lessen the invasive mink's impact on vulnerable native species. However, the extent of the impact of competition likely depends on several factors: (1) the relative density between the native and invasive species, (2) the invasive species' access to spatial and temporal refuges, and (3) the level of naivety of the invasive species in the face of a novel threat, meaning how likely it is to respond appropriately to the threat (Twining *et al.*, 2022).

4.7 Suggestions for future research

Since the diurnal activity of the mink in Agder could be due to a more fish-based diet, I would recommend examining the difference in diets of mink between the impact and control region. Assumptions from this study suggest that the more nocturnal mink activity in Vestland is due to a higher proportion of nocturnal prey in their diet, whilst the more diurnal mink activity in Agder is due to Mink being better able to fish in the daylight. I would also recommend looking into the distribution and seasonality of the different potential food sources of mink, particularly rodents, as they likely provide a substantial alternative food source when competing with otter. Comparing the body condition of mink in Vestland and Agder could also give an insight into general health and potential longevity of mink populations. At the same time, it could be interesting to see if mink activity is different in areas where otters were never absent, as this also could give information about the long-term effects of otter on mink.

Because one of the most highlighted problems with mink in Norway is their impact on seabird colonies, it would be interesting to see if mink has more of an impact on seabirds in the south of Norway where otters have not re-established yet. In a seabird report that covers the control area in Farsund, Agder, several species were reported to specifically have been impacted by mink (Olsen, 2022). There were generally few seabirds breeding in the area, and many of the remaining populations seem to have gathered on islands far from land. Whilst seabird colonies in Vestland are not necessarily doing well, this is more so due to lack of food sources, and mink has not been seen as a big problem since the 80s and 90s (Larsen, 2021).

5. Conclusion

There was no significant difference in the sighting frequency of mink in the presence of otters compared to in a control region without otters. This could be due to the large variability in sighting frequencies, which could be improved with more camera locations and data. Mink activity in the presence of otters was kept at a stable level throughout the almost seven-year study period, indicating that otters were able to suppress mink populations in the area.

Furthermore, it is likely that otter had an impact on the activity pattern of mink, although the impact was opposite of what was expected. Mink was more diurnal in the absence of otters, but this could be due to diet choice. The sighting frequency of otters increased over the seven-year study period, and their activity pattern remained stable. Despite increasing otter activity in the impact region, mink activity did not decrease, but remained stable at a relatively low level. This indicates that otters are not able to completely remove mink from coastal ecosystems. However, long term effects are uncertain as it appears mink have fewer litters in the presence of otters.

References

- Artsdatabanken (2023) 'Artskart'. Available at: <https://artskart.artsdatabanken.no/> (Accessed 18.02.2023).
- Altman, N. and Krzywinski, M. (2015) 'Sources of variation', *Nature Methods*, 12(1), pp. 5–6. Available at: <https://doi.org/10.1038/nmeth.3224>.
- Bevanger, K. and Henriksen, G. (1995) 'The distributional history and present status of the American mink (*Mustela vison* Schreber, 1777) in Norway', *Annales Zoologici Fennici*, 32(1), pp. 11–14.
- Bolker, B. *et al.* (2022) 'GLMM FAQ'. Available at: <http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#overdispersion> (Accessed 30.03.2023)
- Bonesi, L., Chanin, P. and Macdonald, D.W. (2004) 'Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift', *Oikos*, 106(1), pp. 19–26. Available at: <https://doi.org/10.1111/j.0030-1299.2004.12763.x>.
- Bonesi, L., Dunstone, N. and O'Connell, M. (2000) 'Winter selection of habitats within intertidal foraging areas by mink (*Mustela vison*)', *Journal of Zoology*, 250, pp. 419–424. Available at: <https://doi.org/10.1017/S0952836900003149>.
- Bonesi, L. and MacDonald, D.W. (2004a) 'Differential habitat use promotes sustainable coexistence between the specialist otter and the generalist mink', *Oikos*, 106(3), pp. 509–519. Available at: <https://doi.org/10.1111/j.0030-1299.2004.13034.x>.
- Bonesi, L. and MacDonald, D.W. (2004b) 'Evaluation of sign surveys as a way to estimate the relative abundance of American mink (*Mustela vison*)', *Journal of Zoology*, 262(1), pp. 65–72. Available at: <https://doi.org/10.1017/S0952836903004448>.
- Bonesi, L. and MacDonald, D.W. (2004c) 'Impact of Released Eurasian Otters on a Population of American Mink: A Test Using an Experimental Approach', *Oikos*, 106(1), pp. 9–18.
- Bonesi, L. and Palazón, S. (2007) 'The American mink in Europe: Status, impacts, and control', *Biological Conservation*, 134, pp. 470–483. Available at: <https://doi.org/10.1016/j.biocon.2006.09.006>.
- Bonesi, L., Strachan, R. and Macdonald, D.W. (2006) 'Why are there fewer signs of mink in England? Considering multiple hypotheses', *Biological Conservation*, 130(2), pp. 268–277. Available at: <https://doi.org/10.1016/j.biocon.2005.12.021>.
- Brooks, M. E. *et al.* (2017). 'glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling'. *The R Journal*, 9(2), 378–400. doi: 10.32614/RJ-2017-066.
- Brudeseth, B. and Evensen, Ø. (2002) 'Occurrence of viral haemorrhagic septicaemia virus (VHSV) in wild marine fish species in the coastal regions of Norway', *Diseases of Aquatic Organisms*, 52, pp. 21–28. Available at: <https://doi.org/10.3354/dao052021>.

- Carlsson, N. *et al.* (2009) ‘Long-term data on invaders: When the fox is away, the mink will play’, *Biological Invasions*, 12, pp. 633–641. Available at: <https://doi.org/10.1007/s10530-009-9470-z>.
- Carvalho, J.C. and Cardoso, P. (2020) ‘Decomposing the Causes for Niche Differentiation Between Species Using Hypervolumes’, *Frontiers in Ecology and Evolution*, 8. Available at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.00243> (Accessed: 12 April 2023).
- Christensen, H. (1995) ‘Determinants of Otter (*Lutra lutra*) distribution in Norway. Effects of Harvest, Polychlorinated Biphenyls (PCB's), Human Population Density and Competition with Mink *Neovison vison*’. Trondheim
- Clode, D. and Macdonald, D. (2002) ‘Invasive predators and the conservation of island birds: The case of American Mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland’, *Bird Study*, 49, pp. 118–123. Available at: <https://doi.org/10.1080/00063650209461255>.
- Crego, R.D., Jiménez, J.E. and Rozzi, R. (2018) ‘Potential niche expansion of the American mink invading a remote island free of native-predatory mammals’, *PLOS ONE*, 13(4), p. e0194745. Available at: <https://doi.org/10.1371/journal.pone.0194745>.
- Day, C.C. *et al.* (2016) ‘Comparing direct and indirect methods to estimate detection rates and site use of a cryptic semi-aquatic carnivore’, *Ecological Indicators*, 66, pp. 230–234. Available at: <https://doi.org/10.1016/j.ecolind.2016.01.039>.
- Delisle, Z.J. *et al.* (2021) ‘Next-Generation Camera Trapping: Systematic Review of Historic Trends Suggests Keys to Expanded Research Applications in Ecology and Conservation’, *Frontiers in Ecology and Evolution*, 9.
- van Dijk, J. *et al.* (2021) ‘Kartlegging av oterfallvilt, oppdatering av otertetthetsindeks, og kartlegging av oterforekomst i Norge 2016–2020’. Norsk institutt for naturforskning NINA. Available at: <https://hdl.handle.net/11250/2729157> (Accessed: 18 April 2023).
- Doherty, T.S. *et al.* (2016) ‘Invasive predators and global biodiversity loss’, *Proceedings of the National Academy of Sciences*, 113(40), pp. 11261–11265. Available at: <https://doi.org/10.1073/pnas.1602480113>.
- Dunstone, N. (1993) *The Mink*. London: T & A D Poyser Natural History.
- Eldegard K, Syvertsen PO, Bjørge A, Kovacs K, Støen O-G og van der Kooij J (2021a). ‘Pattedyr: Vurdering av mår *Martes martes* for Norge. Rødlista for arter 2021’. Artsdatabanken. <https://www.artsdatabanken.no/lister/rodlisteforarter/2021/17465>
- Eldegard K, Syvertsen PO, Bjørge A, Kovacs K, Støen O-G og van der Kooij J (2021b). ‘Pattedyr: Vurdering av oter *Lutra lutra* for Norge. Rødlista for arter 2021’. Artsdatabanken. <https://www.artsdatabanken.no/lister/rodlisteforarter/2021/3729>
- Eldegard K, Syvertsen PO, Bjørge A, Kovacs K, Støen O-G og van der Kooij J (2021c). ‘Pattedyr: Vurdering av rødrev *Vulpes vulpes* for Norge. Rødlista for arter 2021’. Artsdatabanken. <https://www.artsdatabanken.no/lister/rodlisteforarter/2021/6714>

- Eldegard K, Syvertsen PO, Bjørge A, Kovacs K, Støen O-G og van der Kooij J (2021d). 'Pattedyr: Vurdering av røyskatt *Mustela erminea* for Norge. Rødlista for arter 2021'. Artsdatabanken. <https://www.artsdatabanken.no/lister/rodlisteforarter/2021/16806>
- Erlinge, S. (1972) 'Interspecific Relations between Otter *Lutra Lutra* and Mink *Mustella Vison* in Sweden', *Oikos*, 23(3), pp. 327–335. Available at: <https://doi.org/10.2307/3543171>.
- Findlay, M.A. *et al.* (2017) 'Developing an empirical approach to optimal camera-trap deployment at mammal resting sites: evidence from a longitudinal study of an otter *Lutra lutra* holt', *European Journal of Wildlife Research*, 63(6), p. 96. Available at: <https://doi.org/10.1007/s10344-017-1143-0>.
- Fiskeri- og Kystdepartementet (2013) 'Fiske i Sør - En situasjonsbeskrivelse og forslag til tiltak'.
- Fox, J. and Weisberg, S. (2019). An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. URL: <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Fylkesmannen i Aust- og Vest-Agder (2017) 'Forvaltningsplan for sjøfuglreservatene i Vest-Agder'. Rapport 3/2017.
- Genovesi, P. *et al.* (2012) 'Alien mammals in Europe: updated numbers and trends, and assessment of the effects on biodiversity', *Integrative Zoology*, 7(3), pp. 247–253. Available at: <https://doi.org/10.1111/j.1749-4877.2012.00309.x>.
- Gil-Sánchez, J.M. and Antorán-Pilar, E. (2020) 'Camera-trapping for abundance estimation of otters in seasonal rivers: a field evaluation', *European Journal of Wildlife Research*, 66(5), p. 72. Available at: <https://doi.org/10.1007/s10344-020-01409-7>.
- Griffen, B.D., Guy, T. and Buck, J.C. (2008) 'Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator', *Journal of Animal Ecology*, 77(1), pp. 32–40. Available at: <https://doi.org/10.1111/j.1365-2656.2007.01304.x>.
- Guidos, S. *et al.* (2023) 'Colony-nesting gulls restrict activity levels of a native top carnivore during the breeding season', *Remote Sensing in Ecology and Conservation* [Preprint]. Available at: <https://doi.org/10.1002/rse2.326>.
- Harrington, L.A. *et al.* (2009) 'The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression', *Ecology*, 90(5), pp. 1207–1216. Available at: <https://doi.org/10.1890/08-0302.1>.
- Harrington, L.A. *et al.* (2010) 'The accuracy of scat identification in distribution surveys: American mink, Neovison vison, in the northern highlands of Scotland', *European Journal of Wildlife Research*, 56(3), pp. 377–384. Available at: <https://doi.org/10.1007/s10344-009-0328-6>.
- Harrington, L.A. *et al.* (2012) 'Dive performance in a small-bodied, semi-aquatic mammal in the wild', *Journal of Mammalogy*, 93(1), pp. 198–210. Available at: <https://doi.org/10.1644/10-MAMM-A-351.1>.

- Harrington, L.A. *et al.* (2020) ‘Current status of American mink *Neovison vison* in Great Britain: a review of the evidence for a population decline’, *Mammal Review*, 50(2), pp. 157–169. Available at: <https://doi.org/10.1111/mam.12184>.
- Harrington, L.A. and Macdonald, D.W. (2015) ‘Riparian mustelids in the Upper Thames: a case of alien invasives versus native competitors’, in D.W. Macdonald and R.E. Feber (eds) *Wildlife Conservation on Farmland Volume 2: Conflict in the countryside*. Oxford University Press, p. 0. Available at: <https://doi.org/10.1093/acprof:oso/9780198745501.003.0007>.
- Heggberget, T.L.M. (2007) *Kalking av sure vassdrag, reetablering av oter, mink og vannspissmus. Sluttrapport, NINA Rapport*. 245. Norsk institutt for naturforskning NINA. Available at: <http://hdl.handle.net/11250/2443837> (Accessed: 20 April 2023).
- Heggberget, T.M. (1996) ‘En kunnskapsoversikt for eurasiatisk oter *Lutra lutra*; grunnlag for en forvaltningsplan.’, *NINA Oppdragsmelding*, 439.
- Heggberget, T.M. (1998) ‘Livshistorie og bestandsdynamikk hos norsk oter’, *NINA Oppdragsmelding*, 569. Available at: <https://www.nina.no/archive/nina/pppbasepdf/oppdragsmelding/569.pdf> (Accessed: 18 April 2023).
- Heggberget, T.M. and Christensen, H. (1994) ‘Reproductive Timing in Eurasian Otters on the Coast of Norway’, *Ecography*, 17(4), pp. 339–348.
- Heggøy, O. & Øien, I. J. (2014) ‘Conservation status of birds of prey and owls in Norway’. NOF/BirdLife Norway - Report 1-2014. 129 pp.
- Hudgens, B.R. and Garcelon, D.K. (2011) ‘Induced changes in island fox (*Urocyon littoralis*) activity do not mitigate the extinction threat posed by a novel predator’, *Oecologia*, 165(3), pp. 699–705. Available at: <https://doi.org/10.1007/s00442-010-1761-7>.
- Kruuk, H. (2006) *Otters: Ecology, Behaviour and Conservation*. Oxford, UNITED KINGDOM: Oxford University Press, Incorporated. Available at: <http://ebookcentral.proquest.com/lib/bergen-ebooks/detail.action?docID=431023> (Accessed: 6 March 2023).
- Landa, A. and Guidos, S. (2020) ‘Bycatch in local fishery disrupts natural reestablishment of Eurasian otter in western Norway’, *Conservation Science and Practice*, 2(7), p. e208. Available at: <https://doi.org/10.1111/csp2.208>.
- Larsen, T. (2021) ‘Sjøfuglane i Sogn og Fjordane. Hekkebestandar i sjøfuglreservata 2014-2020’. Statsforvaltaren i Vestland, miljøvernavingdelinga, rapport 2-2021.
- Lenth, R. V. (2016). ‘Least-Squares Means: The R Package lsmeans’. *Journal of Statistical Software*, 69(1), 1-33. doi:10.18637/jss.v069.i01
- Li, Q. *et al.* (2022) ‘Trophic niche differentiation between invasive and native frog species in urban wetlands of Kunming, China’, *Global Ecology and Conservation*, 40, p. e02318. Available at: <https://doi.org/10.1016/j.gecco.2022.e02318>.
- Linders, T.E.W. *et al.* (2019) ‘Direct and indirect effects of invasive species: Biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning’, *Journal of Ecology*, 107(6), pp. 2660–2672. Available at: <https://doi.org/10.1111/1365-2745.13268>.

Lister, B.C. (1976) 'THE NATURE OF NICHE EXPANSION IN WEST INDIAN ANOLIS LIZARDS I: ECOLOGICAL CONSEQUENCES OF REDUCED COMPETITION', *Evolution*, 30(4), pp. 659–676. Available at: <https://doi.org/10.1111/j.1558-5646.1976.tb00947.x>.

Mack, R.N. *et al.* (2000) 'Biotic invasions: Causes, epidemiology, global consequences, and control', *ECOLOGICAL APPLICATIONS*, 10(3), pp. 689–710. Available at: [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2).

McDonald, R.A., O'Hara, K. and Morrish, D.J. (2007) 'Decline of invasive alien mink (*Mustela vison*) is concurrent with recovery of native otters (*Lutra lutra*)', *Diversity and Distributions*, 13(1), pp. 92–98. Available at: <https://doi.org/10.1111/j.1366-9516.2006.00303.x>.

Meyer, S.E. Callahan, M.A., Stewart, J. & Warren, S.D. (2021) 'Invasive Species Response to Natural and Anthropogenic Disturbance'. Side 85-110 i Poland, T.M., Patel-Weyand, T., Finch, D.M., Miniati, C.F., Hayes, D.C., Lopez, W.M. (red.) *Invasive Species in Forests and Rangelands of the United States*. Springer. <https://doi.org/10.1007/978-3-030-45367-1>

Miljødirektoratet (2023) 'Naturbase kart'. Available at: <https://geocortex02.miljodirektoratet.no/Html5Viewer/?viewer=naturbase> (Accessed 30.03.2023)

Mooney, H.A. and Cleland, E.E. (2001) 'The evolutionary impact of invasive species', *Proceedings of the National Academy of Sciences*, 98(10), pp. 5446–5451. Available at: <https://doi.org/10.1073/pnas.091093398>.

Moore, D.S., McCabe, G.P. and Craig, B.A. (2017) *Introduction to the practice of statistics*. 9th edn. New York: Macmillan Education.

Nordström, M. *et al.* (2002) 'Variable Responses of Waterfowl Breeding Populations to Long-Term Removal of Introduced American Mink', *Ecography*, 25(4), pp. 385–394.

Olsen, K. (2022) 'Overvåking av hekkende sjøfugl i Vest-Agders sjøfuglreservater'. BirdLife Norge Avdeling Vest-Agder.

Põdra, M., Gómez, A. and Palazón, S. (2013) 'Do American mink kill European mink? Cautionary message for future recovery efforts', *European Journal of Wildlife Research*, 59(3), pp. 431–440. Available at: <https://doi.org/10.1007/s10344-013-0689-8>.

Poláčková, I. *et al.* (2022) 'The daily and seasonal behaviour of the American mink and the coypu, two invasive species from the Záhorie PLA (Slovakia)', *acta ethologica*, 25(2), pp. 115–123. Available at: <https://doi.org/10.1007/s10211-022-00396-z>.

R Core Team (2021). 'R: A language and environment for statistical Computing'. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Riedman, M. and Estes, J. (2011) 'Predation on seabirds by sea otters', *Canadian Journal of Zoology*, 66, pp. 1396–1402. Available at: <https://doi.org/10.1139/z88-205>.

Ritger, A.L. *et al.* (2020) 'Diet choice in a generalist predator, the invasive lionfish (*Pterois volitans/miles*)', *Journal of Experimental Marine Biology and Ecology*, 524, p. 151311. Available at: <https://doi.org/10.1016/j.jembe.2020.151311>.

- Romero, R. and Guitián, J. (2017) 'Food and feeding habits of Eurasian otter, *Lutra lutra*, and American mink, *Neovison vison*, in an Atlantic island of northwest Spain', *Folia Zoologica*, 66(2), pp. 117–125. Available at: <https://doi.org/10.25225/fozo.v66.i2.a6.2017>.
- Ruiz-Olmo, J. *et al.* (1997) 'Distribution, status and the colonization process of the American mink (*Mustela vison*) in Spain', *Journal of Wildlife Research*, 2, pp. 30–36.
- Salvanes, A.G.V. and Nordeide, J.T. (1993) 'Dominating sublittoral fish species in a west Norwegian fjord and their trophic links to cod (*Gadus morhua* L.)', *Sarsia*, 78(3–4), pp. 221–234. Available at: <https://doi.org/10.1080/00364827.1993.10413536>.
- Sharma, K. *et al.* (2020) 'Conservation and people: Towards an ethical code of conduct for the use of camera traps in wildlife research', *Ecological Solutions and Evidence*, 1(2), p. e12033. Available at: <https://doi.org/10.1002/2688-8319.12033>.
- Slade, A. *et al.* (2023) 'Indirect effects of pine marten recovery result in benefits to native prey through suppression of an invasive species and a shared pathogen', *Ecological Modelling*, 476, p. 110216. Available at: <https://doi.org/10.1016/j.ecolmodel.2022.110216>.
- Smith, T.M. and Smith, Robert L (2015) *Elements of ecology*. Edited by Robert Leo Smith. Boston, Mass: Pearson.
- Sodhi, N.S., Brook, B.W. and Bradshaw, C.J.A. (2009) 'V.1 Causes and Consequences of Species Extinctions', in *V.1 Causes and Consequences of Species Extinctions*. Princeton University Press, pp. 514–520. Available at: <https://doi.org/10.1515/9781400833023.514>.
- The Norwegian Directorate for Nature Management (2011). 'Scientific basis for action plan against American Mink in Norway Invasive American Mink (*Neovison vison*): Status, ecology and control strategies'. DN-utredning 6-2011
- Thieurmel, B. and Elmarhraoui, A. (2022). 'suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase'. R package version 0.5.1. <https://CRAN.Rproject.org/package=suncalc>
- Thom, M.D. *et al.* (2004) 'Female American mink, *Mustela vison*, mate multiply in a free-choice environment', *Animal Behaviour*, 67(5), pp. 975–984. Available at: <https://doi.org/10.1016/j.anbehav.2003.09.008>.
- Tilman, D. (2004) 'Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly', *Proceedings of the National Academy of Sciences*, 101(30), pp. 10854–10861. Available at: <https://doi.org/10.1073/PNAS.0403458101>.
- Twining, J.P. *et al.* (2022) 'Restoring vertebrate predator populations can provide landscape-scale biological control of established invasive vertebrates: Insights from pine marten recovery in Europe', *Global Change Biology*, 28(18), pp. 5368–5384. Available at: <https://doi.org/10.1111/gcb.16236>.
- Wagnon, C.J. and Serfass, T.L. (2016) 'Camera traps at northern river otter latrines enhance carnivore detectability along riparian areas in eastern North America', *Global Ecology and Conservation*, 8, pp. 138–143. Available at: <https://doi.org/10.1016/j.gecco.2016.08.010>.

Wearn, O.R. and Glover-Kapfer, P. (2019) 'Snap happy: camera traps are an effective sampling tool when compared with alternative methods', *Royal Society Open Science*, 6(3), p. 181748. Available at: <https://doi.org/10.1098/rsos.181748>.

Wellman, S. and Haynes, J. (2009) 'Diel Activity Patterns of Mink, Neovison vison , Change with Habitat', *Canadian Field Naturalist*, 123. Available at: <https://doi.org/10.22621/cfn.v123i4.1005>.

Appendix

Study design



Figure I Example of what a camera trap location looks like.
Photo: Idun Kjoberg

Examples of camera-trap activity



Figure II Examples of species frequently caught on camera: Eurasian otter (*Lutra lutra*) (A), White-tailed eagle (*Haliaeetus albicilla*) (B), American mink (*Neovison vison*) (C), Red fox (*Vulpes vulpes*) (D).
Photos: © NINA, Oter Vestlandet