Interactions between Eurasian otters (*Lutra lutra*) and American mink (*Neovison vison*) in western Norway: A camera trap study over space and time

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Front page: The Eurasian otter (*Lutra lutra*) and the American mink (*Neovison vison*). Photos taken by Steven Guidos and Øistein Moholt, respectively.

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Abstract

Classic ecological theory suggests that a large amount of niche overlap between two competing species will lead to the decline or exclusion of the less dominant species. However, despite competition being a major evolutionary force within assemblages of closely related organisms, it is difficult to test for in the field. The recent return of the Eurasian otter (*Lutra lutra*) to parts of its historic range in Norway presented a rare opportunity to examine the effects of competition on an invasive competitor, the American mink (*Neovison vison*), which has managed to colonize much of the country after the otter was exterminated from many parts of its historic range by extensive hunting.

Theoretical and anecdotal evidence suggests that over time, otter should outcompete mink in areas it has reestablished. However, most of this evidence is based on studies conducted in limnic ecosystems, and little is known of this relationship in the coastal marine environment. This study is the first to examine the competitive relationship of otter and mink over time in a coastal ecosystem using wildlife cameras. Cameras were placed at nested locations in the coastal fjord regions of Norway to examine how local otter and mink populations fluctuate over a three-year timeframe in an area recently reestablished by otter. This was compared to another location where otter and mink have cohabited for roughly thirty years. I found that over the course of the experiment, the number of mink sightings on camera in the area recently reestablished by otter significantly decreased, while that of the otter increased. Mink populations have disappeared in areas where otters have been present for long periods of time, at least in the context of small, local scales. Mink were significantly less active in periods of increased otter activity, which supports existing evidence that the relationship between the two species relies on interspecific aggression. Mink also decreased their amount of activity around midnight, which coincided with the timeframe in which otter were most active. This study lends support to the anecdotal evidence that suggests otter are dominant competitors to mink in areas they cohabit, although the potential for otter to permanently eradicate mink from large areas is uncertain. The displacement of mink by otter will likely have impacts on species that are heavily preyed upon by mink and their competitors. More information is needed as to what extent otter displace mink from various types of ecosystems, and what effects this will have on local seabird, rodent and native mustelid species throughout Norway.

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1. Introduction

Invasive predators are considered to be one of the most important causes of species extinctions and biodiversity loss worldwide (Doherty et al., 2016; Vitousek et al., 1997). Only a few ecosystems have evaded their impacts, with especially damaging effects being recorded from insular ecosystems (Blackburn et al., 2004; Courchamp et al., 2003). Once established, invasive predators often form complex relationships within the native ecosystems, and therefore pose a significant problem for management (Glen & Dickman, 2005; Shea & Chesson, 2002). One such predator that has become notorious throughout Europe for its damaging effects on native wildlife is the American mink (*Neovison vison*).

American mink were introduced to Europe for the purpose of the fur farming in the 1920's (Bevanger & Ålbu, 1986; Macdonald & Harrington, 2003). Soon after their introduction escapees began establishing wild populations around these fur farms. At around the same time in the 1930's the former Soviet Union deliberately began to release American mink throughout its native ecosystems to establish a harvestable population (Aliev & Sanderson, 1970). The size of such releases could be substantial, and in the years up to 1971 the release of up to 20, 400 mink at over 250 locations was documented (Pavlov & Korsakova, 1973). The cumulative result of these escapes and intentional releases being that American mink are now well established throughout much of Europe, including Scandinavia, Russia, Spain, France, Germany and the British Isles (Aliev & Sanderson, 1970; Bonesi & Palazon, 2007; Gerell, 1967; Smal, 1988; Wildhagen, 1956).

In Norway, the success of the American mink may be in part related to the absence of one if its competitors, the Eurasian otter (*Lutra lutra*) throughout most of the country while the mink was expanding, a pattern found in other parts of Europe (Lever, 1978; Linn & Chanin, 1978). In this time period many populations of otter in Europe were suffering due to pollution and overhunting (Chanin & Jefferies, 1978; Strachan & Jefferies, 1993). Now, as the otter population has started to recover in Norway both species have begun to share the historic range of the otter. As otter and mink share a similar niche in regards to habitat use and diet they are considered to be direct competitors of one another. Classical theory suggests that when two organisms share a large overlap in niches and inhabit the same area that one will eventually be outcompeted, this method is commonly referred to as "the Competitive Exclusion Principle" (Elton, 1946; Hardin, 1960). Competition should favor the otter, as they have a 7:1 size advantage over the mink, and are better adapted to take advantage of aquatic food resources (Bonesi & Macdonald, 2004c; Clode & Macdonald, 1995; Dunstone, 1979; Nolet et al., 1993). The otter's superior hunting abilities in water are a result of better eyesight under water, larger surface areas of webbing between toes and greater oxygen reserves (Dunstone, 1993; Dunstone & Gorman, 1998; Dunstone & Sinclair, 1978; Erlinge, 1968). Besides indirect competition for food, otter have been shown to directly outcompete mink by means of aggression. Bonesi et al. (2000) was the first to record an otter stealing fish from a mink, and others have also recorded mink hair being present in otter scat (also known as "spraints"), indicating possible predation upon mink (Grigor'ev & Egorov, 1969). Likewise, wounds on otters from mink have been recorded (V. Simpson pers. comm.), further indicating that direct interactions between the two species are probably aggressive.

American mink have been associated with problems for native prey species and competitors everywhere they have spread (Macdonald & Harrington, 2003). The invasive mink are at least partially blamed for the collapsing stocks of species such as the water vole (*Arvicola amphibius*) in Britain (Macdonald & Strachan, 1999; Woodroffe et al., 1990), ground nesting riparian and seabird species throughout Europe (Clode & Macdonald, 2002; Craik, 1995, 1993; Ferreras & Macdonald, 1999; Gerell, 1967; Nordström et al., 2003) and for the disappearance of the native European mink (*Mustela lutreola*) from much of its original range (Maran & Henttonen, 1995; Põdra et al., 2013). In Norway, mink have received much of the blame for many of the failing seabird colonies, amongst other factors (Anker-Nilssen et al., 2006; Byrkjeland, 2015). Efforts to eradicate mink in parts of Europe by means such as live trapping have been met with limited success, although it has been shown that extermination may be possible in small, isolated regions such as islands (Nordström et al., 2003). The success of the American mink is likely due to a combination of its adaptability in exploiting different niches, its generalist diet, high fecundity and its increased survival rate at low population numbers due to a density dependent survival rate (Clode & Macdonald, 1995; Dunstone, 1993). All are qualities of which have been shown to increase an invasive species' effectiveness in establishing a region (Ebenhard, 1988). However, if reestablishing otters can outcompete mink or function to control their populations then we should expect positive impacts on the native prey fauna and mustelid assemblages in areas of otter and mink cohabitation. This, however, will likely be dependent on the extent to which mink can avoid competition with the native otter.

Competition between two species that share a common niche can be avoided in several ways. Namely, the less dominant species may begin to exploit different parts of the ecosystem, switch to consuming different prey types or shift activity patterns (Smith & Smith, 2015). Such relationships have been found by previous studies of otter and mink, with mink changing their diets to include more terrestrial and avian prey in the presence of otter, forage in less optimal habitats, and also switch from being mostly nocturnal to diurnal (Bonesi et al., 2004; Bonesi & Macdonald, 2004a; Bueno, 1996; Clode & Macdonald, 1995; Harrington et al., 2009b). However, these relationships have been shown to vary between regions and ecosystems and are likely highly dependent on the quality of habitat in regards to food resources and environmental heterogeneity (Melero et al., 2012; Melquist et al., 1981). In Norway, Heggberget (2001) found that field reports and informants indicate less mink in areas with otter following the natural reestablishment of the species along the coastline, with the assumption being that mink were avoiding areas of otter occupation. This, however, is mostly based on anecdotal evidence, as there has yet to be a quantifiable relationship between the activity patterns of the two species in Norway.

Bonesi and Macdonald (2004c) found that mink occurrence in a river system in England decreased from 77% site occupation to 23% after just one year of artificial otter reestablishment. Other studies and reports have recorded less mink in areas after natural otter reestablishment (Erlinge, 1972; Jefferies, 2003; Strachan & Jefferies, 1996), although reductions in mink populations over time are predicted to be less dramatic in areas where otter reestablish naturally (Bonesi & Macdonald, 2004c). In general, the detailed spatial overlap of the two species is poorly understood (Harrington et al., 2009a), and some authors conclude that that otter and mink may be able to coexist, as has been shown between coastal North American river otter (*Lontra canadensis*) and mink (Ben-David et al., 1996; Melquist et al., 1981).

In this study I attempted to determine if reestablishing otter populations had a reducing effect or alter the activity patterns of local mink populations over time and space in the fjord systems of western Norway. Wildlife cameras (camera traps) have recently been used to effectively monitor changes in site occupation of mink and activity patterns of otter over time (Crego et al., 2018; González-Esteban et al., 2004; Green et al., 2015; Guter et al., 2008; Rheingantz et al., 2016), although no studies have yet attempted to study otter and mink competition through use of camera traps. By placing out camera traps at common otter and mink marking spots in an area recently recolonized by otter I measured changes in sighting frequency of both species over time and compared this to areas that have supported otter populations for longer periods of time. As the first cameras were placed in the field in 2016 of the area recently established by otters, I measured any change in sighting frequency and activity patterns of either species over a three-year timeframe. I also placed cameras north of the immediate area of reestablishment to enable comparison of sighting frequencies of both species between areas that differ in time since otter reestablishment by at least 30 years. As the cameras gave detailed information on the activity patterns of both species, I also measured if the circadian activity patterns of mink changed over time in response to otter reestablishment of an area.

I predicted that over time, otter sightings would become more prevalent in the area they recently reestablished, and mink would become less. At the same time, there should be a higher frequency of otter sightings and less mink sightings at the northern study location, which has held a viable population of otter for longer amounts of time, compared to the south. Also, mink should alter their activity to become more diurnal and less nocturnal, while the otter's activity patterns would not change. Lastly, I predicted that the sighting frequency of mink during a given timeframe would be dependent on the amount of otter activity recorded in an area.

2. Materials and Methods

2.1 Species characteristics and distribution

Competition between otter and mink and the subsequent changes in activity between the two species is likely reliant on a number of variables. Factors such as past and present distribution, differences in diet, niche breadth, territorial size, timing of mating season and fecundity should all play a role in shaping population dynamics over time and therefore the biology of the two species is key to the methodology of this study.

2.1.1 Otter distribution

The Eurasian otter is a mid-sized mustelid species native to Norway. There are some regional differences within Europe, but in Norway Eurasian otters typically weigh around 6-9 kg as adults (Kruuk, 2006; Yom-Tov et al., 2006), depending on sex, with males being the larger. Otters display typical mustelid morphology, characterized by elongated bodies and dark brown fur over most of the body, with the coat fading to a lighter brown color on the ventral side. Up until the early 1900's, the otter occurred along the entire coastline and all major tributaries on the Norwegian mainland up to around one thousand meters above sea level (Christensen, 1995). Following this period, the otter population began a steep decline, presumably as a result of good fur prices and national bounties (Heggberget, 1996). By the time the species earned its nationwide protection in 1982, only small and sporadic populations were left in the northern county of Nordland and the far east of Norway in Hedmark (Christensen, 1995; Heggberget, 1998). However, by the 1970's the small northern population of otter began to spread southwards along the coast (Heggberget & Myrberget, 1979). Today, the otter has reached the border between the counties of Hordaland and Rogaland and looks to be continuing its spread to the south (van Dijk et al., 2016).

2.1.2 Mink distribution

American mink were introduced to Norway in 1927 for the purpose of fur farming (Hagen, 1966; Øvrebø, 1951). Escapees from these fur farms quickly settled into Norwegian ecosystems and within a 35 year period had managed to colonize 80-85% of the Norwegian mainland (Bevanger & Henriksen, 1995). By 1993, every county in Norway had reported established mink populations within their respective regions. As mink are also a riparian mustelid species they share a similar morphology to that of the otter, with dark brown fur and a dense, water-repellant coat, however the overall body size is about seven to eight times smaller than that of the otter (Clode & Macdonald, 1995; Dunstone, 1979). Coastal males weigh about 1 kg and females are on average around 0.5 kg (Clode et al., 1995). Due to the fact that mink are considered a high-risk species in Norway (Gederaas et al., 2012) and their negative impacts on novel ecosystems (Macdonald & Harrington, 2003) mink trapping is currently being carried out on a small-scale, uncoordinated basis, with eradication efforts focusing mainly around important seabird colonies (Byrkjeland, 2015). However, as these eradication efforts are only concentrated in small areas the American mink persists throughout Norwegian ecosystems.

2.1.3 Important ecological aspects for otter and mink

Both species are dependent on aquatic ecosystems for food (Dunstone & Birks, 1987; Johnson, 1985; Kruuk, 1995). Otters are mainly a piscivorous predator, with a diet consisting of roughly 80% fish (Mason & Macdonald, 1986; McDonald, 2002). Invertebrates, amphibians, birds and small mammals make up most of the rest of their diet, dependent on time of year, type of habitat and prey abundance (Bonesi et al., 2004; Bueno, 1996; Clode & Macdonald, 1995; Erlinge, 1972; Kruuk, 2006; Roche et al., 1995). Mink share a similar diet to otter, although usually less dependent on fish. A study by Dunstone and Birks (1987) found only around 40% of coastal mink scats contained fish. As mink are generalist and opportunistic predators their diet is more dependent on prey abundance (Dunstone, 1993) and shows a higher plasticity than that of the otter when in the presence of competitors, with some studies showing mink consuming more mammalian and terrestrial prey in the presence of otter populations (Bonesi et al., 2004; Bueno, 1996; Erlinge, 1972).

Both otter and mink territorial range is dependent on sex and quality of habitat in regards to feeding and proper denning locations (Birks & Linn, 1982; Clode et al., 1995; Dunstone, 1978; Dunstone & Birks, 1987; Halliwell & Macdonald, 1996; Hatler, 1976). Both species inhabit a smaller territorial range in marine habitats compared to freshwater (Birks & Linn, 1982; Dunstone & Birks, 1987; Kruuk & Hewson, 1978; Yamaguchi & MacDonald, 2003), which suggests more favorable foraging conditions along marine shorelines. Both species exhibit a very similar territorial system, with male territories often encompassing several smaller female territories within the male’s controlled area (Bonesi, 1996; Kruuk, 2006). Male territories are intrasexually exclusive for both species. Female territories for both otter and mink can overlap, although each female usually has a “core area” which is exclusive to other females (Dunstone, 1993; Gerell, 1970; Ireland, 1990; Kruuk & Moorhouse, 1991). As mink and otter spend the vast majority of their time near water, habitat size is most often expressed as the length of waterway an individual inhabits (Dunstone & Birks, 1987; Gerell, 1970).

Coastal mink territories are generally between 1.2 – 1.4 km and 2.2 – to 2.5 km for females and males, respectively (Bonesi, 1996; Ireland, 1990). Otter territories are larger than those of mink, with coastal females inhabiting an area between 4.7 – 6.4 km and males an area of up to 19.3 km (Kruuk & Moorhouse, 1991), however, the data for coastal male otters is based upon a comparatively small dataset. As saltwater damages the insulating quality of both otter and mink fur over time (Bonesi et al., 2000; Hayden & Harrington, 2000; Kruuk, 2006), access to freshwater within territories could possibly be an influencing factor on distribution of each species within the marine environment.

Male mink tend to be especially active during the breeding season, in which they leave their own territories in search of mates (Dunstone, 1993). This generally occurs between mid-February and mid-April, although this can vary between years (Gerell, 1970). Mink juveniles of both sexes are also more active around October, the time at which they disperse and establish their own territories (Yamaguchi & MacDonald, 2003). Otter in Norway display no distinctive breeding season throughout the year, although there is a birth peak during the summer and autumn (Heggberget, 1993). Therefore, activity levels of otter should not be as dependent on mating behavior as those of mink are. This is in comparison to the well-studied otter populations of Shetland in which otters only breed in summer (Kruuk, 2006).

2.2 Study area

The study area is located on the west coast of Norway and is composed of two transects running both parallel and perpendicular to the coastline (Figure 2.1B). The first transect runs west to east starting at Fjelbergøya and ending within the Åkrafjorden in Hordaland County (Figure 2.1C). The transect is approximately 20 km long (59° 45’ N, 05° 66’ E to 59° 44’ N, 6° 02’ E) and is composed of five nested locations. The second transect runs north to south from Hyllestad in Sogn & Fjordane County to the Kvinnherad and Etne municipalities in southern Hordaland. The transect spans an area of roughly 160 km (61° 11’ N, 05° 17’E to 59° 43’ N, 05° 42’E) and consists of two nested locations (Figure 2.1D & E). Hereafter each of these transects will be referred to as “Transect WE” and “Transect NS,” respectively.

The coastline is characterized as a stereotypical fjord system, with long saltwater inlets lined by steep-sided, mountainous terrain cutting into the mainland. Within these inlets the topography is made up of many islands of varying sizes and irregular shorelines. Most of the shorelines are made of bedrock that gently slopes into the water or of small boulders. Wave action throughout the study region is generally low, as all sites are relatively sheltered by groups of barrier islands to the west. A review of some of the local differences between individual nested locations is outlined in Table 2.1. Annual precipitation in Hordaland averages about 2250 mm with a mean of 202 days with precipitation per year (met.no, 2007). Due to high amounts of rainfall many small freshwater pools and streams are present throughout the study area.

The marine vegetation is similar to that in a region just north of the study area recorded by Heggberget and Moseid (1994), with dense *Laminaria* spp. growth typically fringing the shorelines of each nested location. It was assumed fish species and density were comparable to those found by Heggberget (1993) in which taxa such as Gadidae, Cottidae, flatfish and butterfish are present in high concentrations, although varying throughout the year. Several species of rodents inhabit the study area as well including red squirrels (*Sciurus vulgaris*), Norwegian rats (*Rattus norvegicus*) and wood mice (*Apodemus sylvaticus*). Native meso-carnivores in the region that are potential competitors of otter and mink include the red fox (*Vulpes vulpes*), stoats (*Mustela erminea*), weasels (*Mustela nivalis*) and pine martens (*Martes martes*).

Throughout much of the study area accidental drowning in fishing equipment is still a large concern to the overall health of the otter population (Heggberget, 2007). Data collected by the Norwegian Institute for Nature Research (NINA) indicates this problem is especially relevant in Hordaland, which regularly records the highest amounts of annual otter deaths due to bycatch of all coastal counties in Norway (van Dijk et al., 2016). Otter deaths are especially prevalent around the Bergen area (A. Landa, unpubl.). Data available through Artsdatabanken.no was used to track otter and mink deaths around the study area during the experimental timeframe, although there is likely a large amount of underreporting, especially for mink. Numbers of reported deaths in an area are therefore a minimum, at best. Unfortunately, deaths due to human activity likely rendered one of the original nested location’s (located on Askøy, an island outside of Bergen) data biased, and was therefore excluded from all statistics and figures. This location was to originally be included in Transect NS, located directly between the northernmost nested location and the southernmost. The number of otters killed within ~10 km of this nested location just prior to and within the studied timeframe was 5 animals, 2 of which were reported in late 2018.

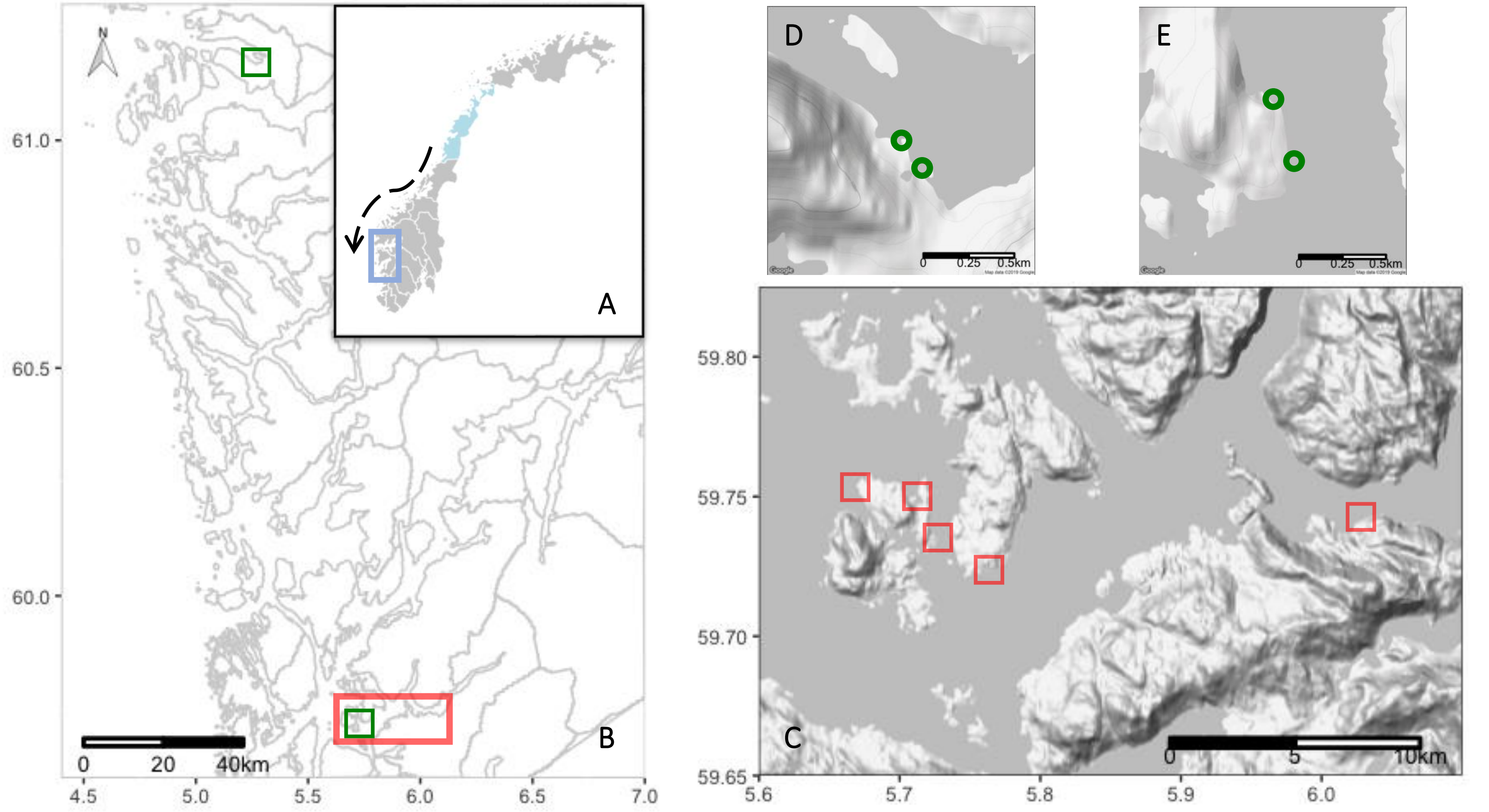

Figure 2.1 Map (A) depicts the study area, indicated by blue box; blue shaded region and dashed arrow indicate area and direction of which otter reestablishment spread from. Map (B) depicts Transects WE and NS, red and green, respectively. Map (C) depicts Transect WE, nested locations indicated by red boxes. Nested locations from left to right are as follows: Fjelbergsund, Nordhusvågen, Sydnessund, Halsnøy and Fyret. Maps (D) and (E) depict nested locations of Transect NS (Hyllestad = D, Sydnessund = E), individual camera locations indicated by green circles. The X and Y-axes of Maps B and C are longitude and latitude, respectively. (Map data from the Norwegian Mapping Authority, Kartverket and R studio Google maps).

Table 2.1 Table specifying characteristics of each nested location. Note; “NL” = Nested location, “HY” = Hyllestad, “FJ” = Fjelbergsund, “NO” = Nordhusvågen, “SY” = Sydnessund, “HA” = Halsnøy, “FY” = Fyret, “FW” = freshwater, “M” = mainland. Otter deaths are ≤ 10 km from NL.

NL	**Coordinates (WGS84)**		**Island size** (km^2)	**Initial camera placement**	**# Cameras**	**Reported otter deaths 2015-18**	**Nearest human disturbance** (m)	**General characteristics**
	Lat.	**Lon.**						
HY	61°18’	05°29’	M	Aug. 2018	2	0	~100	Large FW pool and otter trails through dense vegetation. Sprainting activity near fjord shoreline. Small seabird breeding colony ~300 m from NL. Small farm ~ 100 m from NL.
FJ	59°75’	05°67’	4.9	Feb. 2016	2	1	>500	NL situated on bedrock embankment. Surrounded by forested area. Small FW pool and large amounts of sprainting activity at both camera locations. Small marsh just inland of NL.
NO	59°45’	05°42’	4.9	Mar. 2016	1	1	~200	NL within small bay/inlet. Single camera situated on rock outcrop. Dense vegetation and forest around NL. FW absent. Several summer cottages at the end of inlet and a small dock.
SY	59°73’	05°73’	4.9	Feb. 2016	2	0	~400	NL on rocky embankment, surrounded by forest. Small FW pools dependent on rain. Otter trails through vegetation. Small oyster farm nearby.
HA	59°43’	05°46’	38	Apr. 2016	1	0	>500	Shoreline composed of small boulders. Situated in small ravine, FW stream when raining. Devoid of human activity in area. Several small rock beaches on either side of NL, with boulders of varying sizes.
FY	59°44’	06°02`	M	Jun. 2016	1	0	>500	NL within large boulders next to shoreline. Located in steep ravine, forested area surrounding NL. Several marking sites within area. No FW.

Transect WE: The study area composing Transect WE was chosen because of the recentness of otter re-colonization to the area. As the first recent otter recording in the area was in 2012, when an otter was caught as bycatch in fishing equipment, the experiment takes place in a time and space in which we will be able to measure how the mink population is affected as the otter population becomes more established throughout the region. A total of five nested locations were selected for the purpose of this experiment within Transect WE (Figure 2.2C).

Four years prior to the experiment, otter returned to the area and by the beginning of the experiment they could be found at all study locations within the experimental region. As found by Bonesi and Macdonald (2004c), mink populations may change drastically after only a year a of experiencing competition from newly introduced otter, at least in fresh water ecosystems. Therefore, it is likely that the resident mink populations may have begun to alter their activity by the time the experiment began. As the otter is thought to have recolonized west-to-east in Transect WE, the easternmost nested site at Fyret is likely the most recent area of otter reestablishment of the nested locations.

Transect NS: A total of two nested locations were studied in Transect NS (Figure 2.1 D & E). Each of these nested locations was selected based on how long ago they were recolonized by otter. The northernmost location (Hyllestad) was selected due to that fact that it has supported a solid otter population for over 30 years (Heggberget, 2001). This is compared to the southernmost location (Sydnessund), which has only recently been recolonized by otter around the year 2012 (A. Landa pers. comm.). Sydnessund is also included as a nested location in Transect WE (Figure 2.2C). As Hyllestad has supported a solid otter population for approximately 30 more years than Sydnessund, it is likely there will be differences in sighting frequencies of otter and mink and activity patterns between the two locations.

2.3 Methodology and processing

2.3.1 Camera traps compared to traditional methods

Camera traps have shown to be an efficient and non-invasive technique to study the behavior of mammals (O’Connell et al., 2011; Rowcliffe et al., 2014). To date, several studies have focused around assessing various otter and mink species activity patterns by means of camera traps (Crego et al., 2018; Day et al., 2016; González-Esteban et al., 2004; Leuchtenberger et al., 2014; Rheingantz et al., 2016; Wagnon & Serfass, 2016). Despite the amount of camera trap studies done on otter and mink, this study is the first that attempts to relate the change in otter and mink sightings frequencies to each other over time and space using wildlife cameras.

A common methodology for surveying otter population trends has been analyzing the varying distribution of scats in an area over time (Chanin, 2003; Crawford, 2003; Green & Green, 1987, 1980; Guter et al., 2008; Jones & Jones, 2004). However, it was decided to use camera traps over this method due to several factors. These factors being; relatively few studies exist that have related mink abundance and distribution to scats (Bonesi & Macdonald, 2004b) compared to otter, sampling biases of scat frequency and location between seasons (Conroy & French, 1987; Kruuk, 1992; Yoxon & Yoxon, 2014) and mink deposit scat much less frequently than otters do, which can lead to false conclusions (Bonesi & Macdonald, 2004b). Therefore, it has been recommend to not use scat frequencies to compare otter and mink populations within an area (Bonesi & Macdonald, 2004b). Also, a recent study has shown that camera traps more accurately record otter activity than scat counting (Guter et al., 2008), and they are therefore recommended over scat analyses (Day et al., 2016).

Using wildlife cameras does however come with its own set of disadvantages. Perhaps the most obvious disadvantage being that they only offer a glimpse into the overall habitat use of each area. To offset this, cameras were placed in locations that were likely to be used equally by both species. This was aided due to the fact that both otter and mink use the same areas of habitat (Bonesi & Macdonald, 2004c) as well as the same marking spots (Wagnon and Serfass, 2016). Both species also likely compete over the same den locations within respective territories. However, changes in the camera capture frequency of each species may not be representative of the entire population of an area. Instead, we are limited to making inferences only about the frequency of sightings at each nested location over time, not the entire population of a region.

Glen et al. (2013) suggests that a potential pitfall of using wildlife cameras may be that they are biased towards capturing images of large species compared to smaller (i.e. otters are easier to capture than mink), while Lerone et al. (2015) further adds that infrared cameras may have trouble capturing images of semi-aquatic mammals that have a pelt that is saturated with cold water. I acknowledge that both of these factors could be potential biases, however, mammals as small as wood mice were consistently caught on camera and there were many instances of otters captured that were exiting freshwater pools in winter, where the water temperature could be assumed to be just above freezing. Therefore, I suggest the potential biases of camera traps proposed by Glen et al. (2013) and Lerone et al. (2015) to likely be negligible, and the data collected in this study should not be significantly biased in these regards.

2.3.2 Experimental design

Each of the nested locations was equipped with 1 – 2 wildlife cameras. Two types of cameras were used, the Reconyx ^{TM} HyperFire 2 (Reconyx Inc., Holmen, Wisconsin, USA) and the Cuddeback ^{TM} E2 (Nontypical Inc., Green Bay, Wisconsin, USA). Both cameras were set to capture 3 images per motion sequence separated by one second between pictures. There was no quiet period between each set of pictures. I assumed there was no difference between the abilities of each type of camera to capture otter and mink as they both have a ¼ second trigger after detecting motion and both have been successfully used simultaneously in a study by Wagnon and Serfass (2016) as well. The cameras were placed on metal supports and bolted to exposed rock, facing the direction of a marking spot. All cameras were fitted with an identification tag and placed between 20 and 40 cm above the ground. Visitation by both otter and mink was seen to occur within the same day as camera installation; therefore, it was assumed that neither camera installment nor routine checking had any effect on activity level of either species in the area.

All cameras were placed at common otter and mink marking spots (“latrines”), which were located by using a combination of local, historical trapping knowledge, tracking footprints along the shoreline after snowfalls and by field surveys conducted in the general areas of the nested locations prior to the experimental timeframe. Marking spots were distinguished by the presence of scats and discoloration of rocks at common urination points. Other indicative markings included pathways through dense vegetation and bedding areas. Considering the long length of the experimental timeframe and distance between study areas, selecting sites that could be accessed every two to three months was key for all nested locations. Detailed images of the equipment, marking spots and experimental field setup can be found in Appendix A.

In order for all nested locations to be comparable within each transect they had to fulfill the requirement of being equally accessible by both otter and mink. Therefore, all cameras were located within ~15 m of the shoreline, shared a similar elevation, substrate, local vegetation and amount of human disturbance. Considering this area of shoreline is an essential habitat for fulfilling dietary and life history aspects of both species, it should be unbiased in regards to activity levels of either species. Also, considering that both otter and mink are reliant on the marine environment I only chose to focus on the interactions between otter and mink close to the shoreline, as this is the place where competition will likely be the most intense.

Depending on currents, a 1-2 km broad body of water can be a sufficient obstruction to mink colonization (Bevanger & Henriksen, 1995). Therefore, all nested locations on islands were located within this threshold to the mainland or located within an island chain that bridged this distance. Nested locations were spaced so that a distance of at least 3 km by way of coastline separated them. As this distance exceeds that of the territorial expanse of both male and female coastal mink, each nested location should be independent in regard to mink sighting frequency. Both male and female otter territories exceed this distance however, and it is likely that in Transect WE, only the nested location of Fyret is independent of the other four. Nested locations of Transect NS should be completely independent regarding both species as these locations are separated by a distance of over 160 km from each other.

Mink eradication efforts occurred in parts of Hordaland county during the course of the studied timeframe (Byrkjeland & Haugland, 2015), but these locations were far enough away from the study area that they should have no to minimal effects on the populations of mink I studied (> 6 km, linear distance). Furthermore, as no large perturbations to the mink population occurred during the experiment, such as a release from a fur farm, it can be assumed that any change to the mink sighting frequencies at each location could be attributed to the establishing otter population in the area.

Initial camera placement in Transect WE commenced between January and February 2016. Cameras were placed at Hyllestad (Transect NS) in August of 2018. Additional cameras were added to the Sydnessund and Fjelbergsund locations as the experiment progressed in 2017 to provide more reliable data collection within these areas. Extra cameras were placed a maximum of 400 m of the original so both would provide information on the same groups of otter and mink. Cameras were checked once every 2-3 months in an effort to minimize the chance of dead cameras remaining in the field for long amounts of time. Despite this, camera failure left only 79% of the days in which cameras were in the field with usable data. Data collection lasted until December 2018. Data was sorted based on the presence of otter and mink, with activity level being separated on an hourly basis. Within this definition, an otter or mink that appeared one hour or more after the last observation of the respective species was considered a separate observation. This was done in an effort to reduce pseudoreplicates and is similar to or slightly more conservative than related studies (Di Bitetti et al., 2010; Gómez et al., 2005; Leuchtenberger et al., 2014; Rheingantz et al., 2016). If multiple animals were sighted within the same picture, such as when a family group was present, this was also considered to be one sighting. Sightings of pups of both species were registered when present, although no attempt was made to quantify the number of young accompanying the mother. This was avoided as the chance of all pups being present within the area that was photographed at the same time was considered to be low, and once pups began to approach the size of their mothers it became increasingly difficult to tell them apart, especially when spaced at different distances to the camera.

2.4 Statistical analysis

Statistical analyses relating to sighting frequency changes over time were based on total monthly sightings recorded at each of Transect WE's nested locations, similar to Day et al. (2016) and Wagnon and Serfass (2016). In cases where more than one camera was used at a nested location, I averaged the data together for all months that contained overlapping data to negate the sampling bias of having more than one camera. In months where there was no overlapping data, such as prior to a second camera being installed or if one of the cameras malfunctioned, the number of sightings of the respective month was based on the total amount of sightings of the remaining camera. Changes over space were done only throughout Transect NS, as it was the only transect in which the nested locations were located sufficiently far enough away from each other to expect any differences in sighting frequency in relation to latitude. Data analyses for changes over space were based on daily presence and absence values and frequency of visitation per day over a four-month period. All data analyses, statistics and graphs were done using the programs R (version 3.4.1, R Foundation for Statistical Computing, 2016) and Microsoft Excel, 2011. Statistical significance for *p*-values was set at the 0.05 level.

2.4.1 Comparing nested locations over time

The aim of this analysis was to compare what happened to both otter and mink over time at each individual nested location. Comparing the relationship of otter and mink populations in this way was only possible for the nested locations part of Transect WE, as Transect NS does not have a long enough time series to make any significant conclusions in regards to changes in sighting frequencies over time. To compare the relationships of each respective species' sighting frequency over time at each nested location I used a generalized linear model (GLM) with time as a predictor and total sightings per month as a response. Overdispersion was measured using the Fano factor (Fano, 1947). This method tests for overdispersion by dividing the residual deviance of a model by the degrees of freedom (Agresti, 2002) (Equation 1). If the resulting dispersion parameter was above a value of "1" the model was considered overdispersed. As a quasi-Poisson model can account for overdispersion in a dataset (Hoef &

Boveng, 2007), any nested location in which overdispersion was present was tested with a GLM fitted with a quasi-Poisson model. Any months in which the cameras malfunctioned or there was not a complete set of data were excluded from the analyses.

$$F = \frac{\sigma_W^2}{\mu_W}$$

Equation 1. The Fano factor equation, calculated by dividing the ratio of variance by degrees of freedom.

A generalized linear mixed effects model (GLMM) was used to assess the combined nested location sighting frequency over time in Transect WE. Nested location was set as a random effect factor in the model and autocorrelation between months was also added as an additional factor. Only nested locations in Transect WE that tested positive for mink presence within the first six months of the experiment were included in the analyses. This was done in an effort to limit the analyses to only nested locations in which it was certain that mink were present before the otter reestablishment, in an effort to limit bias of individual nested locations.

2.4.2 Comparing nested locations over space

The purpose of this analysis was to determine if there are any differences in sighting frequencies of mink and otter between the northern and southern nested locations (Transect NS). As mink populations in the northern nested location have cohabited the area with otter for approximately 30 more years than those in the south, there will likely be differences in sighting frequencies between the two regions. As mink established throughout the study region before otters reestablished, any differences between patterns of mink occurrence at each nested location may be treated as a function of time since otter reestablishment. This test was only possible for Transect NS, as the nested locations of Transect WE were spaced at most within c.a. 20 km of each other and this was not considered to be a sufficient distance to account for any significant differences in sighting frequencies over space.

As the most recent camera in Transect NS was installed at the Hyllestad location as late as August 2018, the other location of Transect NS was then also limited to comparisons within the timeframe of September to December 2018. Comparisons concerning the respective species were based on two parameters; presence and absence values and number of times each species was active per day. Sampling effort was dependent on how many days a camera was operational during the compared timeframe. Chi-square tests were used to compare both otter and mink frequency of occurrence and frequency of sightings at each respective location.

2.4.3 Relationship between otter and mink monthly sightings

The aim of this test was to find if there is a general relationship between monthly otter and mink sightings at the same point in time and to determine if the amount of otter sightings per month acts as a regulatory factor upon mink activity. To do this I aggregated all monthly otter and mink sightings from each nested location within both transects into one model and used a GLM to test if monthly otter sightings acted as a predictor for monthly mink sightings.

2.4.4 Comparing diurnal rhythmic activity patterns

Otter and mink diurnal rhythmic activity was comparable using two methods. The first grouped time of activity into six, four-hour categories similar to that of Harrington et al. (2009b). Although instead of using an arscine-transformed variable to measure differences in activity levels at each time period between years, analyses was based on total number of sightings in each time period at each individual camera location. This was done because arcsine-transforming data can lead to nonsensical predications of non-binomial data (Warton & Hui, 2011). I used a GLMM and set time of activity as the predictor and number of sightings in each time category as the response. This was weighted relative to year to account for differences in the number of sighting frequencies between years. Individual camera site was set as a random effect factor. Individual camera locations within Transect WE were used instead of nested locations to include the maximum number of sightings while reducing bias between nested locations with different numbers of cameras. This method was only usable for Transect WE, as this method is reliant on relatively large sample sizes to give proper estimations of activity between time periods. Therefore, only camera sites that had a functioning camera for at least 75% of the year (9/12 months) were included in analyses. This was done in an effort to limit bias, considering that in some locations missing up to 25% of the year would leave only a small number of sightings left and this would bias the distribution of sightings in each timeframe throughout a year. This resulted in Transect NS being excluded from this type of analyses, as cameras were only active for a 4-month period.

The second method of assessing changes in diurnal rhythmic activity of either species related amount of activity to timing of dusk and dawn and was used to assess changes over time (Transect WE) and space (Transect NS). Dawn and dusk were defined as the periods in which the sun height is below -12° and +12°, similar to Rheingantzet et al., (2016). Each day of the study period was assigned a dusk and dawn time available through by the R package "suncalc" (Thieurmel & Elmarhraoui, 2019). Otters in Transect WE were mostly nocturnal; it was therefore hypothesized that mink would alter their activity over time to become more diurnal. Change in activity over time and space was based upon individual sightings combined from all camera locations in Transect WE and Transect NS, respectively. Nocturnal activity was defined as activity happening between dusk and dawn, with diurnal activity being the opposite. Changes in nocturnal and diurnal activity patterns over time (Transect WE) were analyzed using a Chi-square test, in which number of nocturnal sightings were compared to total sightings between years. Changes in activity patterns over space (Transect NS) were compared using a Chi-square test, in which nocturnal sightings were compared to total sightings between different latitudes over a 4-month timeframe.

3. Results

3.1 General observations and recordings

A total of six nested locations were included for analyses from both transects. Between all nested locations, a total of 2458 individual sightings were registered, 1835 of these being otter and 623 were mink. A large amount of variation occurred between nested locations in regard to total sightings and number of recorded months, the overall results of each location are depicted in Table 3.1. The total number of camera traps days between all nested locations was 7423, although the number of days in which the cameras were functional was significantly lower, 5868 days (79%). The cameras were able to capture a range of animals of differing sizes (Figure IV, Appendix B) including small rodents and birds, native carnivores such as red foxes and pine martens as well as large cervid species such as red deer (*Cervus elaphus*). However, sighting frequencies of species other than otter and mink were not quantified.

Table 3.1 Table showing the total number of sightings at each location as well as the average number of sightings per month over the course of the studied timeframe. Total sightings at locations with more than one camera were based on combined monthly sighting averages. Recorded months is based on the number of months a nested location's camera(s) was functional.

Transect	**Species**	**Location**	**Total sightings**	**Recorded months**	**Sightings / month ($\bar{x}$ ± SD)**		
					2016	2017	2018
NS	Otter	Hyllestad	83	4	-	-	**16.9** ± 7.6
NS	Mink	Hyllestad	0	4	-	-	**0** ± 0
WE	Otter	Fjelbergsund	311	30	**10.3** ± 4.4	**6** ± 4.5	**13.5** ±10.5
WE	Mink	Fjelbergsund	29	30	**1.8** ± 2.7	**0.3** ± 0.64	**1** ± 1
WE	Otter	Nordhusvågen	94	17	**2.3** ± 2.3	**7.3** ± 3.5	-
WE	Mink	Nordhusvågen	112	17	**10** ± 9.7	**4.7** ± 2.3	-
NS & WE	Otter	Sydnessund	466	35	**11.8** ± 5.4	**12.4** ± 7.4	**15.6** ± 3
NS & WE	Mink	Sydnessund	125	35	**4.8** ± 3.6	**2.7** ± 3	**3.3** ± 5.3
WE	Otter	Halsnøy	322	27	**8** ± 3.6	**18.7** ± 8.3	**7.9** ± 4.3
WE	Mink	Halsnøy	40	27	**2.6** ± 2.4	**0.9** ± 0.7	**1.3** ± 1.3
WE	Otter	Fyret	42	21	**3** ± 2.4	**1.3** ± 1.3	**1.9** ± 2.4
WE	Mink	Fyret	215	21	**11.7** ± 11	**9.6** ± 7.3	**9.8** ± 7.7

In Transect WE, otter pups were sighted throughout all times of the year, although in general were most common in winter (Figure V, Appendix C). Otter pups were sighted at nearly all nested locations of Transect WE in early to mid-2016, except for Fyret, where pups were present for the first time in December 2017. This likely indicates Fyret as the most recent nested location established by otter. Mink pups were sighted at only 2 nested locations; all sightings were in mid-summer. The sightings were at Fyret in 2016 and Sydnessund, 2017, after which no mink pups were sighted at either location.

3.2 Changes in sighting frequency over time, Transect WE

All nested locations within Transect WE showed either a gradual decline in the number of mink sightings per month to no change throughout the experimental timeframe (Figure 3.1). Despite the apparent gradual decline of mink sightings over time at each nested location, a GLM comparing mink sightings over time found that none of these declines were considered significant (*p*>0.05). A total of three locations showed an increase in the number of otter sightings over time while the other two locations showed no change to a decline in the number of sightings per month (Figure 3.1). Only two of the nested locations in Transect WE recorded a significant increase in the amount of otter sightings per month over time, Sydnessund (*p*=0.04, *F*=4.23, df=33) and Nordhusvågen (*p*=0.001, *F*=18.49, df=15). It should be noted that Nordhusvågen only had data available for the years 2016 and 2017 due to consistent camera failure in 2018.

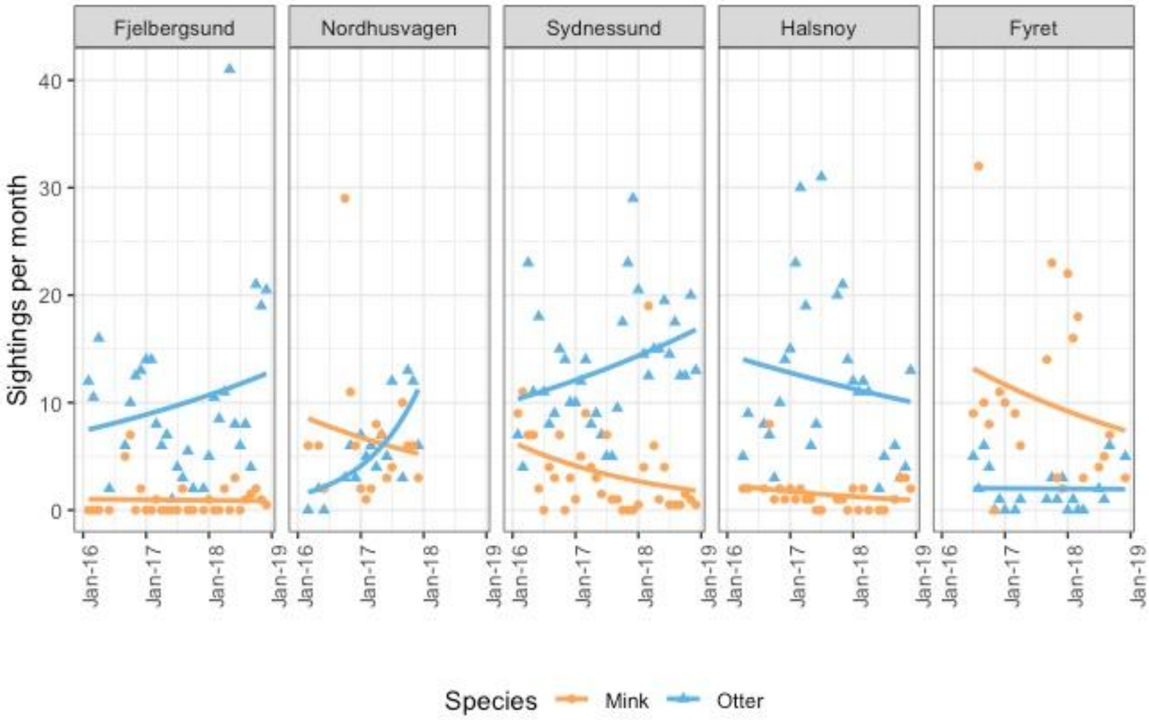

Figure 3.1 The change of otter and mink sighting frequencies over the experimental timeframe in Transect WE. Solid lines indicate the average change over time. Data is absent for the year 2018 at Nordhusvågen due to camera failure.

The combined nested locations of Transect WE depict a gradually decreasing amount of mink sightings throughout the three-year timeframe of the experiment while that of the otter slowly increases (Figure 3.2). Despite a significant amount of variation between nested locations the overall amount of mink sightings of the combined nested locations has significantly declined (*p*=0.048, df=95). Although the combined sighting frequency of otter in Transect WE shows a positive trend over time, the number of sightings in Transect WE has not increased significantly in the three-year study timeframe (*p*>0.05, df=95). This may be in part due to the large amount of variation in sighting frequency between nested locations. The mean ± SD changes in monthly otter sightings per month for the years 2016 to 2018 rose slightly from 7.9 ± 5.4 to 10.3 ± 8.1, respectively. The mean ± SD changes for mink over the same time period were 5.7 ± 7.0 to 3.6 ± 5.6 sightings per month, respectively.

Figure 3.2 The change in overall sighting frequency of otter and mink over time in Transect WE. The data is composed of all nested locations that tested positive for mink presence within the first six months of the timeframe (i.e. all locations excluding Fjelbergsund).

3.3 Differences in sighting frequency over space, Transect NS

Comparisons between the nested locations of the north (Hyllestad) and south (Sydnessund) were based on the timeframe in which overlapping time periods of data recording occurred between the two regions (September – December 2018). Out of 244 sampling days, mink were not sighted once at the northernmost nested location of Hyllestad (Figure 3.3), despite the camera being placed in seemingly optimal mink habitat. This is compared to the southern location of Transect NS, Sydnessund in which mink were present 9 days out of 214 (4%). The frequency of mink sightings was limited to once per day. This is in comparison to otter, in which it was normal to record activity throughout multiple points of the day in both transects. As mink were not captured on camera at Hyllestad throughout the experimental timeframe they were present a significant amount of days more in the south than in the north (χ^2=8.3, *p*=0.004, df=1). Comparisons between the amounts of activity per day were not possible given the lack of mink sightings up north.

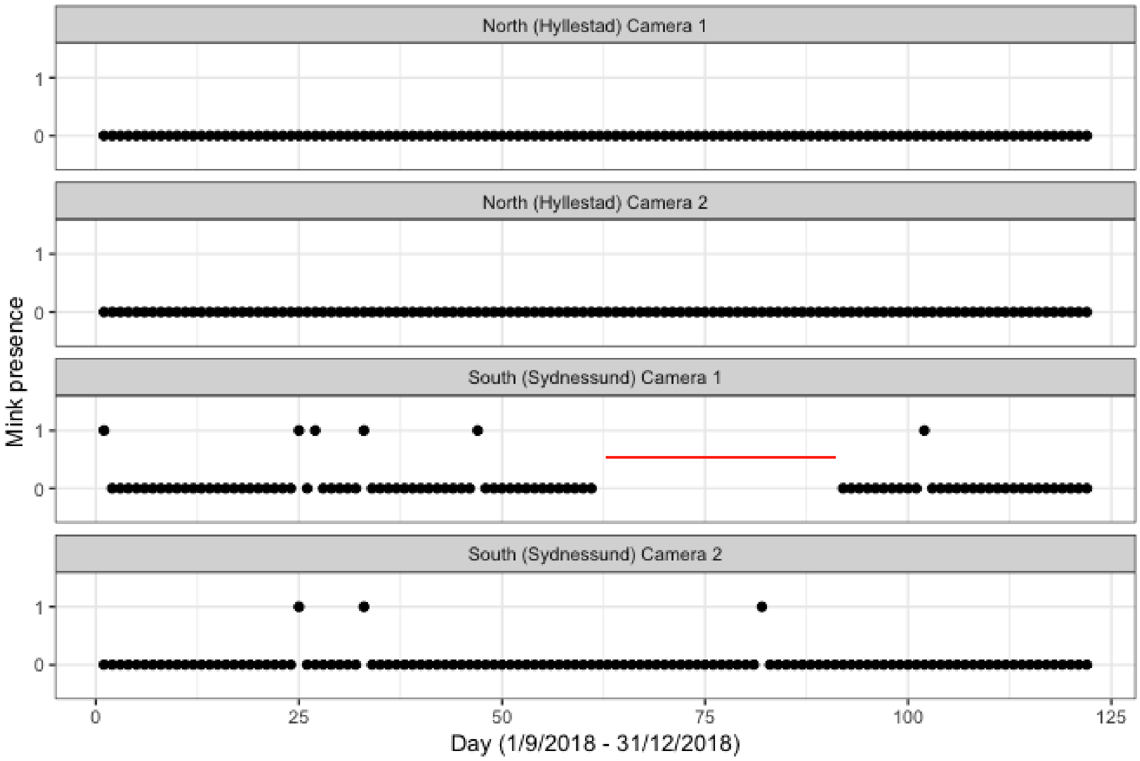

Figure 3.3 The number of days in which mink were present at each camera in the north compared to the south. The red line indicates days in which the camera was inactive. Presence and absence is ranked as follow: 1 = present, 0 = absent.

In the north, the Hyllestad location recorded positive otter sightings 86 out of 244 sampling days (35%). In the south at Sydnessund, otter were present 76 days out of 210 (36%) (Figure 3.4A). A Chi-square test revealed there to be no significant difference between the frequency of amount of days otter were sited between the north and the south (χ^2 = 0, *p*=1, df=1), indicating that by the year 2018 the nested location of Sydnessund is nearing the level of establishment of Hyllestad.

However, otter were more active at the northernmost nested location, with up to four sightings per day per camera. This is in comparison to otter in the south, which were sighted a maximum of twice per day per camera during the compared timeframe (Figure 3.4B). Otters were sighted significantly more per day at Hyllestad compared to Sydnessund (χ^2= 3.96, *p*=0.05, df=1), with 37% of the days in which otters were active up north included two or more sightings per day (32/86 days) compared to just 17% down south (13/76 days).

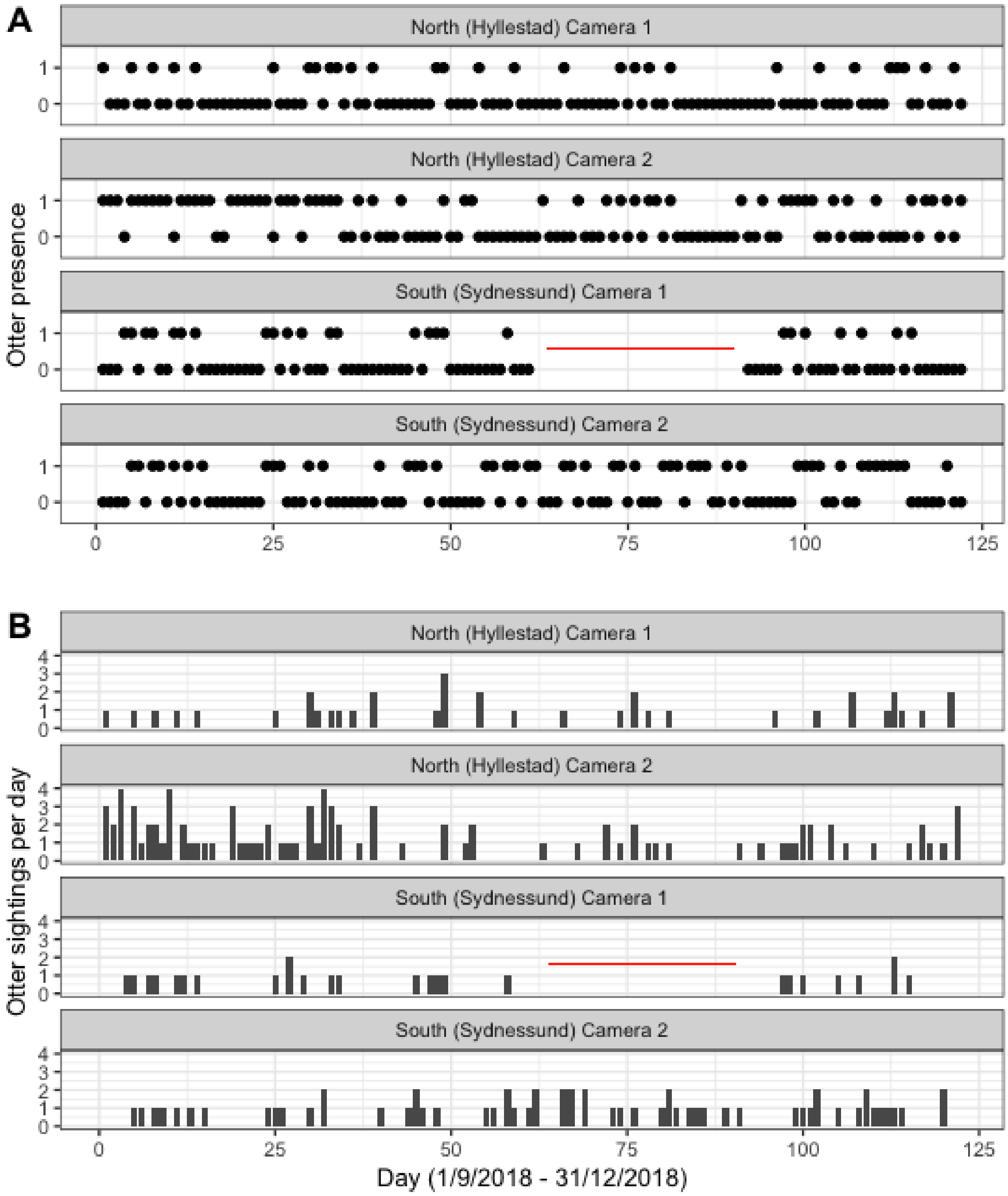

Figure 3.4 The number of days otter were active at each camera in the north compared to the south (A) in relation to how many times otter were active per day between the two regions (B). The red lines indicate camera failure. Days in which cameras were not active were excluded from analyses. Presence and absence (part A) is ranked as follows: 1 = present, 0 = absent.

3.4 Otter's effect on mink

When monthly sightings of otter and mink at all nested locations were combined it was found that otter presence functions to regulate that of mink on a monthly basis (Figure 3.5). As the number of otter sightings increase at a nested location, mink sightings dramatically decrease within the same month, which indicates possible avoidance by mink of areas with high amounts of otter activity. A GLM with monthly otter sightings set a predictor found this relationship to be highly significant (p<0.001, F=28.4, df=134).

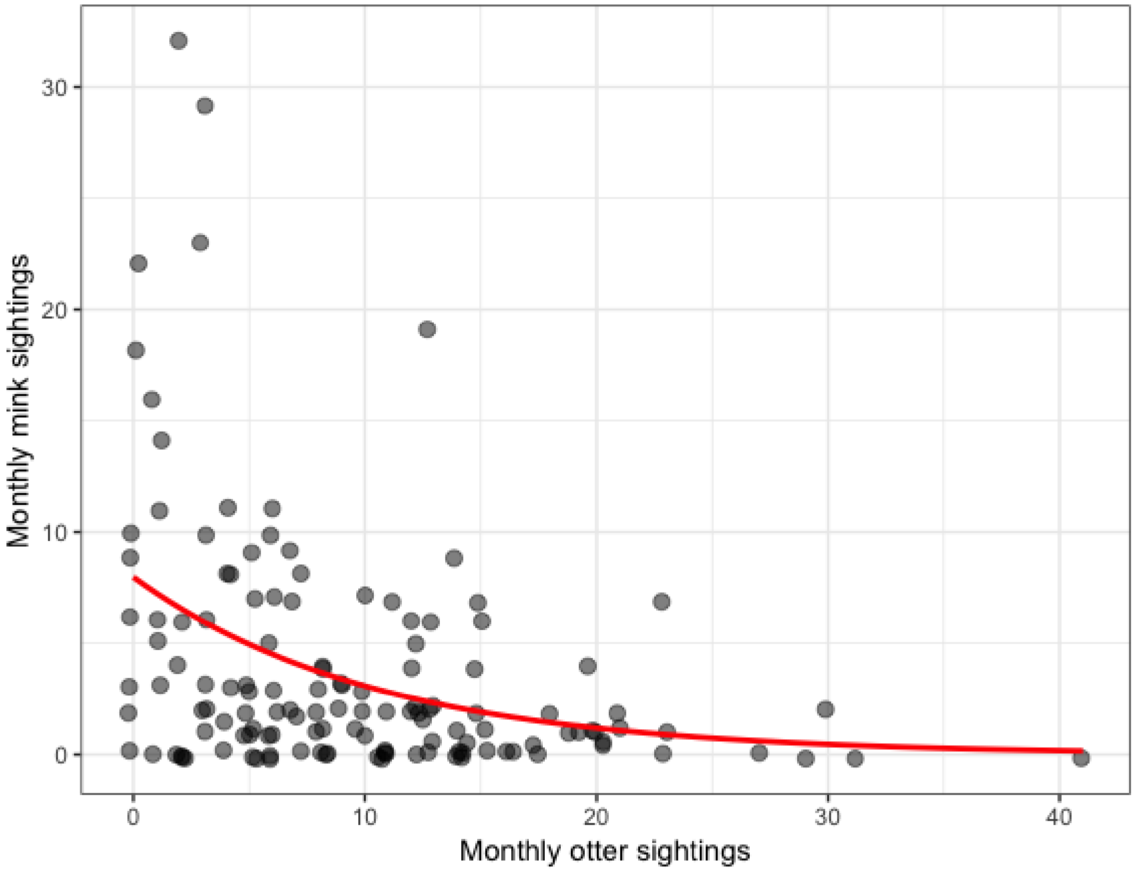

Figure 3.5 The relationship of monthly otter and mink sightings from all nested locations. Monthly sightings of mink decline as otter sightings increase. The red line indicates the line of best fit. Points are offset and transparent to display overlap.

3.5 Change in rhythmic activity over time, Transect WE

Otter sightings were concentrated predominantly between the hours of 20:00 and 8:00, inside of which, approximately 88% and 83% of the sightings occurred in 2016 and 2018, respectively (Figure 3.6). Activity levels between years were very similar, ranging between an average of ≤ 1% and 36% of sightings within a four-hour period. As expected, the percentage of otter sightings at differing time intervals did not vary from the beginning to end of the experiment as each year showed a characteristic peak in activity around midnight and a very low percentage of activity occurring between the hours of 8:00 and 20:00. There were no significant changes in sighting frequency of otters within any of the time intervals between years. A more detailed overview can be found in Appendix D.

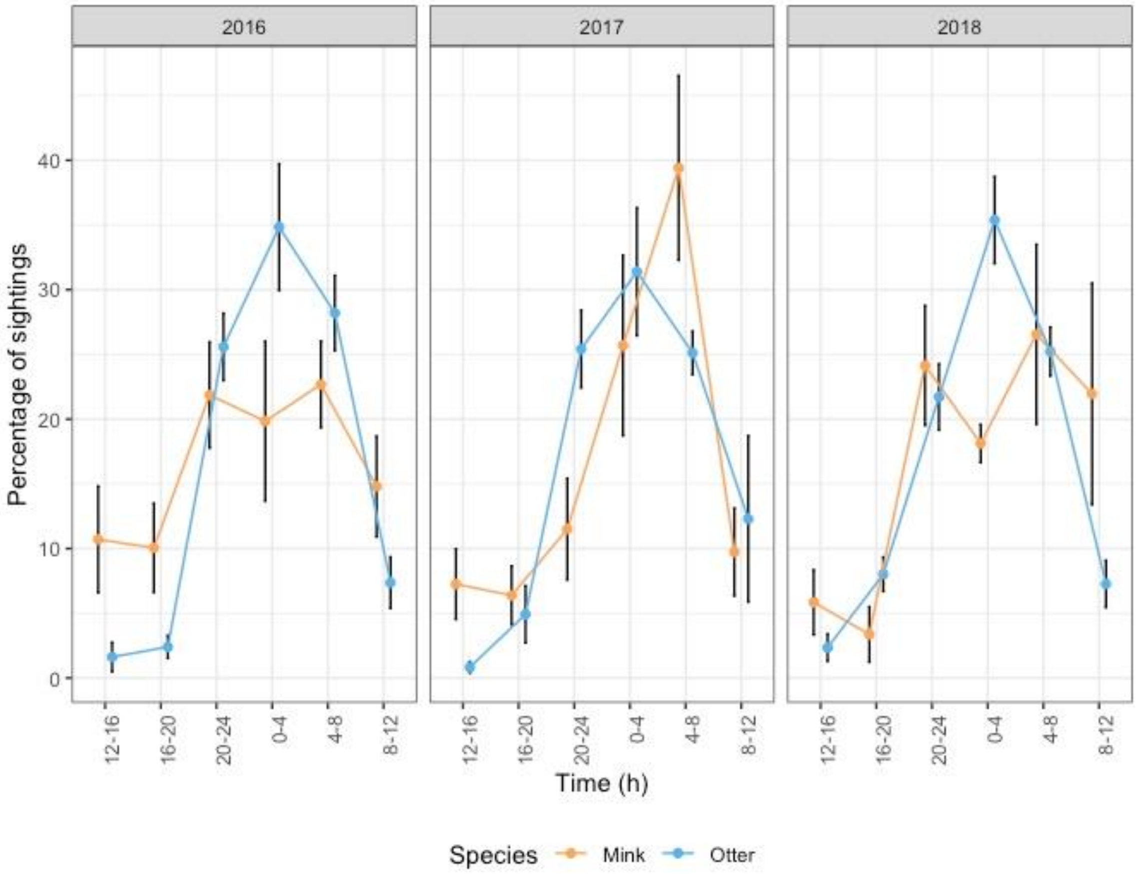

Figure 3.6 The percentage of sightings of both otter and mink at different hours of the day. Time is based on the 24-hour clock. A time of "0" refers to midnight and "12" is midday. Points indicate average values and black lines indicate standard deviation.

Mink sightings varied approximately the same as that of otters within years, ranging between values on average of ≤ 4% and 39% of sightings within a four-hour period (Figure 3.6). However, unlike otters there was some variation between years, and the peak in amount of sightings per time period was not as pronounced as that of the otter. Mink in general were more active over a larger period of the day and depicted a less steep peak in activity during the night. Mink instead were most active between the hours of 20:00 and 12:00, although mink activity in 2017 deviated from this slightly. In general, mink activity was highest within the timeframes of 20:00 – 24:00 and 4:00 – 8:00, with a slight decrease in activity between the two timeframes at which time the otters were most active.

Between 2016 and 2018, mink became less active during the middle of the night and during daylight hours, instead becoming increasingly active around the time periods related to dusk and dawn. Mink became significantly less active between the hours of 8:00 – 12:00 (*p*=0.02, est.=0.98) and 12:00 – 16:00 (*p*=0.01, est.=-1.32). By 2018, the number of sightings increased significantly within the time periods of 20:00 – 24:00 (*p*=0.005, est.=1.16) and 4:00 – 8:00 (*p*=0.001, est.=1.32), with less activity being observed at 00:00 – 4:00 (*p*=0.01, est.=1.04). This indicates mink activity became less well spread throughout the night, as was observed in 2016 and became concentrated more around the hours of dusk and dawn.

Significant differences in activity patterns for mink in all timeframes were only apparent when comparing data from years 2016 and 2018. There were no statistically significant changes in the number of sightings per timeframe between adjacent years, except for the time period 20:00 – 24:00 in which mink sightings significantly increased from 2017 to 2018 (*p*=0.03, est=0.98). Therefore, most of the marked changes in sighting frequencies of the other respective timeframes appear to be gradual.

Total sightings of otter and mink at all camera locations of Transect WE can be found in Figure 3.7. Otter activity is dependent on the amount of daylight throughout the year, while mink activity is more varied. The proportion of otter sightings between dusk and dawn did not change over the course of the study, with 82% of sightings being at night in 2016 followed by 80% in 2018. Otter appear to be active over a larger amount of time in the winter compared to summer, probably relating to the decreased amount of sunlight present in winter.

The timing of mink activity changed from the beginning of the experimental timeframe to the end. Mink sightings at night increased from 46% of all sightings in 2016 to 65% in 2018. Although there appears to be a trend in mink switching to more nocturnal activity, it was not significant (χ^2=3.57, *p*=0.059, df=1). Mink activity appears to be more related to the timing of dusk and dawn than otter, as more activity is concentrated around these time periods than in the middle of the night (0:00 – 4:00).

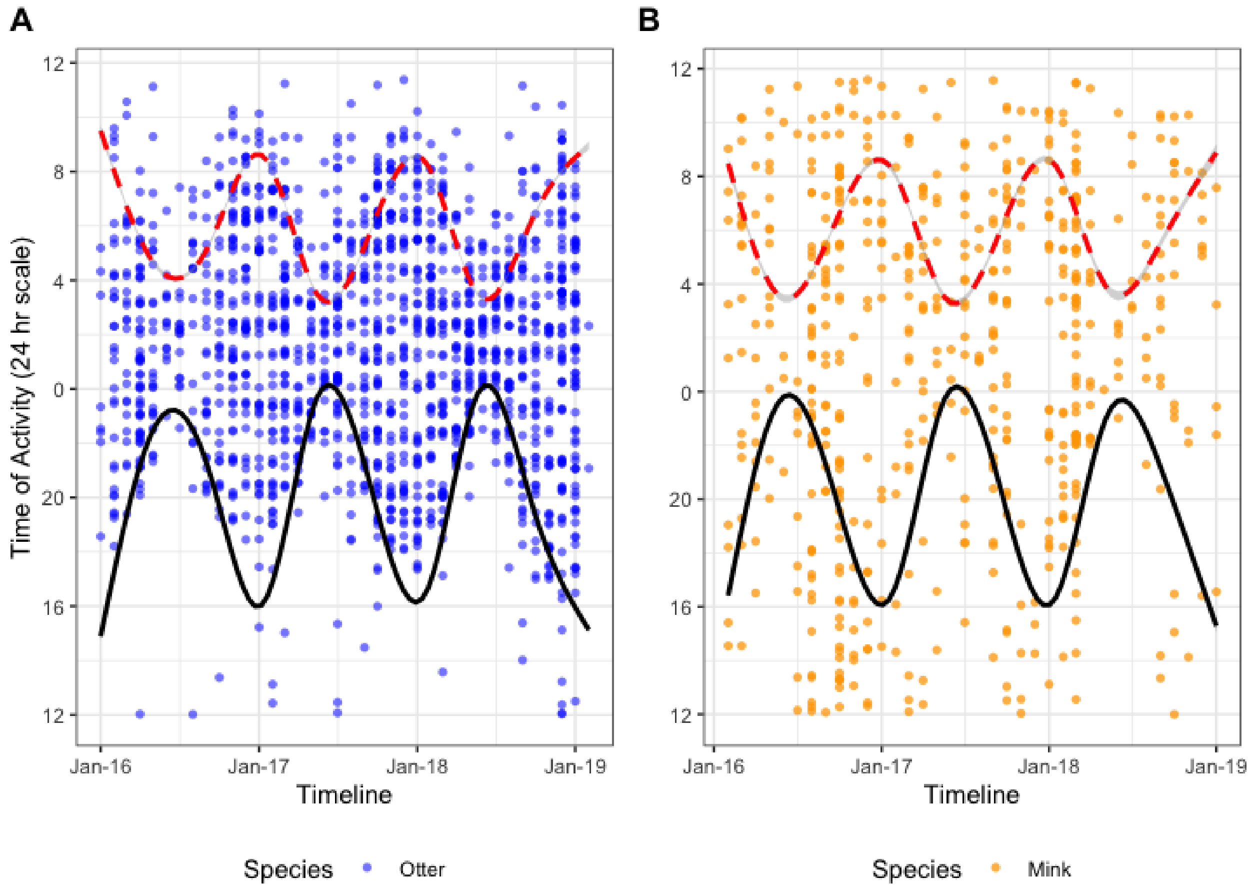

Figure 3.7 The total combined captured time of activity for otter (A) and mink (B) from all cameras in Transect WE. Time of activity based on a 24-hour scale, with 0 = 12 am (midnight) and 12 = 12 pm (midday). Dawn (dashed red line) and dusk (solid black line) were based on date, latitude (59°73'N) and longitude (05°76'E) of Transect WE.

3.6 Differences in rhythmic activity over space, Transect NS

As mink were not found at Hyllestad during the experimental timeframe, comparisons between rhythmic activity patterns over space were limited to otters. At the northernmost location of Hyllestad otters were significantly less nocturnal than those located further south at Sydnessund (χ^2=5.57, *p*=0.02, df=1), with approximately 72% (n=134) of sightings taking place between dusk and dawn at Hyllestad, while at Sydnessund this number rose to 87% (n=90).

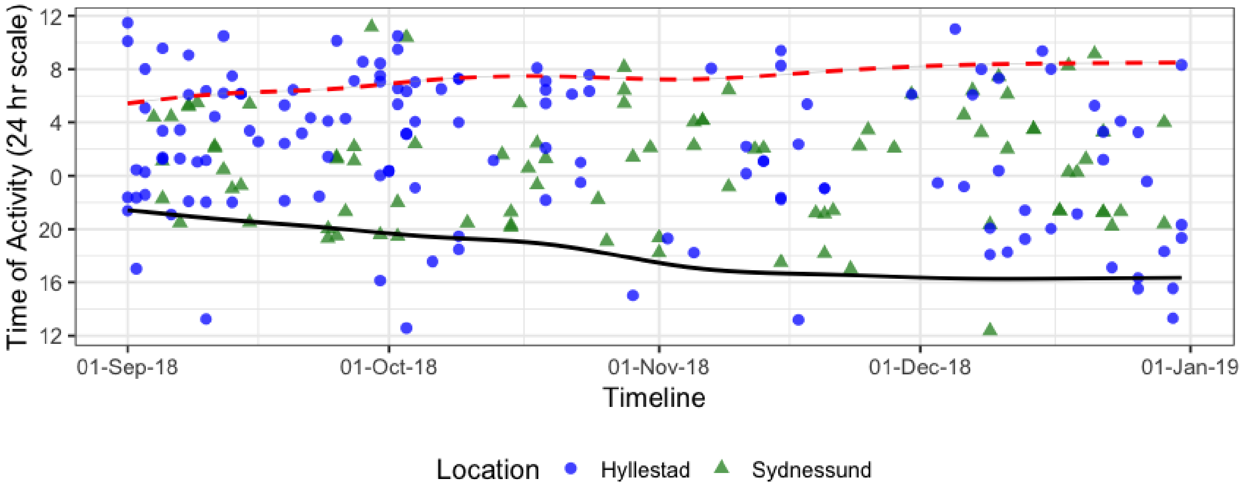

Figure 3.8 A comparison between the time at which otter were sighted between the northern nested location of Transect NS (Hyllestad) and the southern (Sydnessund). Time of activity based on a 24-hour scale, with 0 = 12 am (midnight) and 12 = 12 pm (midday). Dawn (dashed red line) and dusk (solid black line) were based on date, latitude (60°40'N) and longitude (05°30'E) of Bergen city, which is located directly between the nested locations of Transect NS.

4. Discussion

4.1 Sighting frequencies over time, Transect WE

The results of this study demonstrate that otter have a reducing effect on mink populations over extended timeframes, at least in the context of nested locations, although the reducing effect appears to be less dramatic than that found by Bonesi and Macdonald (2004c), in which the amount of sites occupied by mink in the Thames river system decreased from 77% to just 23% after one year of an intentional otter reintroduction. However, fundamental differences in the type of reintroduction, time since reintroduction, methods of surveying and type of habitat likely play a role in this difference. Indeed, where otters reestablish naturally, mink decline much more slowly than in areas where they are intentionally reintroduced (L. Bonesi, unpubl.).

When examined individually, all nested locations recorded a decrease in the number of mink sightings over time, although the degree of this decrease was not consistent between all locations. It is known that the characteristics of the habitat close to a riverbank will affect the length of time the two species may coexist (Bonesi & Macdonald, 2004a), with the same likely being true for coastal-living North American river otters and American mink (Melquist et al., 1981). Despite all nested locations fulfilling the optimal habitat requirements for mink, described in detail by Ben-David et al. (1996), it is possible that differences in the structure of local habitats may be responsible for some of the variation in sighting frequencies between nested locations over time. This may be especially relevant to Fyret, which compared to the other locations of Transect WE had a greater amount of large boulders and crevices in the surrounding area. This local topography could plausibly create a greater amount of escape routes for mink in the presence of otter and may lessen the effects of interspecific aggression, which could be partially responsible for the high amount of monthly mink sightings recorded at Fyret throughout the course of the experiment. Therefore, although all nested locations were selected based on shared habitat characteristics, slight variations in local environmental heterogeneity could be a potential bias on the results of this study.

It is also possible that the placement of nested locations within individual mink and otter territories may have influenced the amount of sightings over time of each species. For example, if by random chance a nested location was placed within a “core area” shared by both species where interspecific territories overlap, one could expect higher encounter rates between otter and mink and a faster decrease in the number of mink sightings recorded over time. However, this potential bias may be negated by the fact that otter and mink live in a linear habitat in which their movements are restricted to areas along bodies of water, seldom venturing from these regions (Yamaguchi et al., 2003). This landscape configuration forces them to a narrow strip of coastline, and therefore subjects them a relatively high chance of interspecific encounters. A similar hypothesis was formulated to describe the effects of a linear habitat on the predation rate of water voles by American mink. This phenomenon, known as the "Tightrope hypothesis" suggests that mink and water voles would be more likely to co-exist if they were not dependent on the bankside vegetation of British rivers (Barreto et al., 1998). A similar relationship is likely existent for otter and mink, therefore negating bias of where cameras are placed in relation to core areas.

Three of the five nested locations showed a general increasing trend in the number of otter sightings per month over the course of the study. The three locations, Fjelbergsund, Nordhusvågen and Sydnessund are all located on the same island, and therefore possibly share the same resident otter population. Halsnøy and Fyret showed a decreasing trend in otter sightings per month to no trend, respectively. Despite the negative trend in otter sightings at Halsnøy over time, mink sightings remained depressed throughout the course of the study, which indicates that even when otter numbers in an area fluctuate, mink populations remain depressed once displaced. Similar findings were found by Bonesi and Macdonald, (2004c), in which otter functioned to permanently displace mink, even after otter densities in an area decreased following an intentional reintroduction. Monthly otter sightings were on average lowest at the nested location of Fyret, this, coupled with the fact that otter pups were first sighted at this location over a year after all other locations is supportive of the hypothesis that this nested location is the most recent area of otter reestablishment. Yet, even with the relatively low levels of otter activity compared to the other nested locations, the overall frequency of mink sightings is negative over time.

Although all nested locations recorded a gradual decrease in the sighting frequency of mink over the course of the study, none of these decreases were significant, which is possibly a result of both the relatively short studied timeframe and the fact that mink and otter coexisted within Transect WE for at least four years prior to the start of the experiment. Bonesi and Macdonald (2004c) found that reintroduced otter significantly decreased the amount of resident mink in an area within the first year of cohabitation. In the year following the mink population stabilized at a low density, despite the otter population having expanded and being less dense than the previous year in which the mink population significantly dropped.

Although no information exists on the population dynamics of otter and mink in the area prior to the beginning of the experiment, the low number of monthly sightings of mink found at both Fjelbergsund and Halsnøy likely indicates that the resident mink populations had already been displaced prior to the start of the study. As the first camera traps were implemented four years after otter were initially reported in the study area, it is possible that the most dramatic effects of their reestablishment on the mink population went unrecorded.

It is also possible that marked changes in the sighting frequencies pertaining to individual nested locations will only become apparent over longer timeframes. This is especially relevant to mink populations living within coastal ecosystems. Access to alternate food sources and increased environmental heterogeneity are commonly known to enhance to degree to which close competitors may coexist (Begon et al., 1990; Smith & Smith, 2015). Marine coastal habitats are especially productive ecosystems, and the high abundance of food resources in coastal habitats may lessen competition between competitors and facilitate a more gradual decline of the less competitive species. Evidence suggests that in their native range, American mink can coexist in coastal ecosystems with North American river otters due to the apparent abundance of prey and by making use of the large amount of habitat heterogeneity in coastal ecosystems to exploit different parts of the shoreline (Melquist et al., 1981). Indeed, most of the anecdotal evidence of otter outcompeting mink over time takes place over significantly longer timeframes than the present study and assesses populations within freshwater systems (Bonesi et al., 2006; Erlinge, 1972; Kauhala, 1996; McDonald et al., 2007; Strachan & Jefferies, 1996).

Monthly sighting values from individual nested locations were pooled from Transect WE to gain a better understanding of what the sighting frequencies were over a larger geographic area. Although none of the nested locations alone depicted a significant decrease in mink sightings over time, when combined into one model the overall number of mink sightings per month significantly decreased over the studied timeframe. Alongside this, monthly otter sightings throughout the region increased, although not markedly. This lack of a marked increase in the otter population is likely due to a large amount of variation in monthly sighting frequencies of otter within nested locations as well as the inclusion of the nested location Fyret in the model, which continuously record low monthly values of otter activity throughout the study.

4.2 Sighting frequencies over space, Transect NS

Within the four-month timeframe in which comparisons between nested locations of Transect NS was possible, mink were never sighted at the northern nested location at Hyllestad (total camera trap days = 244). This finding lends support to anecdotal evidence that suggests less mink occur in areas that have been reestablished by otter in Norway (Heggberget, 2001). Within the same timeframe mink were sighted a total of nine times in the southern location of Transect NS (Sydnessund), which lags behind in regards to time since otter reestablishment by approximately 30 years (total camera trap days = 209).

Although mink were not sighted at Hyllestad during the experimental timeframe, it cannot be said with certainty that they are absent at the nested locations throughout all times of the year, considering the compared timeframe was for a period of only four months. However, the timeframe in which cameras recorded data at Hyllestad does directly overlap with one of the two time periods throughout the year in which mink populations are especially active, as juveniles actively search for and establish their own territory around the month of October (Ireland, 1990; Yamaguchi & MacDonald, 2003). Therefore, the lack in sightings of even transient individuals at Hyllestad is likely indicative of a resident population that has been very reduced and scattered, or altogether gone from the area.

Surprisingly, the amount of days otter were present up north was not markedly different than down south during the compared timeframe, which lends further support that the otter population is becoming better established in the southern study region, at least at Sydnessund. However, although the number of days in which otters were sighted between the two nested locations was almost the same, the amount of otter activity occurring at Hyllestad per day was significantly greater than that of Sydnessund. The difference in sighting frequency of mink between the compared nested locations may therefore be less dependent on the amount of days otter are active per month at a given location and more contingent upon the number of times otter are active per day and the amount of time mink have coexisted with otter in an area.

It is possible that another explanation for the pattern of mink sightings decreasing over time and the absence of mink at Hyllestad is that otter have simply displaced mink from the coastline rather than reduce the local population. Although the methodology used in this study cannot provide evidence otherwise, I consider this hypothesis unlikely. The topography of the fjord systems in western Norway is such that only the shoreline provides ideal habitat for mink, with areas inland of the shoreline generally ascending to steep-sided, mountainous terrain, the topography of which is believed to have initially slowed the expansion of mink in western Norway (Bevanger & Henriksen, 1995). Also, areas just inland of the coastline are much less productive ecosystems and are already inhabited by a relatively large assemblage of native mustelid species including pine martens, stoats, weasels, and other small carnivores like the red fox. The dietary overlap of these mustelid species is already considerable (Brugge, 1977; King, 1980; King & Moors, 1979); therefore, levels of exploitation competition in inland systems would likely be substantial, making a long-term invasion by mink even more difficult. Although competition specifically between weasels, stoats and mink has not been properly studied (Powell et al., 1983), experiments from the British Isles provide evidence that competition between invasive mink and the native otter and polecat (*Mustela putorius*), a similar sized, terrestrial mustelid to the mink, leads to reduced body mass relative to length in sympatric mink populations (Harrington et al., 2009b). This, theoretically, could lead to reduced levels of fitness and reproductive failure in mink living amongst similar-sized native mustelid species in the long-term, and a similar relationship may be expected among the native mustelid assemblage in western Norway.

4.3 Patterns in monthly sighting frequencies

I found that the amount of mink sightings at a nested location is highly dependent on the amount of otter sightings within the same month. Results indicate as the number of otter sightings per month at a nested location increased, the number of mink sightings recorded significantly decreased. This suggests that the amount of mink activity in an area is dependent on that of the otter. This also implies that the absence of otter from a nested location during short timeframes may facilitate a temporary niche expansion for mink, in which mink can take advantage of local food sources in the absence of otter. Therefore, the long-term ability for mink populations to coexist in the presence of otter may be dependent on the extent to which otter are active in an area over long periods of time.

It is likely that this pattern of activity between the two species is a result of interference competition, rather than exploitation competition for several reasons. The first is that mink only appear to become especially active at a nested location in times when the amount of otter sightings are lowest, which is indicative that mink are choosing to avoid these areas when otters are especially active. Similar relationships are found between mink and white tailed sea eagles, in which mink actively decrease activity and avoid areas where eagle densities are highest (Salo et al., 2008). Secondly, the absence of mink at Hyllestad was made even more exceptional by the apparent abundance of small mammals caught on camera. Although not quantified, small mammals such as rats, wood mice and red squirrels were continually sighted at Hyllestad, which indicates a substantial alternative food source for mink to exploit under the competitive pressure of otter. However, no mink were captured on camera at this location during the study period. Lastly, the two carnivore species differ greatly in size, which suggests competition between the two will be aggressive (Case & Gilpin, 1974). Interspecific competition through aggression is common in many intraguild predator relationships (Palomares & Caro, 1999), such as wolves (*Canis lupus*) limiting distribution of coyotes (*Canis latrans*) (Dekker, 1989; Fuller & Keith, 1981), coyotes limiting that of red foxes (Major & Sherburne, 1987; Sargeant et al., 1987; Voigt & Earle, 1983) and red foxes affecting the distribution of arctic foxes (*Vulpes lagopus*) (Hersteinsson & MacDonald, 1992). An example of intraguild exclusion through aggressive interactions in mustelids is between invasive American mink and the smaller, native European mink, in which the former tends to limit the distribution and activity patterns of the latter (Maran & Henttonen, 1995; Põdra et al., 2013; Sidorovich et al., 1999, 2000). Otters have previously been recorded acting aggressively towards mink (Simpson, 2006), and results from this study agree with others which imply competition is based on interference (Dunstone, 1993; Erlinge, 1972; McDonald et al., 2007).

4.4 Changes in rhythmic activity over time, Transect WE

I found that over time, mink decreased diurnal activity and became more nocturnal in Transect WE, despite the resident otter population being predominantly nocturnal. This contradicts the results found by Harrington et al. (2009b), which indicated that mink switched to more diurnal activity in the presence of otters, assumedly as a means of avoiding competition. The results of this study would seem to indicate that competitive pressure from the resident otter population is not enough to force mink to switch their activity patterns to being mostly diurnal. However, when analyzing specific time intervals, it is clear that mink significantly decreased amount of activity during the time period 0:00 – 4:00, which corresponds to the time period in which otter were most active in Transect WE. At the same time, mink significantly decreased activity during daylight hours over the course of the study and markedly increased activity during periods associated with dusk and dawn.

The finding that mink became both less active at night and during the middle of the day, opting the focus activity patterns around dusk and dawn is likely the result of several factors acting simultaneously. Competition with otter during night is the most probable explanatory factor that has resulted in mink being sighted less during late night hours. However, the avoidance of daytime activity by mink suggests some sort of risk associated with foraging in daylight. One such risk associated with daytime foraging is increased susceptibility to predation by avian predators. Large raptor species, such as the white-tailed eagle (*Haliaeetus albicilla*) and golden eagle (*Aquila chrysaetos*) are predators of mink (Johnsen et al., 2007; Sulkava et al., 1997; Tjernberg, 1981). Although no studies focus on interactions between golden eagles and mink, it is known that white-tailed eagles can potentially shape mink activity patterns where the two species overlap (Salo et al., 2008). Both golden and white-tailed eagles have experienced population increases in western Norway over the past several decades (Folkestad, 2006; Folkestad & Probst, 2013; Kålås et al., 2010) and it is possible mink are being squeezed between competitive pressure from otter and predation pressure from eagles, resulting in the mink's increasingly crepuscular activity patterns observed in this study.

4.5 Differences in rhythmic activity over space, Transect NS

Otter sightings at Hyllestad tended to also predominantly happen between the hours of dusk and dawn (72%), although not as much as at the southern location of Sydnessund, at which 87% of sightings were nocturnal. As no mink were sighted at Hyllestad during the experimental timeframe, this difference in affinity for nighttime activity by otter could be a possible determining factor in potential ability for coexistence between otter and mink populations. In conjunction with otter being overall more active at Hyllestad compared to Sydnessund, the timing of activity was spread more throughout the day rather than being concentrated almost exclusively at night. By being active throughout a larger part of the day, mink may potentially be unable to avoid competition by altering activity patterns to time periods in which otter are not active, which would be a contributing factor to the absence of mink at Hyllestad.

4.6 Will otter and mink coexist?

The fate of mink represents an important conservation issue in Norway, as mink are invasive and likely at least partially responsible for some of the collapsing stocks of ground nesting seabirds in areas they have invaded (Byrkjeland, 2015). In smaller mustelid species, it is known that larger, generalist predators like the long-tailed weasel (*Mustela frenata*) predate upon smaller, more efficient species such as the least weasel (Polderboer et al., 1941). Differences in foraging efficiency and slight differences in the types of prey available to each of these predators, based on their differing body sizes is the main explanation for their abilities to coexist in the same habitat (Rosenzweig, 1966). A similar mechanism may be in place for otter and mink that could lead to coexistence, although in the case of otter and mink the otter is both larger and the specialist predator (Bonesi & Macdonald, 2004c). Also, the mink’s potential to exploit alternative food sources away from the shoreline may facilitate a means by which the two species can coexist. Despite many studies that suggest mink can adapt their diets under competitive pressure of otter (Bonesi et al., 2004; Bueno, 1996; Clode & Macdonald, 1995; Erlinge, 1972), little is known of this phenomenon in Norway. This in itself warrants further studies concerning local alternative prey abundances inland of the coastline and throughout the fjord systems of western Norway.

In their native range, American mink do coexist in many areas with the North American river otter. Evidence from this study suggests that the occurrence of mink in western Norway is negatively affected by competition with the superior Eurasian otter, and that once established otter have the ability to permanently suppress mink populations in areas they cohabit, at least in the context of nested locations. However, mink are still sighted throughout much of Norway, even in areas where otter were never eradicated from and have boasted sound populations far longer than those examined in this study. This may be related to a finding by Christensen (1995), who found that in western Norway, mink are positively associated with human settlements and agricultural land in the presence of otter, whilst no preference is shown between wilderness and agricultural or developed land in the absence of otter. This is a possible indication that otter will outcompete mink from the otter’s preferred habitat in western Norway, although mink may find a potential refuge near areas of human activity, as otter display a strong aversion to human disturbance (Kruuk, 1995). Open agricultural land is not considered to be ideal habitat for mink (Yamaguchi et al., 2003), therefore preference of mink for these areas in the presence of otter is further evidence that mink are being outcompeted from wild habitats in western Norway and are relegated to less optimal habitats. However, given the potential refuge of agricultural land and human settlements, it is unlikely that otter will completely eliminate mink from Norway, although they will probably be able to suppress mink populations in areas they cohabit, at least in ecosystems similar to those examined in this study.

Also, the large number of otters drowned in fishing equipment, especially in western Norway may function as a local competitive release for mink and promote coexistence of the two species. Indeed, several otters were drowned just prior to and during the experimental timeframe in close proximity ($\leq$ 10 km) to several of the nested locations. The frequent use of shallow water fyke nets throughout Transect WE, coupled with the large amount of underreporting of drowned otters in Norway (A. Landa, unpubl.), means these numbers are likely underestimated. Improved methods of reporting accidentally killed otter and mink are needed to understand how this process influences local population dynamics, as this could have been a significant influencing factor on sighting frequencies for several nested locations in Transect WE.

The return of the otter represents a potential large-scale natural reestablishment success of an iconic species in Norway. At the same time, continued otter reestablishment will likely function to limit the amount of mink present in coastal ecosystems throughout the country, which could have positive impacts on the future reproductive success of seabirds in areas that mink have been displaced. However, these cascading effects will be likely be dependent on the amount of otter activity present throughout the year near seabird colonies, and more research is necessary to better understand these processes.

4.7 Concluding remarks

This study represents a further contribution to past evidence proposing that otter have a reducing effect on mink populations where they have reestablished and for the first time lends quantitative support to the anecdotal evidence that suggests mink are negatively associated with areas of otter inhabitation in western Norway. This study also provides further evidence that the relationship between invasive mink and native otter is dominated by interference competition rather than competitive exclusion, as mink actively avoid locations where otters are most active, even when alternative food sources are abundant. However, the long-term ability of otter populations to suppress mink remains uncertain, as the studied timeframe was relatively short and permanent effects may only become apparent over longer spans of time. Although mink appear to be displaced from natural ecosystems, more studies are needed to assess local population dynamics of the two species near areas of human inhabitation, as these places may serve as a refuge to mink and therefore promote the long-term existence of this invasive species in Norway. Likewise, mink may facilitate coexistence by altering rhythmic activity patterns to avoid competition with otter, as was seen in this study. More information is needed as to what extent mink may survive in natural ecosystems inland of the coast and to what extent each species is active around seabird colonies, especially during the breeding season. If the return of the otter to western Norway functions to outcompete mink from areas around seabird colonies, the natural reestablishment may function as a cost-effective mechanism by which seabird recruitment is enhanced in the future by lessening the effects of an invasive predator in coastal Norwegian ecosystems.

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Appendix A – Experimental design

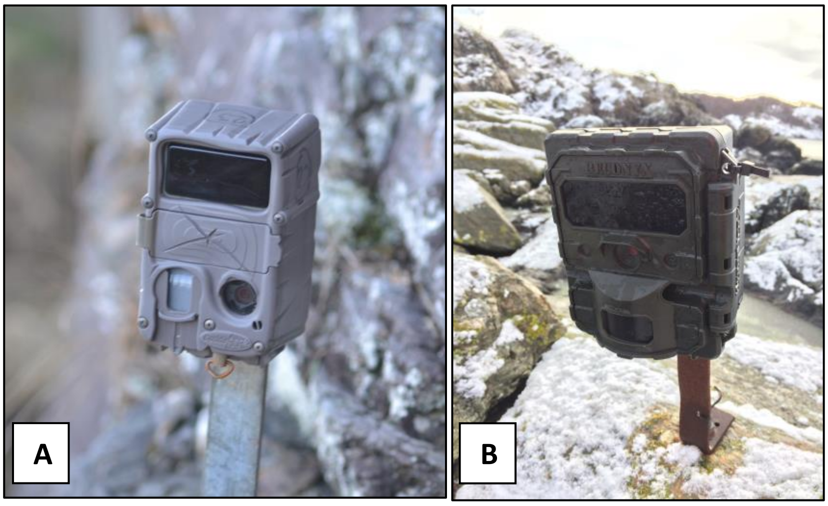

Figure I. The two types of cameras used in the study. “A” = the Cuddeback ™ E2 (Nontypical Inc., Green Bay, Wisconsin, USA), “B” = the Reconyx ™ HyperFire 2 (Reconyx Inc., Holmen, Wisconsin, USA). Photos: Steven Guidos

Figure II. The typical camera setup at a nested location. The nested location shown is Halsnøy (Transect WE). Note the camera facing the two marking spots, inside the yellow circles. Photo: Steven Guidos

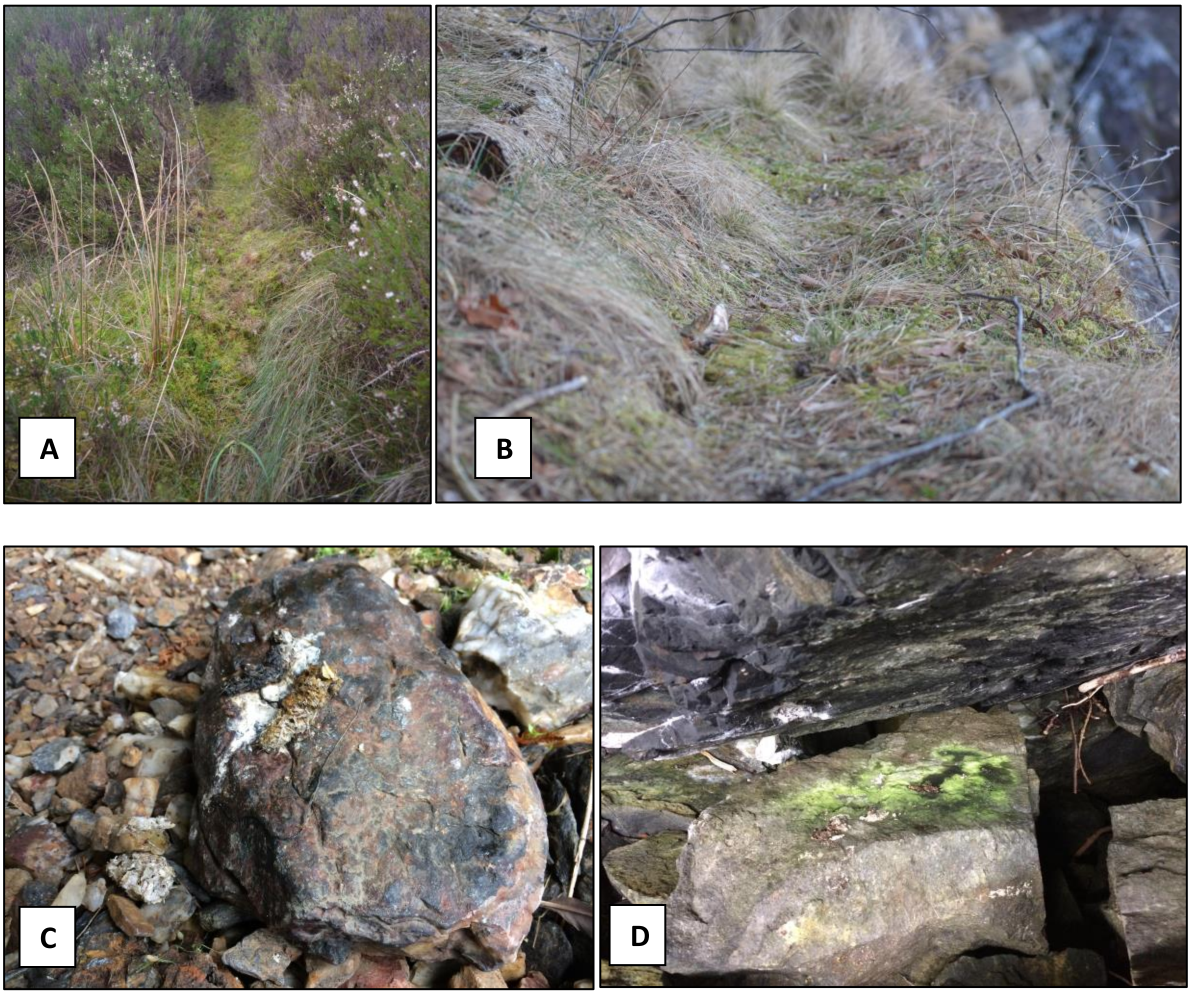

Figure III. Common marking charactersitics of otter and mink. “A” and “B” are trails through vegetation made by otters, although also likely used by mink as well. “C” is an otter scat (~ 4-5 cm). “D” is a common marking area for both otter and mink, note the green discoloration of the rock, indicative of frequent urination. Numerous scats are visible on top of the rock. Photos: Steven Guidos

Appendix B – Examples of species captured on camera

Figure 1V. Examples of various species consistently caught on camera at different nested locations. Species and locations are as follows: "A" = otter, (*Lutra lutra*), Nordhusvågen; "B" = mink (*Neovison vison*), Nordhusvågen; "C" = wood mouse (*Apodemus sylvaticus*), Hyllestad; "D" = red deer (*Cervus elaphus*), Fjelbergsund; "E" = red fox (*Vulpes vulpes*), Hyllestad; "F" = red squirrel (*Sciurus vulgaris*), Hyllestad. All photos owned by the Norwegian Institute for Nature Research.

Appendix C – Otter and mink pup sightings

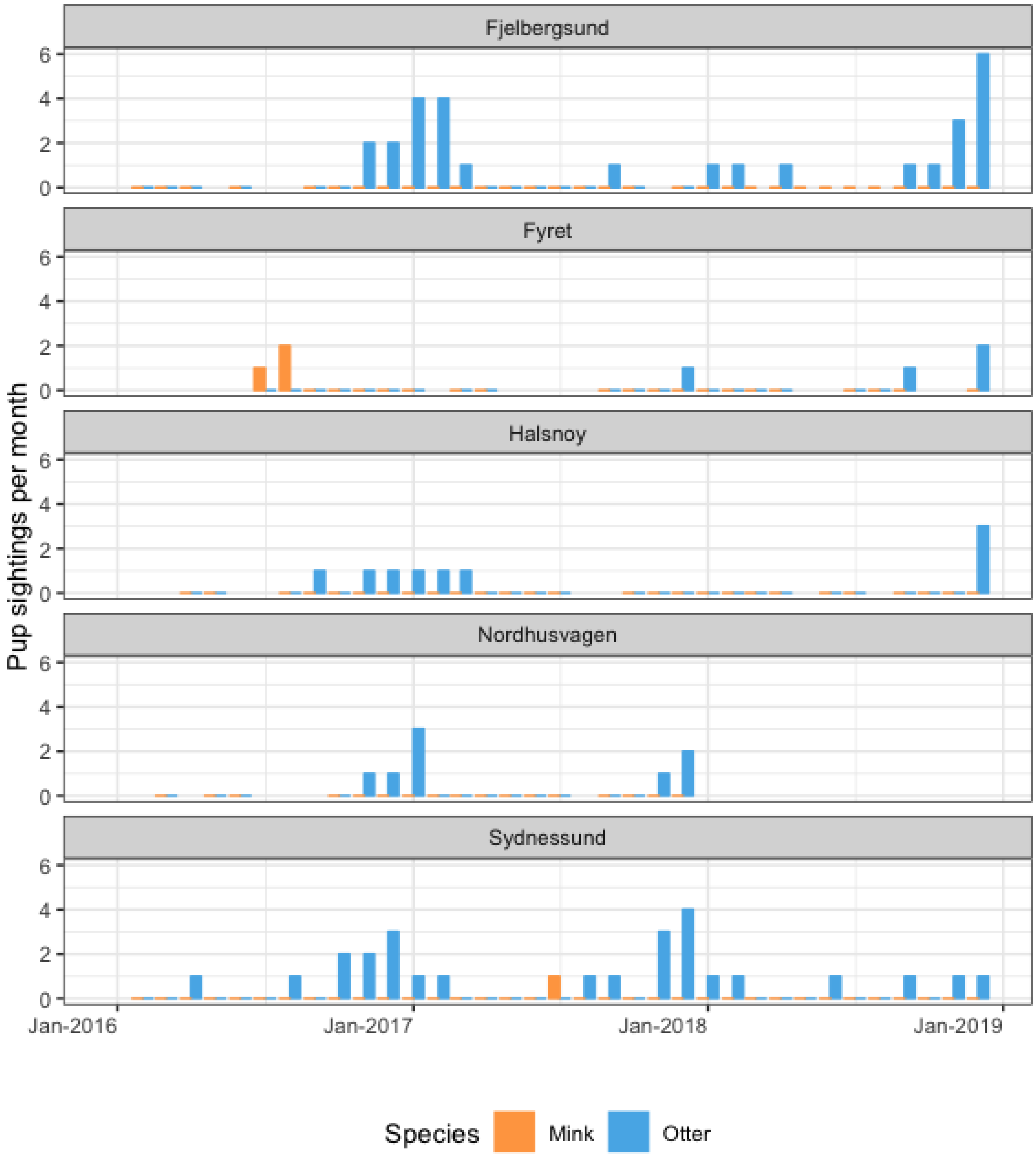

Figure V. The number of pup sightings per month at each of the nested locations in Transect WE over the course of three years. Data from nested locations with two cameras were combined and averaged.

Appendix D – Additional statistical results

Table I. Overview of the generalized linear model results for each nested location of Transect WE. Formula: Monthly sightings ~ Time, family = quasi-Poisson. Monthly sightings over time are specified by each nested location and species. Significant values are indicated in bold text.

Nested Location	**Species**	**df**	**Residual deviance**	***F***	***p***
Sydnessund	Otter	33	71.4	4.2	**0.047**
Sydnessund	Mink	33	124.5	3.03	0.091
Fjelbergsund	Otter	29	150.1	1.26	0.271
Fjelbergsund	Mink	29	65.3	0.03	0.874
Nordhusvågen	Otter	15	24.3	18.49	**<0.001**
Nordhusvågen	Mink	15	70.14	0.37	0.551
Halsnøy	Otter	25	123.6	0.58	0.452
Halsnøy	Mink	25	37.5	1.54	0.227
Fyret	Otter	19	46.8	0.0	0.955
Fyret	Mink	19	117.6	1.05	0.318

Table II. The change in amount of activity recorded at different timeframes of the day from the year *2016 to 2018*. Data is representative of all individual cameras in Transect WE. Significant values are indicated in bold text. Formula: Number of sightings in each timeframe ~ Timeframes * Year + (1|Camera), family = Poisson. Timeframe is based on a 24-hour clock, time “0-4” is equivalent to “00:00” to 4:00”.

Species	**Timeframe**	**Estimate**	**Std. Error**	***p***
Mink	12-16	-1.320	0.4115	**0.001**
Mink	16-20	0.470	0.479	0.326
Mink	20-24	1.163	0.422	**0.006**
Mink	0-4	1.049	0.432	**0.015**
Mink	4-8	1.320	0.411	**0.001**
Mink	8-12	0.986	0.434	**0.023**
Otter	12-16	0.575	0.688	0.403
Otter	16-20	0.479	0.742	0.518
Otter	20-24	-0.598	0.688	0.384
Otter	0-4	-0.388	0.684	0.571
Otter	4-8	-0.575	0.688	0.403
Otter	8-12	-0.651	0.728	0.372

Table III. The change in amount of activity recorded at different timeframes of the day from the year *2016 to 2017*. Data is representative of all individual cameras in Transect WE. Significant values are indicated in bold text. Formula: Number of sightings in each timeframe ~ Timeframes * Year + (1|Camera), family = Poisson. Timeframe is based on a 24-hour clock, time "0-4" is equivalent to "00:00" to 4:00".

Species	**Timeframe**	**Estimate**	**Std. Error**	***p***
Mink	12-16	-0.583	0.352	0.097
Mink	16-20	-0.107	0.422	0.799
Mink	20-24	0.175	0.376	0.642
Mink	0-4	0.624	0.366	0.089
Mink	4-8	0.583	0.352	0.098
Mink	8-12	0.206	0.383	0.591
Otter	12-16	0.522	0.688	0.447
Otter	16-20	0.066	0.748	0.930
Otter	20-24	-0.599	0.687	0.416
Otter	0-4	-0.702	0.686	0.306
Otter	4-8	-0.522	0.688	0.448
Otter	8-12	-0.378	0.723	0.601

Table IV. The change in amount of activity recorded at different timeframes of the day from the year *2017 to 2018*. Data is representative of all individual cameras in Transect WE. Significant values are indicated in bold text. Formula: Number of sightings in each timeframe ~ Timeframes * Year + (1|Camera), family = Poisson. Timeframe is based on a 24-hour clock, time "0-4" is equivalent to "00:00" to 4:00".

Species	**Timeframe**	**Estimate**	**Std. Error**	***p***
Mink	12-16	-0.737	0.434	0.090
Mink	16-20	0.577	0.529	0.274
Mink	20-24	0.988	0.458	**0.031**
Mink	0-4	0.425	0.453	0.349
Mink	4-8	0.737	0.435	0.090
Mink	8-12	0.780	0.469	0.096
Otter	12-16	0.052	0.512	0.917
Otter	16-20	0.414	0.542	0.445
Otter	20-24	-0.039	0.512	0.939
Otter	0-4	0.314	0.509	0.537
Otter	4-8	-0.053	0.512	0.918
Otter	8-12	-0.272	0.522	0.622