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Behavioral responses to olfactory attractants at camera traps: a study of three carnivores in a boreal ecosystem

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Preface

This master thesis is part of the Red Fox Project at the Norwegian University of Life Sciences (NMBU), which is led by researcher Richard Bischof at NMBU. The project conducts research on the behavior of red foxes in order to improve the management of the species.

First and foremost, I would like to thank my supervisor, Richard Bischof, for all the help and support during the fieldwork, the statistical analysis and the writing, and for sharing knowledge and ideas with me. I am very grateful for the opportunity to participate in the Red Fox Project.

I would also like to thank John Odden, senior research scientist at the Norwegian Institute for Nature Research (NINA) and general manager of the Scandinavian lynx project (SCANDLYNX) Norway, for letting me use NINA's camera traps during the fieldwork. Great thanks to Hannah Weber, engineer at NINA, for teaching me how to use the camera traps, answering all my questions and helping me with supplies whenever I needed it. Thanks also to Neri Horntvedt Thorsen, research fellow at NINA, for helping me with the selection of the camera sites. Thank you to Roar Økseter, engineer at NMBU, for helping me with the preparation of the lure sticks.

A special thank you to my fellow colleague Sigurd Bakken for the cooperation during the fieldwork, and for the friendship during the writing process. It has been a pleasure working with you.

Ås, May 10, 2018

Ellen Nordrum Brøste

Abstract

Camera trapping is an efficient and minimally invasive method for studying wildlife ecology and behavior. In camera trap studies, it is important to consider the detection probability to get reliable estimates of e.g. species abundance and occupancy. One way of increasing detection probability is the use of olfactory attractants, commonly referred to as scent lures. Scent lures are natural or synthetic scents based on food, animal scent or plant materials, which purpose is to attract animals through olfaction. Even though scent lures are used in a wide range of research, few have studied how animals behave at scent lures stations at camera traps. Studying animal behavior at scent stations can provide information about the mechanisms by which scent lures change detection probability.

In this study, carried out in southeastern Norway, camera trap photos were used to analyze the behavior of carnivores at 30 scent stations using five different scent station treatments; skunk (*Mephitis mephitis)*-based, red fox (*Vulpes vulpes*)-based and castor (*Castor canadensis*)-based lures, synthetic fermented egg (SFE), and distilled water (control). Each scent station received all five treatments, and each treatment was replaced every 14 days (± 3 days). Three medium-sized carnivore species were detected and thus included in the study: the red fox, the European badger (*Meles meles*) and the European pine marten (*Martes martes*).

This study revealed species-specific behavioral responses to scent lures at camera traps. Red foxes spent more time with red fox- based and skunk based lures and were more likely to visually inspect these lures, indicating attraction towards them. Badgers held a shorter distance to castor-based and skunk-based lures and had more contact with the skunk-based lures. Pine martens displayed aversion towards skunk-based and red fox-based lures by keeping a longer distance. Surprisingly, none of the target species responded to the food-based lure.

The findings in this study implies that the effect of a single scent lure varies both across species and across the behavioral responses of a given species. The choice of lure to attract a given species should thus depend also on the purpose of its use.

Sammendrag

Bruk av viltkamerafeller er en effektiv og lite invaderende metode for å studere dyrs økologi og atferd. I studier er det viktig å ta hensyn til oppdagelsessannsynlighet for å oppnå pålitelige estimater av for eksempel en arts tallrikhet eller tilstedeværelse. En måte å øke oppdagelsessannsynligheten på er bruk av olfaktoriske tiltrekningsstoffer, også kalt luktlokkemidler. Luktlokkemidler er naturlige eller syntetiske luktstoffer basert på mat, lukt fra dyr eller plantematerialer, hvis hensikt er å tiltrekke dyr via dyrs luktesans. Selv om luktlokkemidler er brukt i et bredt spekter av forskning har få studert hvordan dyr oppfører seg ved luktlokkemidler ved viltkamerafeller. Studier av dyrs atferd ved luktlokkemidler kan gi informasjon om mekanismene som gjør at luktlokkemidler endrer oppdagelsessannsynlighet.

I denne studien, utført i Sørøst-Norge, ble bilder fra viltkamerafeller brukt til å analysere rovdyrs atferd ved 30 luktstasjoner ved bruk av fem ulike luktstasjonsbehandlinger; stinkdyr (*Mephitis mephitis*)-baserte, rødrev (*Vulpes vulpes*)-baserte og bever (*Castor canadensis*)-baserte luktlokkemidler, syntetisk fermentert egg (SFE), og destillert vann (kontroll). Hver luktstasjon mottok alle de fem behandlingstypene, og hver behandlingstype ble byttet ut hver 14. dag (± 3 dager). Tre mellomstore rovdyr ble avbildet og dermed inkludert i studien: rødrev, europeisk grevling (*Meles meles*) og europeisk mår (*Martes martes*).

Denne studien avslørte artsspesifikke atferdsresponser på luktlokkemidler ved kamerafeller. Rødrever brukte mer tid ved rødrevbaserte og stinkdyrbaserte luktlokkemidler, og var mer tilbøyelige til å visuelt inspisere disse luktlokkemidlene, noe som indikerer tiltrekning mot disse. Grevlinger holdt kortere avstand til beverbaserte og stinkdyrbaserte luktlokkemidler, og hadde mer kontakt med stinkdyrbaserte luktlokkemidler. Mårene viste aversjon mot stinkdyr-baserte og rødrevbaserte luktlokkemidler ved å holde større avstand. Overraskende nok responderte ingen av artene på det matbaserte luktlokkemidlet.

Funnene i denne studien antyder at effekten av et enkelt luktlokkemiddel varierer både på tvers av arter og på tvers av en gitt arts atferdsresponser. Valget av luktlokkemidler for å tiltrekke en gitt art bør dermed også avhenge av hensikten med bruken av middelet.

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1. Introduction

Camera trapping is an important method in ecology, allowing insight into the life of animals that would otherwise be hidden from us (O'Connell et al., 2011). The use has increased rapidly throughout the past few decades (McCallum, 2013), and the method has developed from the use of simple equipment to advanced technology (O'Connell et al., 2011). Camera trapping is a minimally invasive method, as animals are surveyed without direct human interactions (MacKay et al., 2008) and thus, the method causes little disturbance on fauna (O'Connell et al., 2011). The method is also time- and resource efficient (O'Connell et al., 2011), and enables researchers to survey larger areas than what would be possible with observations ((Kays & Slauson, 2008). Camera trapping is used for answering questions about a range of ecological topics, from nest predation (Buler & Hamilton, 2000), feeding ecology (Weckel et al., 2006) and population estimates (Gould & Harrison, 2018), to activity patterns (Bridges et al., 2004), animal behavior (Kovacs et al., 2017) and species distributions (Ahumada et al., 2011; Buzzard et al., 2017). Camera traps are especially useful for studying rare and elusive species (Karanth et al., 2004), and sometimes, even new species are discovered during camera trap studies (Rovero et al., 2008). The method also allows researchers to study multiple species at once (Chutipong et al., 2017). Photos of animals make research available and understandable for the public, and is a way to raise awareness about species status and conservation (Kays & Slauson, 2008).

Detection probability is of key importance for obtaining reliable estimates and results in studies using camera traps (Harmsen et al., 2011; O'Connell et al., 2011). Detection probability can be defined as "the likelihood that an individual will be detected (photographed or captured) if it is present in a sample unit during the time of the sample" (O'Brien, 2011, p. 73), and is important to consider because it varies in space and time, between species, between individuals of the same species and within the same individual (O'Brien, 2011). Local environmental factors, topography, season and study design are some of the factors that can affect detection probability (Bailey et al., 2004). In camera trapping, the placement and configurations of camera traps within the study area is an important factor (O'Brien, 2011). O'Connor et al. (2017) found that a multiple-camera array increased the detection probability of bobcat (*Lynx rufus*) and Virginia opossum (*Didelphis virginiana*), two cryptic species that are hard to detect. Detection probability can also be increased by placing camera traps along wildlife trails (McCain & Childs, 2008).

One method frequently used to increase detection probability is the use of attractants (Gerber et al., 2012). An attractant is defined by Schlexer (2008) as "any substance, material, device, or technique used to attract a target species" (p. 263). Attractants can be divided into baits, lures and natural attractants, where baits are food-based attractants, lures are attractants based on scent, sound or a visual component, and natural attractants are components belonging to the species' natural environment (Schlexer, 2008).

Attractants based on scent, often referred to as scent lures (though also referred to as olfactory attractants, call lures or long-distance lures) are commonly used in camera trap studies (e.g. Braczkowski et al. (2016), Bridges et al. (2004) and Moruzzi et al. (2002)). The purpose of scent lures is to attract animals through olfaction (Schlexer, 2008). Many animals depend on olfaction to navigate in their environment, and use olfactory cues to find e.g. food and mates, as well as avoiding danger such as potential predators (Ache & Young, 2005). The use of body scent is an important part of both inter- and intraspecific communication in many species (Burgener et al., 2009; Lindgren et al., 1995). In carnivores, scent from specialized scent glands, urine and faeces are used to communicate information about for example territory, mating, movement and behavior (Albone, 1984; Gorman & Trowbridge, 1989). By exploiting the crucial role of olfactory cues, scent lures may increase the number of visits to camera traps and thus increase detection probability (Thorn et al., 2009).

Scent lures can be made from a range of components, but are most commonly based on animal scents, food or plant materials (Schlexer, 2008). Animal scent is used to exploit the interest in conspecifics, potential predators or prey, and animal products such as urine, faeces and scent glands are commonly used (Schlexer, 2008). Animal-based lures can be pure products, but commercial lures are often a mixture of various ingredients (Schlexer, 2008). Examples of commonly used food-based lures are fermented egg (Hunt et al., 2007), fatty acid scent (FAS) (Monterroso et al., 2011), peanut butter (Andelt & Woolley, 1996) blood (Thorn et al., 2009) and fish oil (Jordan & Lobb-Rabe, 2015), while catnip (*Nepeta cataria*) oil (Suárez-Tangil & Rodríguez, 2017) and valerian (*Valeriana officinalis*) oil (Read et al., 2015) are common plant-based lures. Many scent lures have yet to be tested for their effectiveness, and the choice of lure is thus often based on tradition rather than science (Schlexer, 2008)

Although many camera trap studies use scent lures, few have studied the behavioral responses to scent lures at camera traps (but see Andersen et al. (2016) and Wikenros et al. (2017)). Looking at behavior can help us better understand the mechanism by which scent lures change detection probability, e.g. whether animals investigate the lure, mark on it or try to consume it. More time spent at a camera trap station increases the probability that the animal gets photographed, and increases the chance to detect identifying marks (Güthlin et al., 2014) and observe other characteristics like body condition (Carricondo-Sanchez et al., 2017) and sex (Monterrubio-Rico et al., 2018). In addition, increased behavioral activity may also increase the chance of animals leaving tissue or matter suitable for DNA sampling, such as hair (Burki et al., 2010), feces and urine (Andersen et al., 2016), and glandular secretion in the case of marking (Clapham et al., 2014). Thus, knowledge about behavioral responses to scent lures is important for further development of methods used in ecological studies.

The aim of this study is to discover how carnivores in a boreal ecosystem respond to scent lures at camera traps. To accomplish this, I quantify the behavioral responses of three medium-sized carnivores;

the red fox (*Vulpes vulpes*), the European badger (*Meles* meles) and the European pine marten (*Martes martes*), to the presence of five different scent station treatments; skunk (*Mephitis mephitis)*-based, red fox-based and castor (*Castor canadensis*)-based scent lures, synthetic fermented egg (SFE), and distilled water (control). The behavioral responses are investigated analyzing still images from camera traps in a boreal ecosystem in southeastern Norway. The behavioral responses are divided into six classes; time spent at the scent station, distance to the lure, contact with the lure, mouthing the lure, visual inspection of the lure and scent marking. Through this study, I also explore how camera trapping can be used as a method to study animal behavior.

I ask the following research question and two general predictions:

Q1: How do the species-specific behavioral responses vary between the scent lures?
P1: I predict that, compared to the control (water), the three target species will display behaviors that indicate attraction towards food-based scent lures and gland-based scent lures from conspecific or smaller carnivores than themselves.
P2: I predict that, due to risk of intra-guild predation, smaller carnivores will display behaviors that indicate avoidance of gland-based scent lures from larger carnivores, compared to the control (water).

I discuss the implications of the results for the effects of lures on animal behavior and show how animal behavior can be studied using camera traps.

2. Materials and methods

2.1 Study area

The study area (59.36-59.81° N, 10.60-11.60° E) was located in southeastern Norway. The area lies within the counties of Akershus and Østfold, and covers 15 municipalities; Nesodden, Frogn, Oppegård, Ås, Ski, Enebakk, Vestby, Våler, Spydeberg, Eidsberg, Marker, Skiptvet, Rakkestad, Sarpsborg and Råde (figure 2.1). The size of the area was about 2400 km^2 and between 0 and 400 meters above sea level (Kartverket, 2017). The landscape varies from coastline, lakes and agricultural fields to valleys and wooded hills (Klemsdal, 2002). The area lies for the most part within the boreonemoral zone (Moen, 1999). Boreal forests dominate the area, consisting of Scots pine (*Pinus sylvestris)* and Norwegian spruce (*Picea abies)* mixed with deciduous types like silver birch (*Betula pendula)*, downy birch (*Betula pubescens)*, aspen (*Populus tremula)*, grey alder (*Alnus incana)*, oak (*Quercus* spp.), hazel (*Corylus avellana)*, ash (*Fraxinus excelsior)* and elm (*Ulmus glabra)* (Moen, 1999).

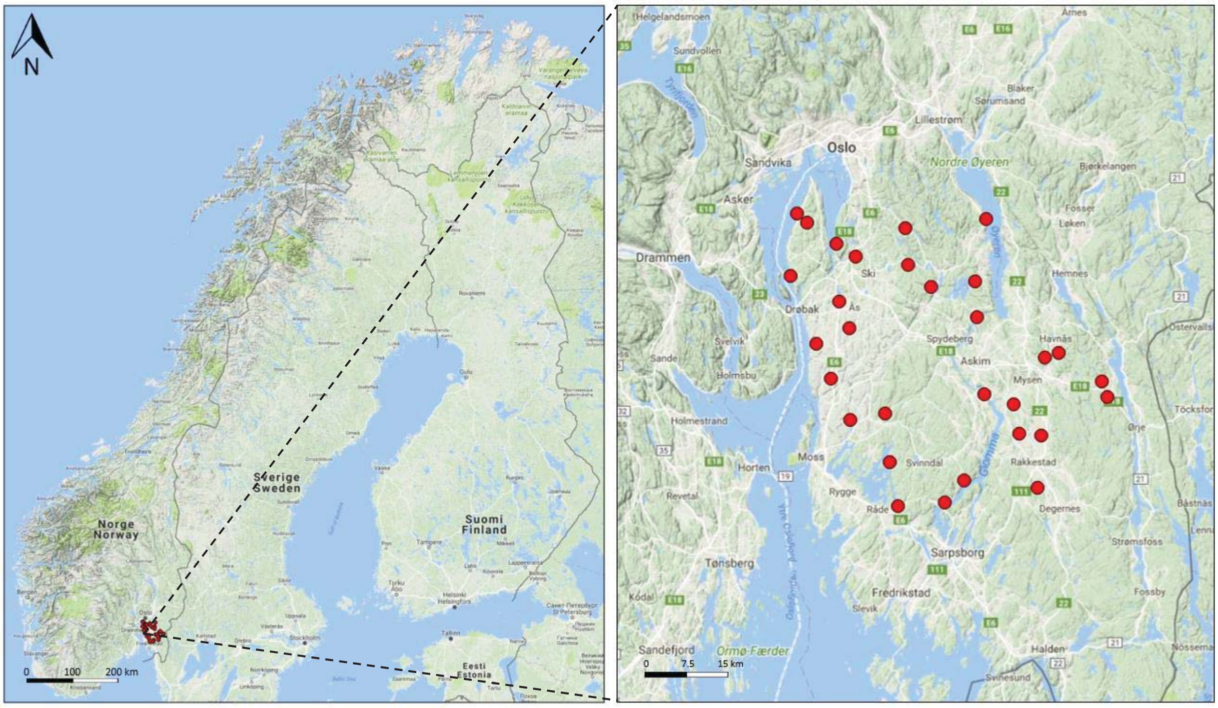

Figure 2.1. The study area in Akershus and Østfold counties, southeastern Norway. The red dots represent the 30 camera trap locations used in the study (Background maps: Map data ©2018 Google, www.google.com/maps).

The growing season (defined as number of days with mean temperature above 5°C) is relatively long compared to other parts of Norway, lasting between 180 and 190 days (Moen, 1999). The climate is milder than expected from the degree of latitude, due to warm winds and oceanic currents, among other factors (Dannevig & Harstveit, 2013). The temperature varies during the year, with mean temperature between -3 and -5 °C in January and between 16 and 17 °C in July (Dannevig, 2009). Yearly precipitation rate is intermediate, with an average of 700-1000 mm (Moen, 1999), and the duration of snow cover (when snow covers minimum 50 % of the ground) is between 50 and 125 days per year (Moen, 1999).

2.2 Study species

In this study, I focus on the three species of wild medium-sized carnivores; the red fox, the European badger and the European pine marten. These species were chosen because previous data from NINA's studies have indicated that these species are abundant in the study area (Odden, 2015), and because other studies have shown that these species respond to scent lures in the wild (Bischof et al., 2014b; Burki et al., 2010; Mortelliti & Boitani, 2008).

The three target species vary in their geographic range but overlap for the most part in Europe. The red fox, who belong to the Canidae family (Larivière & Pasitschniak-Arts, 1996), is found in Europe, Asia, North America and North Africa (Zimen, 1980), and has been introduced to Australia by humans (Australian Government, 2011). It has the widest geographic range of all land-living carnivores (Schipper et al., 2008) and continues expanding its range (Elmhagen et al., 2017; Hjeljord, 2008; MacPherson, 1964). The European badger (henceforth referred to as badger), who belong to the Mustelidae family (Bjärvall & Ullström, 2005), has a much smaller geographic range, covering Europe except the northern parts of Scandinavia and Russia (Roca et al., 2014). The geographical distribution of the European pine marten (henceforth referred to as pine marten), who also belong to the Mustelidae family (Bjärvall & Ullström, 2005), is similar to the badger's, covering most of Europe, except Iceland, Greece, and parts of the Iberian peninsula and Great Britain (Bjärvall & Ullström, 2005; IUCN, 2016).

The red fox and the badger are highly adaptable species when it comes to habitat choices. Both species can exploit a variety of landscape types, from wilderness to urban areas (Baker et al., 2000; Do Linh San et al., 2011; Hartová-Nentvichová et al., 2010), and a variety of habitats (Cavallini & Lovari, 1994; Feore & Montgomery, 1999; Kauhala & Auttila, 2010). The red fox is often found in heterogeneous landscapes and edges between different habitats (Henry, 1986; Lloyd, 1980), while the badger is linked to agricultural landscapes and woodland (Byrne et al., 2012; Feore & Montgomery, 1999), especially deciduous forests (Bjärvall & Ullström, 2005) but also coniferous forest (Brøseth et al., 1995). Both species can also be found at high altitudes in Alpine areas (Balestrieri et al., 2011; Lucherini & Crema, 1995). The pine marten has a narrower use of habitats, partly due to predation by larger animals like red fox (Lindström et al., 1995), Eurasian lynx (*Lynx lynx*) (Linnell et al., 1998) and golden eagle (*Aquila chrysaetos*) (Korpimäki & Norrdahl, 1989). It prefers forest, especially spruce forest, over open landscapes and clear-cuts (Brainerd & Rolstad, 2002; Storch et al., 1990), where it both can hide from predators and find its prey.

Red foxes, badgers and pine martens are generally seen as generalists and opportunists (Panzacchi et al., 2007; Roper, 1994; Storch et al., 1990), and forage alone (Bevanger, 2012; Henry, 1986; Kruuk, 1978). The red fox's diet ranges from fruits (Contesse et al., 2004), berries (D'Hondt et al., 2011) and scavenged meat (Contesse et al., 2004) to small rodents, mountain hare (Needham et al., 2014) and roe deer (Panzacchi et al., 2007). The badger's diet consists of invertebrates, with earthworms as the favorite (Brøseth et al., 1995; Kruuk, 1978; Lucherini & Crema, 1995), plants (Lucherini & Crema, 1995), berries (Brøseth et al., 1995), and vertebrates like birds (Lucherini & Crema, 1995) and small rodents (Brøseth et al., 1995). As the pine marten is an excellent climber, it feeds on squirrels and is a competent nest predator (Storch et al., 1990), but its diet also consists of rodents, birds, hares, berries, insects (Helldin, 2000) and ungulate carcasses (Jedrzejewski et al., 1993).

The circadian activity of the red fox is highly variable. In areas with low levels of human disturbance, the activity is mainly crepuscular (Pandolfi et al., 1997; Servin et al., 1991) and can be diurnal (Lovari et al., 1994), while the activity is nocturnal in human-dominated areas (Díaz-Ruiz et al., 2016). The badger is nocturnal in the sense of aboveground activity, but is active underground during the day, where it stays inside one of the setts in the territory (Do Linh San et al., 2010). The pine marten is also mainly nocturnal, though activity patterns may vary by season (Bevanger, 2012; Zalewski, 2001).

2.3 Study design

In this study, 30 camera trap locations were used. At each camera trap, a scent station was installed with 2 to 6 m between the scent station and the camera. The area between the scent station and the camera was cleared by removing high grass and branches. The scent station consisted of one scent lure stick hammered 20 cm into the ground, leaving 20 cm exposed above the ground. The lure sticks were made of untreated wood of Scots pine or Norwegian spruce with a total length of 40 cm and a cross-section of 2,5 x 5 cm. A 3 cm deep and 1 cm wide hole angled 45 degrees downwards was drilled into each lure stick on the narrow side 2,5 cm from the top of the stick (figure 2.2).

A total of 150 lure sticks were used in the study. The lure sticks were treated with a scent lure, applied with one cotton swab cut in half and soaked in the lure, containing ~ 0.5 mL of lure, and placed in the drilled hole of the lure stick. Cotton swabs with cotton on both ends and paper core were used. The five treatments were (i) skunk-based scent lure (essence of striped skunk anal scent glands), (ii) red fox-based scent lure (grinded red fox scent glands), (iii) castor-based scent lure (castoreum (essence of anal sacs) from American beaver (*Castor canadensis)*), (iv) SFE and (v) distilled water as control. All four scent lures were obtained from F & T Fur Harvester's Trading Post, Alpena, MI, USA.

Skunk-based scent lures have shown positive effect on attracting swift foxes (*Vulpes velox*) (Stratman & Apker, 2014), red foxes (Bischof et al., 2014b), and mountain lions (*Puma concolor*) (Long et al., 2003), and skunk scent is used as a component in many scent lure mixes (F & T Fur Harvester's Trading Post, 2018). The skunks (family Mephitidae) (Wozencraft, 2005) are not native to Europe, and their scent therefore represents a novelty for the species in the study area. The secretion is quite potent and persistent (Stevens, 1945), which makes it effective as a scent lure.

As it was probable that the red fox would be one of the species that would visit the scent stations, fox-based lure was chosen. Lures based on red fox scent glands are used in red fox trapping, and is recommended as a fox attractant in the literature (Schlexer, 2008). Due to the red fox-based lure’s thick consistence, the lure was mixed with glycerol to ease the application.

The castor-based lure was included in the study because it has shown to be effective in attracting red foxes (Bischof et al., 2014b), and has been recommended as lures to attract wolverines (*Gulo gulo*) (Mowat, 2001). In combination with catnip oil, it has been used to attract Eurasian lynx (Schmidt & Kowalczyk, 2006) and Canada lynx (*Lynx canadensis*) (McDaniel et al., 2000).

SFE contains some of the same components that are found in scavenged meet and canid anal glands (Bullard, 1982). Studies have shown positive effects on red foxes (Hunt et al., 2007; Saunders & Harris, 2000; Travaini et al., 1996), kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans)* (Bullard et al., 1983; Roughton, 1982) dingoes (*Canis lupus dingo*) and feral dogs (*Canis lupus familiaris*) (Hunt et al., 2007).

Distilled water was used as control, and the application was performed following the same protocol as the lures to ensure equal treatment. As the lure sticks were novel objects suddenly appearing in the environment, they were assumed to be attractive to animals even without scent lures. The use of lure sticks treated with water as control made it possible to compare the effect of the scent lures with the effect of the lure sticks without scent lures.

The scent stations were randomly assigned to one lure at the time and the lure sticks and lures were replaced every 14 days (± 3 days). After use, the lure sticks were disposed off outside the study area. The lure sticks were placed with the drilled hole facing the wildlife trail if this was present in front of the camera and facing the camera where wildlife trails were absent. Gloves were used in all handling of cameras, lure sticks and lures to prevent cross-contamination and contamination of human scent.

Figure 2.2. Example of scent lure stick with a cotton swab placed in the drilled hole. The lure stick is driven 20 cm into the ground, leaving 20 cm above the ground.

2.4 Data collection

The fieldwork was conducted between September 15 and December 20, 2017. In this study, camera traps from the Norwegian Institute for Nature Research (NINA) were used. NINA uses camera traps to monitor the Eurasian lynx in southeastern Norway as part of the SCANDLYNX project (Odden, 2015). SCANDLYNX is a Scandinavian research project on the Eurasian lynx (Odden, 2015; SCANDLYNX, 2017). Camera traps were placed specifically with the goal to photo-capture lynx, and were therefore placed in steep terrain, on ledges or facing the cliff bases, often close to wildlife trails. The cameras were pointing perpendicular to the wildlife trail at locations where a wildlife trail was present. Each camera was mounted on a tree between 0.2 and 1 m above ground.

Thirty of NINA's camera locations were used during the study, with one camera trap per location and a minimum of 2.3 km between the locations. Five different models of RECONYX™ (address: 3828 Creekside Ln, Ste 2, Holmen, WI 54636, USA, www.reconyx.com) cameras were used: HC500 HyperFire Semi-Covert IR (with infrared light), HC600 HyperFire High Output Covert IR (with invisible flash), PC800 HyperFire Professional Semi-Covert IR (with infrared light), PC900 HyperFire Professional Covert IR (with invisible flash), and PC850 HyperFire Professional White Flash LED (with white light and LED flash). The number of cameras of each model used in the study was not registered. The cameras were operating 24 hours per day every day during the study period. The cameras were set to take three photos per trigger with up to two photos per second, using the *rapidfire* setting. The *no delay* function was used to enable the cameras to take a new series of photos one second after the other if triggered. Using the *time lapse* function, the cameras were set to take one photo per day to assure that the cameras were operating. The cameras were set to high resolution and high sensitivity (for more information, see Odden (2015)).

2.5 Data processing

All photos from the camera traps were sorted, and photos of red foxes, badgers and pine martens were kept for further analysis. Each photo of the target species was analyzed by registering the six behavioral responses listed below. The behavioral responses were chosen based on previous studies, and by studying camera trap photos from NINA's research available at http://viltkamera.nina.no. Photos of a given species that were taken within a five-minute interval were assumed to be of the same individual and thus defined as one visit. The behavioral responses were defined and measured as follows:

Time spent at scent stations: Time spent at scent stations was defined as the duration of a visit in seconds. The time an animal spends at scent lures has been used to evaluate attraction and avoidance in both captive (Saunders & Harris, 2000) and wild (Andersen et al., 2016) carnivores, suggesting that more time spent at scent station could indicate attraction, while less time spent could indicate avoidance.

Distance: To get a relative measure of distance across the target species, distance was measured using the body length of the animal in the photo. Body length has been used as measuring unit in other studies on behavioral ecology (e.g. Macdonald et al., 2004). The body length was measured from the base of the ear to the base of the tail. Distance was recorded as the number of body lengths between the lure stick and the part of the animal closest to the lure stick (figure 2.3). Contact between the animal and the lure was recorded as zero body lengths.

Contact: Contact was defined as any contact between the animal's body and the lure stick, regardless of body part, and was recorded as true or false (figure 2.4.a). When there was contact between the animal and the lure stick, it was recorded whether the animal was mouthing the stick.

Mouthing: Mouthing was defined as biting, licking or otherwise contact between the animal's mouth and the stick (figure 2.4.b). In cases where distinguishing between licking and sniffing was not possible, the behavior was recorded as contact and not mouthing. The behavioral response was recorded as true or false.

Visual inspection: Visual inspection of lure was measured by evaluating whether the animal was looking at the lure stick (figure 2.3). In cases where this was not possible to evaluate, the direction of the animal's head was evaluated, i.e. if the head was pointing directly towards the lure stick, this was recorded as visual inspection. The behavioral response was recorded as true or false.

Scent marking: Scent marking is commonly used in studies on behavioral responses to scent lures (Andersen et al., 2016; Bullard et al., 1983; Wikenros et al., 2017). Scent marking was defined as urinating, defecating or deposition of gland secretion (Johnson, 1973). Scent marking was recorded whenever this occurred in the photo, regardless of the location of the marking, i.e. directly on the lure stick, on the ground or on a conspecific individual (figure 2.5). The behavioral response was recorded as true or false.

Figure 2.3. Example camera trap photo of red fox. Body length was measured from the base of the ear to the base of the tail (a), and distance was measured using the number of body lengths between the lure stick and the part of the animal closest to the lure stick (b). In this photo, the red fox is visually inspecting the lure stick.

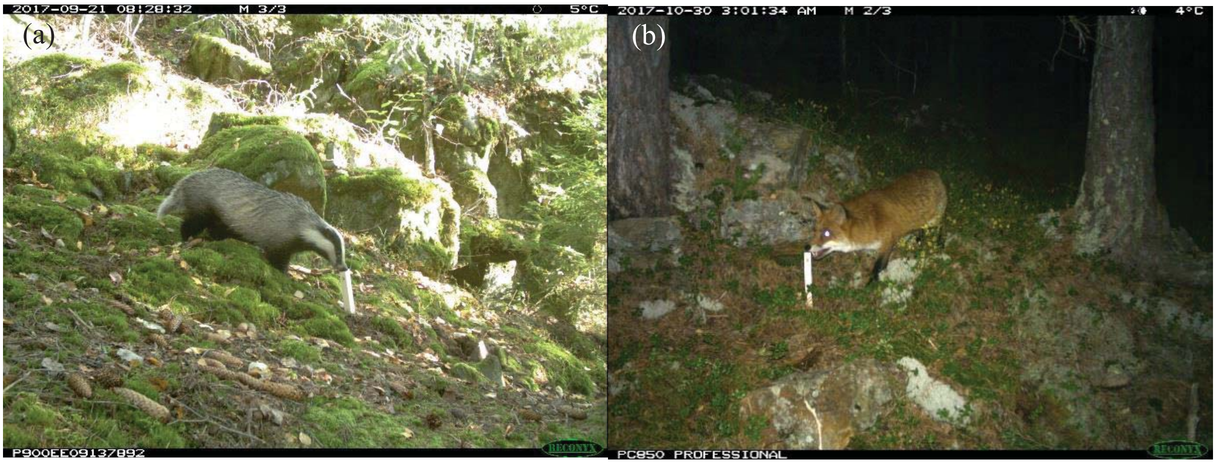

Figure 2.4. Example camera trap photos of contact between badger and lure stick (b) and red fox mouthing a lure stick.

Figure 2.5. Example camera trap photo series of pine marten approximating the lure (a), turning around while touching the lure stick with the front paw (b), scent marking standing on front paws (c), and running off (d).

2.6 Statistical analysis

The open-source language and environment for statistical computing and graphics R version 3.4.3 (R Core Team, 2017) with RStudio version 1.1.414 (© 2009-2018 RStudio, Inc.) was used to execute the statistical analyses. The significance level was $\alpha = 0.05$. The statistical models for each behavioral response are explained below. The results of the model selection process are shown in the appendix (table A.1).

<u>Time spent at scent stations:</u> To estimate the effect of lure type on the time spent at the scent station, the Cox proportional hazards regression model (CPH model) (Cox, 1972) was used to perform a time-to-event analysis. In a time-to-event analysis, also called survival analysis (Kleinbaum & Klein, 2012), time is defined as the time from a given start point (e.g. medical treatment of a patient) until a given event occur (e.g. the patient dies) (Kleinbaum & Klein, 2012). In this analysis, time was defined as seconds until the event occurred, and the event was departure from the scent station (i.e. time between the first and the last photo of a visit). The result of a CPH model is a hazard ratio comparing the likelihood of failure between two groups. The hazard ratios are obtained by exponentiating the coefficients. The scent lures were compared to the control only. To execute the analysis, the R package *coxme* (Therneau, 2018) was used. Time per visit was used as response variable, scent station treatment (skunk-based lure, red fox-based lure, castor-based lure, SFE and control (water)) and days since lure application were used as fixed effects, and camera ID was included as a random effect.

<u>Distance:</u> The effect of the scent lures on the distance between the target animal and the lure stick was analyzed with linear regression using the *lmer* function in the R package *lme4* (Bates et al., 2015) to fit a linear mixed model (LMM). This model was chosen because the response variable, distance, contained decimal numbers. A mixed model was required to include both fixed and random effects. Scent station treatment (skunk-based lure, red fox-based lure, castor-based lure, SFE and control (water)) and days since lure application were used as fixed effects, and camera ID was included as a random effect. The data was aggregated over visit with function set to minimum. The R package *effects* (Fox, 2003) was used to create plots showing the effects of scent station treatment on distance.

<u>Contact:</u> The effect of the scent lures on the animals' contact with the lure was investigated with a logistic regression using logit link function, by fitting a generalized linear mixed-effects model (GLMM) using the *glmer* function in the R package *lme4* (Bates et al., 2015). As the response variable, contact, was binomial, the GLMM was fitted with family *Binomial*. A mixed model was required to include both fixed and random effects. Scent station treatment (skunk-based lure, red fox-based lure, castor-based lure, SFE and control (water)) and days since lure application were used as fixed effects, and camera ID was included as a random effect. The data was aggregated over visit with function set to maximum. The

R package *effects* (Fox, 2003) was used to create plots showing the effects of scent station treatment on contact.

Mouthing: Due to the low number of observations, no statistical analyses were performed on the results for the behavioral response mouthing.

Visual inspection: To explore the effect of the scent lures on the animal's visual inspection of the lure stick, a logistic regression using logit link function was used by fitting a GLMM. The *glmer* function in the R package *lme4* (Bates et al., 2015) was used. Visual inspection was used as the response variable, and because this was a was binomial variable, the GLMM was fitted with family *Binomial*. A mixed model was required to include both fixed and random effects. Scent station treatment (skunk-based lure, red fox-based lure, castor-based lure, SFE and control (water)) and days since lure application were used as fixed effects, and camera ID was included as a random effect. The data was aggregated over visit with function set to maximum. The R package *effects* (Fox, 2003) was used to create plots showing the effects of scent station treatment on visual inspection.

Scent marking: Due to the low number of observations, no statistical analyses were performed on the results for the behavioral response scent marking.

3. Results

The study resulted in 1876 operational camera trap days, of which 336 days with controls, 357 with SFE, 369 with castor-based lures, 360 with fox-based lures and 420 with skunk-based lures. The carnivore species captured by the camera traps during the study period were red fox, European pine marten, European badger, Eurasian lynx, domestic dog (*Canis lupus familiaris)* and domestic cat (*Felis catus)*.

A total of 1279 camera trap photos of the target species were obtained. Examples of photos are shown in figure 3.1. The red fox was the most frequently captured species, followed by the badger and the pine marten (table 3.1). Red foxes were photo-captured at 27 of the 30 camera trap locations, badgers at 14, and pine martens at 12 camera trap locations.

Figure 3.1. Example camera trap photos showing (a) red fox in front of lure stick, (b) badger and (c) pine marten investigating lure sticks.

Table 3.1. The number of camera trap photos, visits, and the number of camera traps where at least one individual of a given species was detected, per species and treatments. The total number of camera trap photos and visits per species is shown at the bottom.

Species/	Red fox			Badger			Pine marten		
Treatment	Photos	Visits	Cameras	Photos	Visits	Cameras	Photos	Visits	Cameras
Control	79	24	13	111	18	5	34	5	4
SFE	87	22	12	16	5	3	75	8	3
Castor	48	14	7	161	10	5	9	2	2
Red fox	136	18	11	63	5	4	45	9	5
Skunk	210	30	18	169	22	8	36	8	5
Total	560	108	-	520	60	-	199	32	-

3.1 Time spent at scent stations

The results from the CPH model were significant for red foxes, while no significant effect of the lures compared to controls was detected for badgers and pine martens (table 3.2). Compared to the control, red foxes were likely to stay longer at a scent station treated with red fox-based lure (coef = -0.85, exp(coef) = 0.43, se(coef) = 0.34, z-value = -2.49, p-value = 0.01), and skunk-based lure (coef = -0.72, exp(coef) = 0.49, se(coef) = 0.31, z-value = -2.34, p-value = 0.02).

Table 3.2. The results of the final Cox proportional hazards model (Surv(duration,event) ~ Treatment + 1|Camera.ID) for red fox, badger and pine marten, showing the effect of the lures compared to the control. Coefficients are on the log scale. Numbers are rounded up to two decimals. Significant z-values and p-values (<0.05) are bold.

Treatment per species	coef	Exp(coef)	se(coef)	z-value	p-value
Red fox					
SFE	-0.23	0.79	0.33	-0.71	0.48
Castor-based lure	0.11	1.12	0.38	0.30	0.76
Fox-based lure	-0.85	0.43	0.34	**-2.49**	**0.01**
Skunk-based lure	-0.72	0.49	0.31	**-2.34**	**0.02**
Badger					
SFE	0.01	1.01	0.66	0.01	1.00
Castor-based lure	-0.42	0.65	0.52	-0.81	0.42
Fox-based lure	-0.24	0.79	0.62	-0.39	0.70
Skunk-based lure	-0.21	0.81	0.37	-0.58	0.56
Pine marten					
SFE	-0.48	0.63	0.59	-0.79	0.43
Castor-based lure	0.85	2.33	0.87	0.97	0.33
Fox-based lure	0.61	1.84	0.59	1.02	0.31
Skunk-based lure	0.69	2.00	0.62	1.12	0.26

3.2 Distance

The analysis of the distance between the animal and the lure revealed differences between badgers and pine martens (table 3.3, figure 3.2). Compared to the control, skunk-based lures (estimate = -2.12, standard error (SE) = 0.66, z-value = -3.23) and castor-based lures (estimate = -1.81, SE = 0.90, z-value = -2.01) had positive effects on distance for badgers. Fox-based lures (estimate = 1.17, SE = 0.31, z-value = 3.74) and skunk-based lures (estimate = 0.81, SE = 0.32, z-value = 2.55) had negative effects on distance for pine martens, compared to the control.

Table 3.3. The output from the LMM (Distance ~ Treatment + 1|Camera.ID) of the effect of treatment on the distance between an individual of a given species and the lure. The numbers are the estimates, standard errors (SE) and t-values for the red fox, the badger and the pine marten. Numbers are rounded up to two decimals. Significant t-values (±2) are bold.

Treatment per species	Estimate	SE	t-value
Red fox			
Intercept (control)	1.84	0.32	**5.77**
SFE	0.28	0.38	0.74
Castor-based lure	-0.11	0.46	-0.24
Fox-based lure	-0.43	0.41	-1.05
Skunk-based lure	-0.16	0.37	-0.43
Badger			
Intercept (control)	2.75	0.62	**4.44**
SFE	-0.84	1.03	-0.82
Castor-based lure	-1.81	0.90	**-2.01**
Fox-based lure	-1.49	1.10	-1.35
Skunk-based lure	-2.12	0.66	**-3.23**
Pine marten			
Intercept (control)	0.00	0.25	0.00
SFE	0.38	0.32	1.18
Castor-based lure	0.75	0.47	1.60
Fox-based lure	1.17	0.31	**3.74**
Skunk-based lure	0.81	0.32	**2.55**

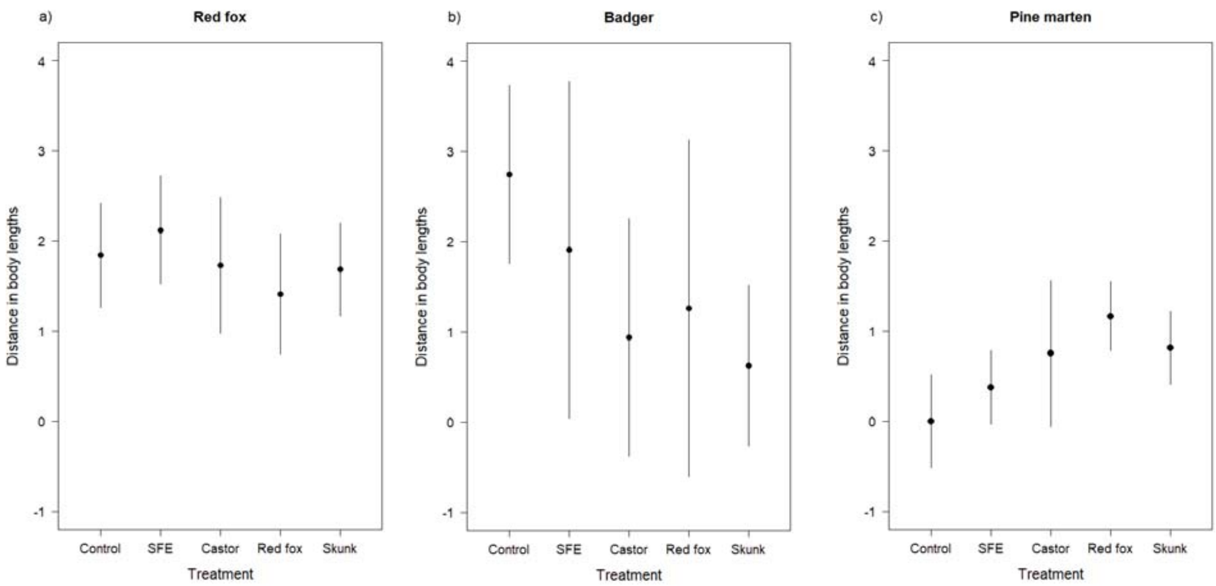

Figure 3.2. The results from the LMM for a) red fox, b) badger and c) pine marten, showing the effect of treatment on distance between the species and the lure stick. The points represent the estimated mean and lines represent the 95% confidence intervals around the mean.

3.3 Contact

Skunk-based lures had a positive effect on the probability of contact between the badgers and the lure (estimate = 2.50, SE = 1.15, z-value = 2.19, p-value = 0.03), and a positive trend was detected for fox-based lures (estimate = 2.51, SE = 1.44, z-value = 1.74, p-value = 0.08) (table 3.4, figure 3.3). No significant effect was detected for red foxes and pine martens, although a positive trend was detected for pine martens at SFE (estimate = 2.46, SE = 1.30, z-value = 1.90, p-value = 0.06).

Table 3.4. The output from the final GLMM (Contact ~ Treatment + 1|Camera.ID) of the effect of treatment on the contact between an individual of a given species and the lure. The numbers are the estimates, standard errors (SE) t-values and p-values for the red fox, the badger and the pine marten. Numbers are rounded up to two decimals. Significant t-values (±2) and p-values (<0.05) are bold.

Treatment per species	Estimate	SE	t-value	p-value
Red fox				
Intercept (control)	-2.59	0.95	**-2.72**	**0.01**
SFE	0.03	1.15	0.03	0.98
Castor-based lure	-0.26	1.40	-0.18	0.85
Fox-based lure	0.02	1.15	0.02	0.99
Skunk-based lure	1.01	0.96	1.06	0.29
Badger				
Intercept (control)	-2.96	1.11	**-2.66**	**0.01**
SFE	-16.98	547.35	-0.03	0.98
Castor-based lure	2.14	1.35	1.59	0.11
Fox-based lure	2.51	1.44	1.74	0.08
Skunk-based lure	2.50	1.15	**2.19**	**0.03**
Pine marten				
Intercept (skunk)*	-1.95	1.07	-1.82	0.07
SFE	2.46	1.30	1.90	0.06
Castor-based lure	-33.05	2.81e+07	0.00	1.00
Fox-based lure	-0.13	1.05	-0.09	0.93
Control	43.91	3.00e+07	0.00	1.00

* Skunk-based lure was used as intercept as there were no variance in the estimates with control as intercept.

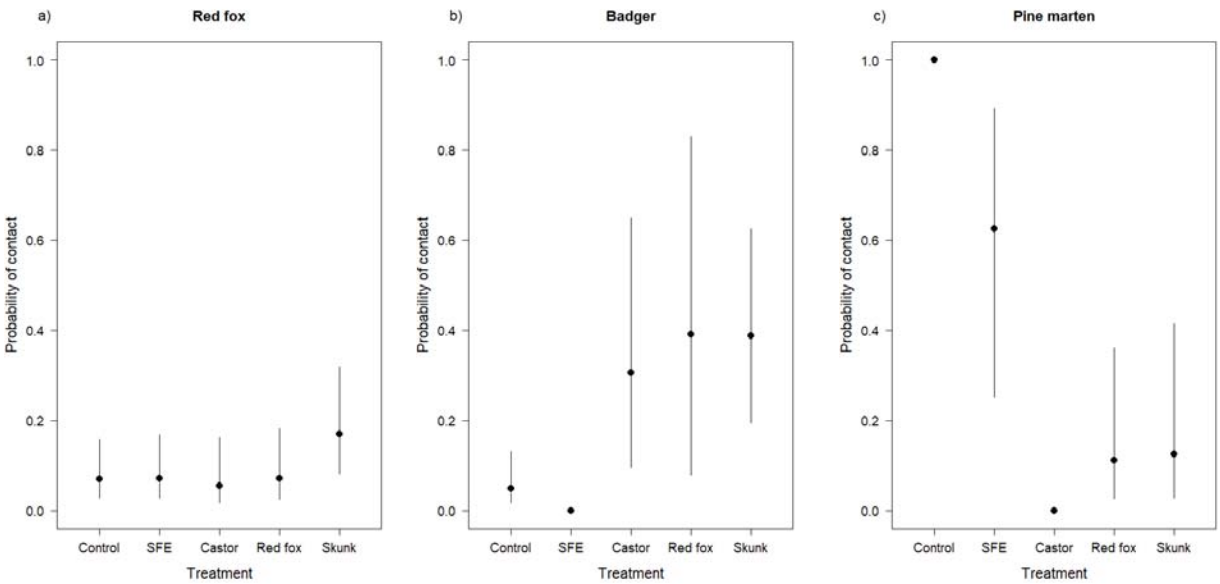

Figure 3.3. The results from the GLMM for a) red fox, b) badger and c) pine marten, showing the effect of treatment on the probability of contact between an individual of a given species and the lure. The points represent the mean and the lines represent the 95% confidence intervals around the mean.

3.4 Mouthing

The red fox was the only species to be photo-captured mouthing the lure stick during the study. Three incidents of mouthing at skunk-treated stations and one at a control station were recorded.

3.5 Visual inspection

Fox-based lures (estimate = 1.94, SE = 0.79, z-value = 2.45, p-value = 0.01) and skunk-based lures (estimate = 1.44, SE = 0.72, z-value = 1.99, p-value = 0.05) (table 3.5, figure 3.4) had a positive effect on the probability of visual inspection by red foxes compared to controls.

Table 3.5. The output from the final GLMM (Visual.inspection ~ Treatment + 1|Camera.ID) of the effect of scent station treatment on the probability of visual inspection of lure. The numbers are the estimates, standard errors (SE), t-values and p-values for red fox, badger and pine marten. Numbers are rounded up to two decimals. Significant t-values (±2) and p-values (<0.05) are bold.

Treatment per species	Estimate	SE	t-value	p-value
Red fox				
Intercept (control)	-1.72	0.62	**-2.78**	**0.01**
SFE	0.74	0.79	0.94	0.35
Castor-based lure	-0.07	1.01	-0.07	0.94
Fox-based lure	1.94	0.79	**2.45**	**0.01**
Skunk-based lure	1.44	0.72	1.99	**0.05**
Badger				
Intercept (control)	-1.25e+00	5.67e-01	**-2.21**	**0.03**
SFE	-3.22e+01	8.03e+06	0.00	1.00
Castor-based lure	1.25e+00	8.49e-01	1.48	0.14
Fox-based lure	8.47e-01	1.08e+00	0.79	0.43
Skunk-based lure	1.07e+00	7.11e-01	1.51	0.13
Pine marten				
Intercept (control)	4.06e-01	9.13e-01	0.44	0.66
SFE	6.93e-01	1.23e+00	0.57	0.57
Castor-based lure	-3.46e+01	1.91e+07	0.00	1.00
Fox-based lure	-1.82e-01	1.13e+00	-0.16	0.87
Skunk-based lure	-4.06e-01	1.16e+00	-0.35	0.73

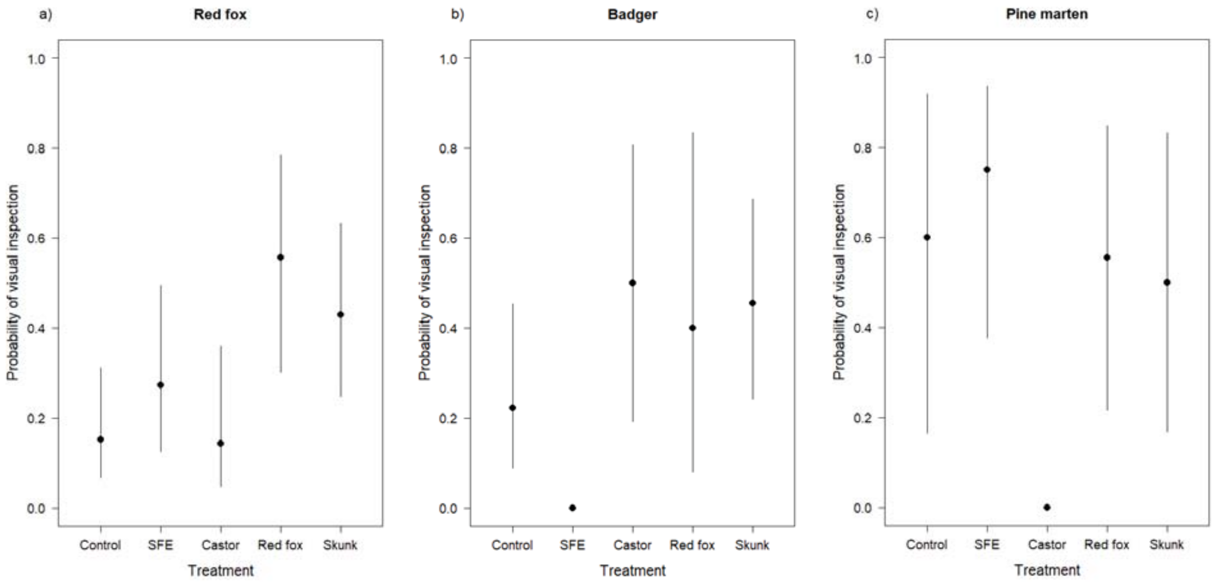

Figure 3.4. The results from the GLMM for a) red fox, b) badger and c) pine marten, showing the effect of treatment on the probability that an individual of a given species would look at the lure stick. The points represent the mean and the lines represent the 95% confidence intervals around the mean.

3.6 Scent marking

Due to small sample size, no statistical analyses were performed to estimate the effect of the lures on marking behavior. The data from the study revealed that pine martens marked most frequently, followed by badgers, and that red foxes seldom scent marked at the scent stations (table 3.6).

Table 3.6. The total number of visits, and the number of visits where scent marking occurred at least once during the visit, per species and treatment for red fox, badger and pine marten.

Species/	Red fox		Badger		Pine marten	
Treatment	Visits	Marking	Visits	Marking	Visits	Marking
Control	24	0	18	0	0	5
SFE	22	1	5	0	7	1
Castor	14	0	9	1	1	1
Red fox	18	0	4	1	8	1
Skunk	30	1	17	5	7	1

4. Discussion

This study revealed pronounced species-specific behavioral responses to scent lures at camera traps. Not only did responses vary depending on lure type and species, but patterns also varied between the different metrics I used to quantify behavior. Red foxes displayed behavior that indicated attraction towards gland-based lures from conspecifics and smaller carnivores, partially supporting **P1**. Badgers displayed behavior that indicated attraction towards gland-based lures from smaller carnivores, also partially supporting **P1**. Compared to the control, food-based lures showed no significant effect on pine martens, rejecting **P1**. However, pine martens displayed behavior that indicated avoidance of gland-based lures, supporting **P2**.

4.1 Behavioral responses to scent lures by red foxes

Red foxes spent more time at scent stations treated with skunk-based lures compared to the control. This attraction behavior is consistent with the findings of Bischof et al. (2014b), where detection probability of red foxes was greater at sites with skunk-based lures compared to control sites. Red foxes did not get closer to or had more contact with the skunk-based lures than what would be expected by chance. As olfactory signals require close investigation to obtain information (Alberts, 1992), this may indicate that skunk-based lures elicit large-scale attraction but micro-scale avoidance in red foxes. Red foxes were also more likely to visually investigate skunk-based lures than the control. This behavior may be interpreted as a signal of attraction or interest. These results indicate that one specific lure may elicit a variety of behavioral responses in the same species.

Red foxes also spent more time at red fox-based lures than what would be expected by chance. This was expected, as predators are known to be attracted to conspecific scent to obtain information (Clapperton et al., 1999). A study in Spain found that red foxes spent time investigating urine from conspecifics, however, they spent more time investigating urine from Eurasian lynx, which do not occur in Spain, than urine from conspecifics (Monterroso et al., 2011). Lynx are larger than red foxes and kill red foxes where the two species coexist (Helldin et al., 2006). The findings from Monterroso et al. (2011) indicate that red foxes spend longer time investigating scents from potential competitors to receive information about potential threats and avoid potential encounters (Banks et al., 2016). As gland secretion and urine may have different functions in scent marking (Johnson, 1973), these two studies are not directly comparable. Comparison of wild and captive animals also requires caution (Benson-Amram et al., 2013). However, the results indicate that scent from larger predators may be more attractive to red foxes than scent from conspecifics and could thus be more suitable as red fox attractants. On the other hand, red foxes in the present study were more likely to visually inspect red fox-based lures than controls, showing that the effect of the lure is strong enough to elicit attraction behavior in red foxes.

SFE had no significant effect on the behavioral responses of red foxes compared to the controls. This is not consistent with the findings of Saunders and Harris (2000), who found that captive red foxes spent more time with SFE than with trimethylamine, a component in anal glands of red foxes. These differences may be due to different methods, as animals may respond differently to lures in captivity than in the wild (Schlexer, 2008). The differences may also be explained by the differences in the lures used in the studies, as a single component of the anal glands may evoke different behavioral responses than grinded scent glands, as used in the present study. The study of Saunders and Harris (2000) found that red foxes spent more time with SFE in the period of winter to spring compared to the period of summer to autumn. As SFE smells like scavenged meat, red foxes' relatively low interest in the SFE-lure during the study period may correlated with red foxes' diet, where scavenged meat makes up a larger proportion of the diet during winter compared to the other seasons (Needham et al., 2014).

4.2 Behavioral responses to scent lures by badgers

The scent lures elicited different behavioral responses in badgers than in red foxes. While red foxes responded equally to castor-based lures and controls, badgers held a shorter distance to castor-based lures compared to the control. The American beaver is not found in Norway (Artsdatabanken, 2018b), but its European relative, the Eurasian beaver (*Castor fiber*) is common in large parts of Norway, including the study area (Artsdatabanken, 2018a). As interactions between Eurasian beavers and badgers are not reported in the literature, it can be assumed that encounters between the two species are rare. Thus, regardless of the similarity or difference between the scent of the American beaver and the Eurasian beaver, the castor-based lure may represent a novelty for badgers. The castor-based lure was the only gland-based lure used in this study that was based on a rodent; the two others were based on carnivores. As it is known that scent from prey attracts predators (Hughes et al., 2010), the castor-based lures may also represent the scent of a potential prey.

Badgers also displayed behavior that indicated attraction towards the skunk-based lures. Badgers both got closer to and had a higher probability of contact with the skunk-based lures compared to the control. However, they did not spend more time at the lures than what would have been expected by chance. Other studies on badgers have reported little effect of scent lures based on sympatric predators on badger attraction (Monterroso et al., 2011; Suárez-Tangil & Rodríguez, 2017). This indicates that lures based on novel scents may be the most effective lures to attract badgers.

As badgers are the same size or larger than red foxes, I predicted that badgers would show attraction towards red fox-based lures (**P1**). The results reject this prediction, as this lure elicited no response in badgers compared to controls. Badgers and red foxes partially overlap in diet and habitat use (Macdonald et al., 2004), and thus, interactions between the two species are likely. A study from England found that badgers were dominant and could be aggressive in encounters with red foxes, while red foxes increased their vigilance (Macdonald et al., 2004). The dominance over red foxes suggests that red foxes represent little threat to badgers, which may be the reason that badgers in the present study showed no response to the red fox-based lures.

4.3 Behavioral responses to scent lures by pine martens

Pine martens are smaller predators than red foxes (Bevanger, 2012), making pine martens vulnerable to predation. Studies from Sweden have found that red foxes kill pine martens and may be important in the regulation of pine marten abundance (Lindström et al., 1995; Storch et al., 1990). It is thus plausible that pine martens would inspect red fox cues with caution. This was found to be the case in the present study, where pine martens held a greater distance to the red fox-based lure compared to the control. This finding is in accordance with Garvey et al. (2016), who found that wild captured stouts (*Mustelida erminea*) were more cautious in their approach to the scent of a larger sympatric predator, the ferret (*Mustela furo*), compared to the scent of a novel predator and the control (water). However, in the study of Garvey et al. (2016), it was also found that stouts spent more time investigating the scent of ferrets than the other scent treatments, indicating attraction towards the scent. This is not consistent with the results from the present study, were no difference in the time spent at the scent stations were detected among the scent lures for pine martens.

Pine martens also stayed further away from the skunk-based lures compared to the control. Striped skunks are larger than pine martens (Bevanger, 2012; Ford & Fahrig, 2007; Gehring & Swihart, 2003), but as the species' geographic range do not overlap, pine martens have no experience with the scent of skunks. The results from Garvey et al. (2016) found no evidence for cautious approach towards a novel predator scent (African wild dog (*Lycaon pictus*) by stouts. However, behavioral responses similar to those found in the present study are found in other mammals. A study on Australian mammals investigated spotted-tailed quolls' (*Dasyurus maculatus*) behavioral responses to the scats of a larger predator, the Tasmanian devil (*Sarcophilus harrisii*) (Andersen et al., 2016). The study found that quolls responded with a higher degree of vigilance compared to the control (no scent) but did not spend more time at the devil scat than at the control.

The behavioral responses of pine martens to red fox-based and skunk-based lures were similar. One explanation is that pine martens are unable to discriminate between the scent of skunks and the scent of red foxes. Urine from red foxes and gland secretion from skunks both contain sulfide components (Andersen & Bernstein, 1975; Whitten et al., 1980). Such explanations have been suggested in studies on other carnivores and evaluated as unlikely (Harrington et al., 2009). An alternative explanation is that pine martens respond similar to the scent of the two larger predators for different reasons, where the reason for avoidance of red foxes is the recognition of a known predator whilst the reason for avoidance of skunks is the pungency of a novel scent. Further investigation of these responses is needed.

4.4 Management advice

The results of this study suggest that the choice of lure should depend on the species of interest and the specific behavioral response desired to elicit. In management of, or research on, red foxes where the animals' maintenance is desirable, lures based on skunk or red fox scent are suitable. Skunk-based lures are recommended lures for badgers in management tasks where contact is required, such as self-triggered traps and DNA sampling devices. In tasks where short distance between the animal and the lure is important, both castor-based and skunk-based lures are suitable for badgers. In the management of pine martens, none of the lures are recommended as attractants, but red fox-based and skunk-based lures can be recommended as repellents.

4.5 Limitations

It is possible that the sample size was too small to yield reliable results, especially for badgers and pine martens. Compared to other ecological studies using camera traps, the number of operational camera trap days was low (Bischof et al., 2014a; Díaz-Ruiz et al., 2016; Monterrubio-Rico et al., 2018). The number of incidents of two of the measured behavioral responses – mouthing and scent marking – was too low to perform statistical analyses. A longer period of fieldwork, or a higher number of camera traps, could have increased the sample size and increased the chance of discovering the true effects of the lures.

The amount of scent lure used may have affected the results. The amount used in this study was ~ 0.5 mL, while in other studies using scent lures the amount range from 0.5 mL (Saunders & Harris, 2000) and 2 mL (Suárez-Tangil & Rodríguez, 2017) to 3-5 mL (Bischof et al., 2014b; Díaz-Ruiz et al., 2016; Monterroso et al., 2011) and 5-10 mL (Stratman & Apker, 2014). It is possible that a larger amount of scent lure could have altered the number of visits and the behavioral responses of the target species.

There are several factors that could have been included in the statistical models to control for their effect. The time since the start of the fieldwork could have been included to assess how the effect varied over time. Camera model and type of flash could have been included to assess whether this affected the behavioral responses. The distance between the lure sticks and the wildlife trails were not recorded. It is possible that the distance may have had an impact and led to incorrect results. In cases where the lure stick was placed close to wildlife trails, animals passing without investigating the scent lures would be recorded as close to the scent lures, leading to erroneous assumptions of attraction. By including the distance between the lure stick and the wildlife trail, this could have been controlled for in the statistical analysis.

5. Conclusion

This study has shown that red foxes, badgers and pine martens vary in their behavioral responses to scent lures at camera traps. Red foxes displayed behavior that indicated attraction towards gland-based scent lures from conspecifics and from skunks. For badgers, gland-based scent lures from skunk and castor elicited behavior that indicated attraction. Pine martens showed no attraction behavior towards the lures but displayed behavior that indicated avoidance towards gland-based scent lures from red foxes and skunks. Surprisingly, none of the target species responded to the food-based lure. The results imply that scent lures based on glands from carnivores are the most effective lures for attracting and detecting red foxes, while novel scents seem to be the most effective lures for attracting and detecting badgers. None of the scent lures tested in this study can be recommended as pine marten attractants, but lures based on scents from larger carnivores seem to be effective as repellents. The findings in this study imply that the effect of a single scent lure varies both across species and across the behavioral responses of a given species. The choice of lure to attract a given species should thus depend also on the purpose of its use.

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Appendix

Table A.1. Model selection by the corrected Akaike Information Criterion (AICc). The models are ranged from most to least complex. The selected models are bold. The numbers are the AICc, the difference between the models (ΔAICc), the Akaike Weight (Wi) and the number of estimated parameters in the model (K). *Lureage* represents days since lure application.

Model ID	Model	AICc	ΔAICc	Wi	K
Time spent at scent stations					
T1	Surv(duration, event) ~ Treatment + Lureage + (1|Camera.ID)	2360.39	1.17	0.34	6
T2	**Surv(duration, event) ~ Treatment + (1|Camera.ID)**	**2359.22**	**0.00**	**0.60**	**5**
T3	Surv(duration, event) ~ 1 + (1|Camera.ID)	2363.78	4.56	0.06	1
Distance					
D1	Distance ~ Treatment + Lureage + (1|Camera.ID)	122.70	0.58	0.43	8
D2	**Distance ~ Treatment + (1|Camera.ID)**	**122.13**	**0.00**	**0.57**	**7**
D3	Distance ~ 1 + (1|Camera.ID)	145.16	23.03	0.00	3
Contact					
C1	Contact ~ Treatment + Lureage + (1|Camera.ID)	95.17	8.58	0.01	7
C2	**Contact ~ Treatment + (1|Camera.ID)**	**93.07**	**6.49**	**0.04**	**6**
C3	Contact ~ 1 + (1|Camera.ID)	86.59	0.00	0.95	2
Visual inspection					
V1	Visual.inspection ~ Treatment + Lureage + (1|Camera.ID)	42.44	4.90	0.07	7
V2	**Visual.inspection ~ Treatment + (1|Camera.ID)**	**41.61**	**4.06**	**0.11**	**6**
V3	Visual.inspection ~ 1 + (1|Camera.ID)	37.54	0.00	0.82	2

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