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Behavioral responses to camera traps: A study on two large carnivores in Norway

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Preface

This thesis is written at The Norwegian University of Life Sciences (NMBU). It marks the end of my two-year master's degree in Natural resource management at the Faculty of Environmental Sciences and Natural Resource Management.

I would like to thank Professor Richard Bischof, for being the best supervisor I could have asked for. Thanks for all your support, time and effort to help me with everything from start to finish. I really appreciate you sharing your knowledge, you have taught me a lot. And thank you Richard for being so including, you made this whole process a great experience!

A massive thank you to John Odden, senior research scientist at the Norwegian Institute for Nature Research (NINA) and project manager of the SCANDCAM project for giving me the opportunity to use NINAs camera trap photos in my study, for answering all my camera related questions and for providing valuable comments on my thesis. To PhD student at NINA Neri Horntvedt Thorsen for answering my questions and for great discussions at the office, thank you. And to Solveig Haug, project associate in SCANDCAM at NINA, thank you for always taking your time to send me all the stuff I asked for. Your quick replies were much appreciated.

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To my friends at NMBU, you made these two years better than I could ever hope for. And all my friends and family at home: Thanks for all your support and for keeping me sane.

Ås, May 2019

Benedicte Lissner Beddari

Abstract

In ecology, camera trapping is commonly used as a non-invasive technique to collect ecological observation data and to monitor populations. The technique is used to address a variety of research questions worldwide. Despite being widely used, few studies have evaluated the potential effects of camera traps on animals, and to my knowledge no studies have quantified to what extent and under which conditions such effects occur.

In this thesis, I have assessed the behavior of two large carnivores in Norway, Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*), using still images captured by camera traps. The aim of the study was to investigate whether the presence of camera traps can cause behavioral changes in wildlife. I recorded behaviors that indicated apparent detection of cameras by visual and/or acoustic contact. Furthermore, other distinct behaviors towards camera was assessed, in addition to the orientation of the animal in a given visit, to detect distinct changes in direction caused by the trap. Finally, I compared behavioral scores between species and camera-specific factors like flash type.

Lynx and wolves both apparently detected cameras (eyes and/or ears pointed directly at the camera) in approximately 11% of the visits, and altered their behavior in response to them. Two different categories of responses were discovered: Responses directly related to an apparent detection (approach, flight, observe and startle) and responses related to the presence camera traps (physical contact, olfactory sensing and squinting). I detected species-specific and camera-specific differences in behavioral impacts. Lynx were more likely to approach the camera, compare to wolves who expressed flight and startle response more pronounced. Flash and different flash types influenced the species differently in how they responded to the presence of camera traps. Both species were found to have pronounced change in orientation when expressing apparent detection responses to camera. My study revealed clear evidence of camera traps being low-invasive, but not non-invasive wildlife monitoring tools. This suggests that camera trap studies should quantify their impact on study species and its effect on inferences.

Sammendrag

Viltkamera er en mye brukt metode benyttet i forskning og overvåking verden over. Det er en effektiv og populær innsamlingsmetode som blir brukt i mange ulike studier. Metoden blir ofte omtalt som en forskningsmetode som ikke påvirker viltet (ikke-invasiv), da forskere ikke trenger å fysisk håndtere studieartene, eller være tilstede under innsamling av data. Det finnes studier som har rapportert om tilfeller av dyr som reagerer på tilstedeværelsen av kamera, men få studier som har tallfestet påvirkningen viltkameraet kan ha på dyr.

I denne studien er det brukt viltkamerabilder av gaupe (*Lynx lynx*) og ulv (*Canis lupus*) i Norge. Disse bildene er brukt til å se etter tegn til at dyr er bevist på viltkameraet og hvordan de responderer på tilstedeværelsen av et fremmed objekt. Det ble registrert om individer oppdaget kamera ved visuell (øyekontakt) og/eller auditiv (begge ørene mot kamera) kontakt. Ved kontakt ble responsen til denne oppdagelsen registrert. I tillegg ble orienteringen av kroppen notert, for å identifisere om bevegelsesmønstret forandret seg ved respons til kamera.

Jeg fant bevis på at både gaupe og ulv oppdager kameraet. To kategorier av respons tilknyttet viltkamera ble registrert: Respons direkte tilknyttet visuell og/eller auditiv kontakt (tilnærming, observering, flukt og redsel) og respons som ikke var direkte tilknyttet en registret oppdagelse av kamera (fysisk kontakt, snusing mot kamera og mysing med øynene). Studien fant arts-spesifikke og kamera-spesifikke forskjeller i ulik grad av oppdagelse og respons og begge arter viste et skifte i bevegelsesretning, som en konsekvens av oppdagelsen av kamera. Disse funnene viser at vilt påvirkes av viltkamera, og antagelsen om at viltkamera er en metode som ikke påvirker vilt er dermed misvisende. Ved bruk av viltkamerabilder i studier, må derfor kameras påvirkning av vilt tas i betraktning.

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1. Introduction

In ecology, camera trapping is commonly used as a non-invasive technique to collect ecological observation data and monitor wildlife (e.g. Caravaggi et al., 2017; Hofmeester et al., 2019; Rowcliffe et al., 2008; Silveira et al., 2003; Weingarth et al., 2013). Camera traps yield visual information in the form of short videos or still images, captured from a fixed position. This method provides the opportunity to generate data on multiple species and research questions at once, over an extended time period (Bridges & Noss, 2011; Newey et al., 2015). It can be done with less effort and greater cost efficiency than other methods, such as the use of radio transmitters or satellite telemetry (Caravaggi et al., 2017). The use of camera traps also does not require direct physical interference with wild animals (Newey et al., 2015). Across the world, camera trapping has been used for decades, with methodology and equipment improving constantly (Kucera & Barrett, 2011). Camera traps have been used to address a variety of research questions, including studies on activity patterns (Ogurtsov et al., 2018), biodiversity (Cheyne & Macdonald, 2011) density and abundance (Di Bitetti et al., 2006), human interference (Ngoprasert et al., 2007), social structure (Morehouse et al., 2016) and species interaction (Bischof et al., 2014a; Milleret, 2011).

Despite its extensive use, few studies have evaluated the behavioral effects of camera traps on animals. Studies have identified animals reacting to camera traps, altering their behavior as a response to the encounter (Glen et al., 2013; Schipper, 2007; Wegge et al., 2004). Meek et al. (2016) conducted a behavior assessment study on four small and medium-sized carnivore species in Australia and found all four species to express detection of and behavior modification caused by camera traps. Studies (not necessarily on behavior) have also reported that animals avoid or escape camera traps (Gibeau & McTavish, 2009; Glen et al., 2013; Schipper, 2007; Séquin et al., 2003; Wegge et al., 2004). Furthermore, animals can be attracted to cameras, which is referred to as trap-happiness (Meek et al., 2016; Weingarth et al., 2013). Camera trap data is often used under the assumption of equal detectability (Larrucea et al., 2007), which refers to the probability of detecting an individual or species at a camera trap when it is present in the area. A change in behavior can generate bias when estimating e.g. abundance and density (Karanth & Nichols, 1998; Larrucea et al., 2007) and this might apply especially if disturbance from camera traps leads to trap shyness or avoidance (Karanth & Nichols, 1998; Schipper, 2007; Séquin et al., 2003). Not only can behavior modification affect the inferences drawn from studies using camera traps, but cameras have the potential of being a disturbance to wildlife and their environment. It is therefore important to understand how camera trapping can impact animal behavior.

In recent years, camera trapping has been implemented in research and monitoring of large carnivores in Norway (Odden et al., 2018). The SCANDCAM project managed by The Norwegian Institute for Nature Research (NINA) and the Swedish University of Agricultural Sciences, collect data using camera traps (http://viltkamera.nina.no/) in both Norway and Sweden. Initially the project was started to monitor Eurasian lynx (*Lynx lynx*) (hereafter referred to as lynx), SCANDCAM now also collects photographic data on other large carnivores, including grey wolves (*Canis lupus*). These images do not only provide evidence of the presence of individuals in space and time, but can give visual information on the behavior in front of camera traps (Blake et al., 2010; Brøste, 2018; Tan et al., 2013). Camera traps often target rare and elusive species (such as lynx and wolves), which make it possible to test for and quantify effects of camera traps on large carnivores.

The aim of this study is to quantify the impact of camera traps on the behavior of two large carnivores (lynx and wolf) in Norway. Still images of lynx and wolves from camera traps were analyzed to assess possible detection of cameras by lynx and wolves and to measure behavioral responses. Indication of visual (eye-contact) and/or acoustic (ear position) contact with the camera was recorded as apparent detection. Following apparent detection, behavioral response such as approach- or flight response to the camera was assessed. Furthermore, the orientation of body and head relative to the trap was recorded to analyze possible changes in orientation, caused by the camera. In this thesis, I pose the following research questions and associated predictions:

- Q1: To what extent and under which conditions are camera traps being detected by large carnivores?
    - P1: I predict that animals will direct their attention to the camera trap by looking at it and/or pointing their ears towards it, and that the probability of and time to apparent detection (ears and/or eyes aimed directly at the camera) differs between lynx and wolves, due to their pronounced differences in behavior (felid vs. canid).
    - P2: I predict that apparent detection of the camera is more likely when the flash is triggered, with white flash being more conspicuous than infra-red and invisible infra-red flashes.

- Q2: Do large carnivores alter their behavior due to camera traps and how do responses differ between species?
    - P1: I predict that apparent detection of a camera will be followed by a response and expect aversive (escape/avoidance) responses to be more pronounced for wolves, due to the species' reputation of cautious behavior.
    - P2: I predict that animals noticing the camera trap will have earlier departure times and a change in orientation.

This study aims to shows how camera trap data can provide behavioral information to quantify the effect they have on study animals.

2. Materials and method

2.1 Study species

In Norway, large carnivores are of great interest among researchers, managers, and the general public. This study focusses on two of the large carnivores in Norway, lynx and wolves. The wolf is the most controversial carnivore in Scandinavia and due to its cautious and wary behavior, it has a reputation of being difficult to camera trap (Boitani & Mech, 2006; Gibeau & McTavish, 2009). Lynx on the other hand, tend to be easier to camera trap due to more inquisitive behavior (Kitchener A, 1998) and is the primary target of SCANDCAM (Tovmo et al., 2018). As both species are widely distributed (wolves throughout the northern hemisphere; Eurasian lynx throughout Eurasia), the results of this study will be of interest also to researchers outside of Norway.

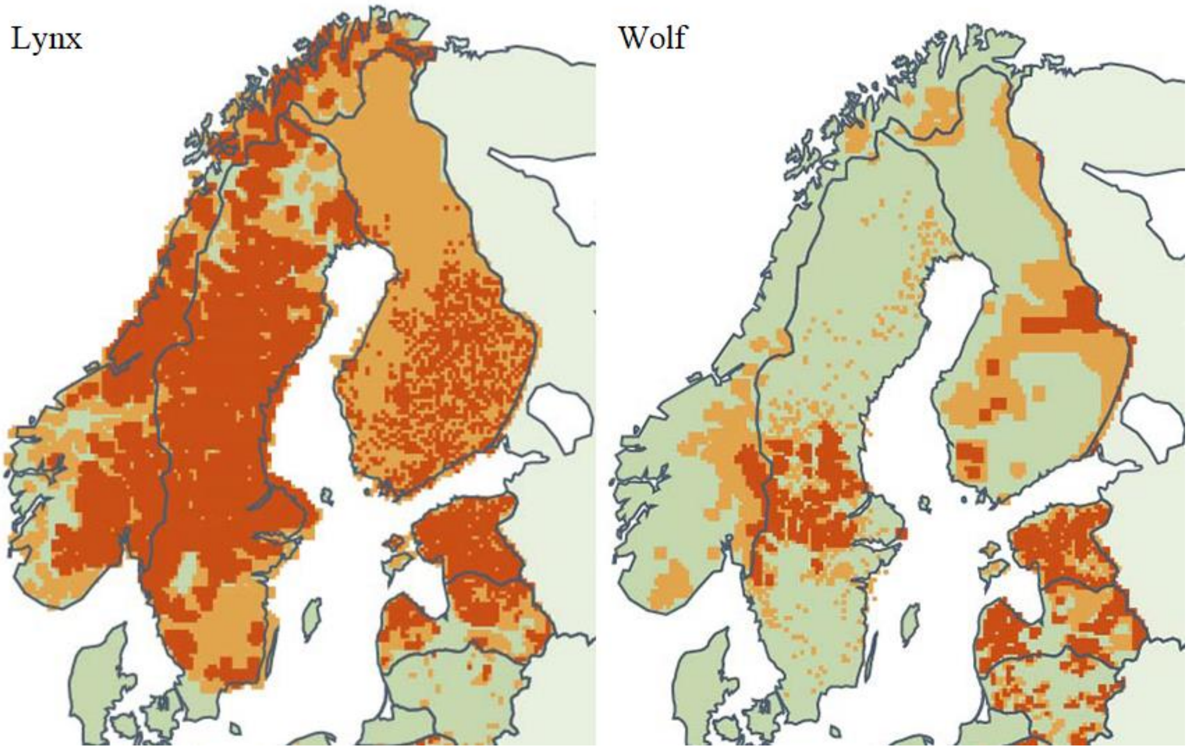

Figure 1: Distribution map for lynx (left) and wolf (right) in Scandinavia and the Baltic region. Red pixels show permanent residents, orange pixels occasional appearance. (http://ec.europa.eu/environment/nature/conservation/species/carnivores/media.htm. Accessed: 22.04.19)

The wolf population in Norway and Sweden had its first documented reproduction in 1978, after being classified as extinct for 14 years (Wabakken et al., 2001). Since then, the Scandinavian population has grown (Trouwborst et al., 2017) (Fig. 1), and today the population is estimated to 401 individuals (Bischof et al., 2019). Of these, 91 of these are considered to use home ranges contained completely within the border of Norway. Wolves claim territories (Jedrzejewski et al., 2001; Mech, 1994) and live in packs normally consisting of a breeding pair, and their offspring (Zimmermann, 2014). Wolf home range size can vary between 260 to 1,600 km^2, depending on prey availability and habitat preferences (Mattisson et al., 2013).

By the early 1900s, lynx hunting almost drove the European population to extinction. However, after being protected by a hunting restriction, there are now approximately 9000 individuals in Europe (Chapron et al., 2014) and an estimated 340 individuals in Norway (Tovmo et al., 2018). Lynx is widely distributed throughout Norway, with the exception of the southwest (Tovmo et al., 2018) (Fig.1). Like the wolf, lynx claim territories, where home range size is determined by prey density and habitat preferences (Herfindal et al., 2005). The territory sizes differ between sexes: Aronsson et al. (2016) found home ranges sizes stretching from 300 – 2300 km^2 for males, and 110–1850 km^2 for females. Lynx are solitary, with the exception of family groups consisting of females and their dependent young (Bego & Zoto, 2004).

Both lynx and wolves are generalist apex predators (Zimmermann, 2014). Moose (*Alces alces*) and roe deer calves (*Capreolus capreolus*) are the most preferred prey for wolves (Gervasi et al., 2012; Sand et al., 2005; Sand et al., 2008). If available, beaver (*Castor fibre*) are preyed upon as well (Sand et al., 2008). Lynx prefer roe deer even at low densities (Odden et al., 2006), and they mainly hunt adults (Gervasi et al., 2012). Second to roe deer, hare (*Lepus timidus*) is an important part of the lynx diet (Odden et al., 2006). However, as generalists, both species also hunt semi-domestic and wild reindeer (*Rangifer tarandus*) (Tveraa et al., 2013), badger (*Meles meles)* (Sand et al., 2008; Sunde et al., 2000) and various bird species like capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) (Sand et al., 2008). In the summertime, free-ranging sheep (*Ovis arie*) could be a part of the diet as well (May et al., 2008; Odden et al., 2006; Sunde et al., 2000).

In Norway, lynx and wolves have similar habitat preferences. Both prefer forest covered areas at low altitude. Lynx prefer slightly lower elevation, more densely forested and rougher terrain than wolf. These small differences in habitat preferences likely arise from two different hunting strategies (May et al., 2008). Wolves often hunt in packs, chasing prey to exhaustion (Wikenros et al., 2009), while lynx stalk prey (Kitchener A, 1998), hence the benefit of more dense forest to stay hidden (May et al., 2008). Worldwide, wolves tend to be a habitat generalist, able to adapt to high elevations as much as low, with lynx more of a forest specialist (Geffen et al., 2004; Linnell et al., 2001). The habitat overlap may originate from distribution restriction in Norway, caused by active removal as a management goal. This could exclude individuals from areas with suitable habitat.

2.2 Study area

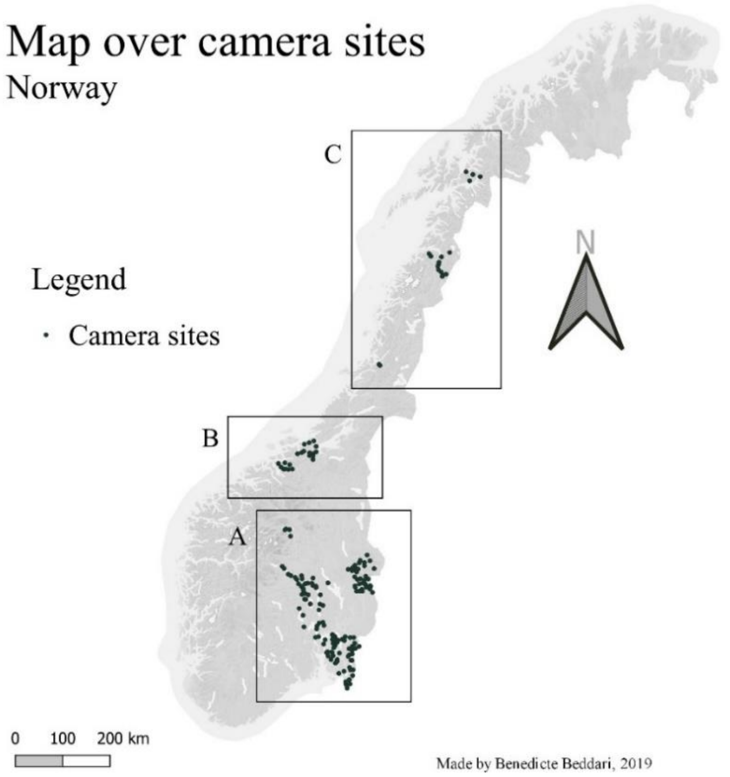

Figure 2: Map of Norway, with the 187 camera sites (dark dots) used in this study. A) southeast region, B) Trønderlag region and C) Nordland and Troms region.

The study area extends over a large part of Norway (59°- 69° N, 8- 16°E, Fig. 2). The southeast region (58.8-61.8°N, 8.8-12°E, Fig. 2A) consists of boreal coniferous forest, dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with silver birch (*Betula pendula*), downy birch (*Betula pubescens*), aspen (*Populous tremula*), alder (*Alnus incana*) and black alder (*Alnus glutinosa*). Forestry and agricultural activity create a mosaic landscape with a wide network of gravel roads. With increasing latitude, the topography changes from relatively flat in the south, to more rugged and elevated terrain in the north. Mean annual temperatures are within 2-6° C in the lower areas, and 0-4° C at higher elevation. Precipitation amounts to 1500 mm per year for the entire area (Norges vassdrags- og energidirektorat, 2019). The study sites in Trønderlag (62.9-63.5°N, 8.4-9.9°E, Fig. 2B) are close to the coast and are characterized by valleys and mountains up to 800 m a.s.l. Forest areas consists of both coniferous-, deciduous- and mixed forest, depending on elevation. Mean temperature ranges between 4-6°C, with annual precipitation above 2000 mm (Norges vassdrags- og energidirektorat, 2019). The study sites in Nordland and Troms (67-68.60° N, 14.9 - 16°E, Fig. 2C) lay in terrain that rapidly changes from coastline to mountainous. Mountains reach up to ~ 1000 m a.s.l, with 12-14% of the counties being covered in bare mountain. The vegetation becomes more alpine, primarily dominated by birch (*Betula pendula* and *Betula pubescens*), but also Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Aspen (*Populous tremula*) and alder (*Alnus incana* and *Alnus glutinosa*) are present as well. The annual mean temperature is -1- 4° C. Precipitation ranges from 2000-4000 mm, with higher precipitation near the coast (Norges vassdrags- og energidirektorat, 2019).

2.3 Camera trapping

The camera trap data (photos) used in this study were obtained from NINAs archive and are part of the SCANDCAM project (http://viltkamera.nina.no/). One of SCANDCAMs ambitions is to develop and evaluate the use of camera traps as a wildlife management tool. Data included in my analysis were collected between April 2013 and September 2018 from the different camera sites.

The intention with NINAs camera traps is to capture still pictures or videos of wildlife, with a focus on large carnivores, especially lynx. Placement of camera traps are not random, but rather targeting areas where wildlife passing is likely to occur. Often this will be on gravel roads, animal trails or, for lynx, along cliffs and similar terrain features. Areas, where NINA are installing camera traps are divided into square grid cells of 50km^2, with one camera mounted in each cell. The camera is installed on a tree, approximately 70 cm above ground, 2 m from the predicted pathway and with a line of sight perpendicular to the expected traveling route (Fig. 3) (Odden et al., 2018).

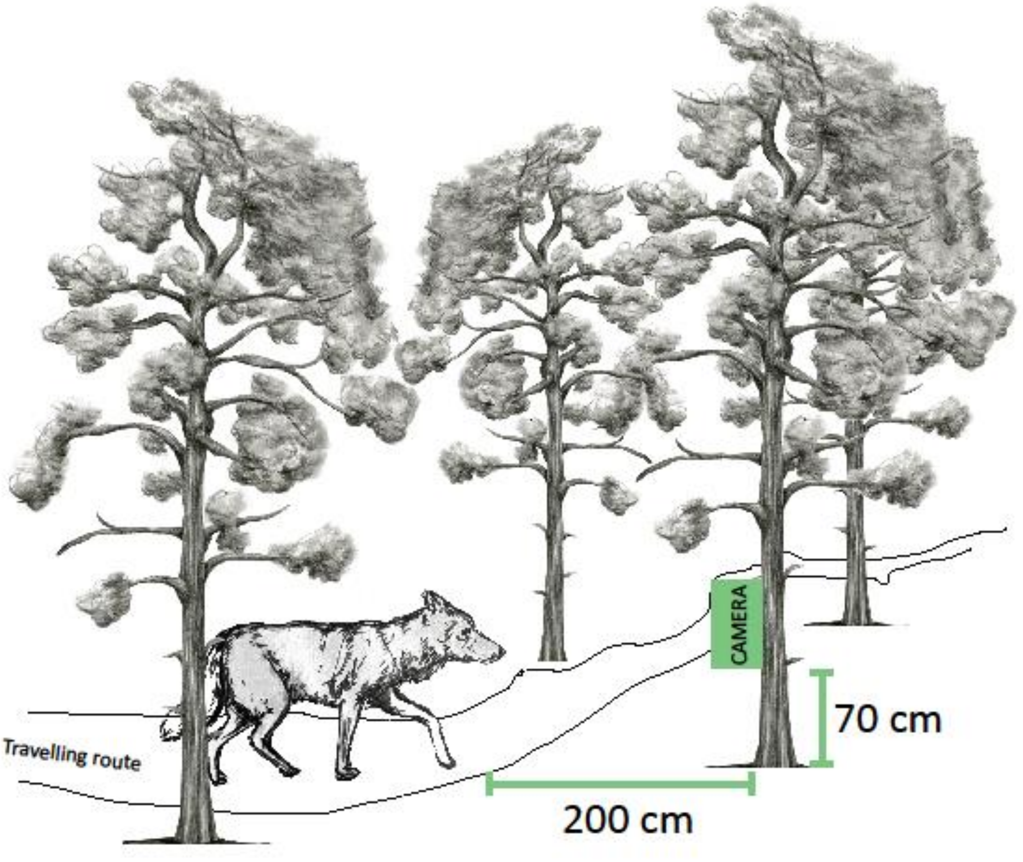

Figure 3: An example of the camera trap set up in the terrain. Cameras are installed on a tree, approximately 2m from the expected traveling path and 70cm above ground. (Illustration: Silje Marie Kristiansen)

In this study, 187 camera locations were used. Five different models of Reconyx^{TM} cameras were deployed at the sites (Table 1). These cameras have passive infrared sensors, which triggers the camera when the infrared field is breached (e.g. when an animal is passing) (Rovero et al., 2013). The camera settings follow a standard SCANDCAM protocol. To obtain the best result, motion sensitivity is set to "high" and trigger interval to "rapid fire". When an animal breaches the infrared field, a series of three pictures are taken with up to two pictures per second. There is no "quiet period" between the intervals, meaning the camera continues taking photos as long as the infrared sensor is triggered. For each camera model, the highest picture quality is chosen. All models have a 42^{o} field of view (www.wildlifemonitoringsolutions.com). There are three types of flash used in my study area. White flash (LED) are present in the Reconyx model PC850. White LED emits white light when triggered. Camera model HC500 and PC800 use red-glow infrared flash. When triggered, the camera will show a small red dot. HC600 and PC900 use invisible infrared flash (hereafter called no-glow), which emits light over 850nm, invisible to the human eye (Meek et al., 2014). The PC850 (LED) will retrieve colored photos at night, whereas models with infrared flash will produce monochrome photos at night (www.nighttraps.com.au). When placing camera traps, NINA deliberately avoid camera models with LED flash, in areas where wolves are expected to be captured. Based on NINAs experiences, wolves tend to react to LED flash and will avoid the camera site (N. Thorsen, pers. comm.).

Table 1: Overview of Reconyx^{TM} camera models used in this study, with the respective flash types and number of cameras used in the study.

Reconyx model	Flash type	No. of cameras
HC500 Hyperfire	Red-glow infrared	27
HC600 Hyperfire	No-glow infrared	24
PC850 Hyperfire Professional White Flash	White (LED)	45
PC900 Hyperfire Professional Covert	No-glow infrared	69
PC800 Hyperfire Professional Semi Covert	Red-glow infrared	22

2.4 Image processing and behavioral assessment

In this study, I included still images from lynx and wolves captured in Norway between 2016-2018 and 2013-2018 respectively. Photos from camera trap sites which were obviously baited, apparently in an urban setting (e.g. next to houses/cabins), images not showing seconds, locations with more than one camera, and images of poor quality (e.g. snow in front of lens, or incomplete images with broken pixels), were excluded.

All behavior assessment/scoring of images was conducted by one observer (myself), to ensure consistent interpretation. There is a chance of responses passing undetected, with responses occurring between sequences of pictures taken, or by being overlooked by the observer. If more than one individual appeared in the same photo, all individuals' behavior was analyzed separately.

Before assessing the behavior in a picture, the camera identification number (camera id) was recorded (given by NINA), date (dd.mm.yyyy), time (Hour:minute:second, Am=00:00-12:00, pm= 12.01:23.59), species (lynx or wolf), and whether the flash was triggered (true or false). The brightness and contrast were adjusted in photos where the background was too dark to interpret the image or to check for additional individuals in darker regions of the image.

To quantify if camera traps cause a change in lynx and wolf behavior, I developed an ethogram, and used it to categorize various aspects of activities and behavior (see descriptions in the following sections). The ethogram was developed by examining the dataset for different types of behaviors. Eye contact with the camera (visual contact) and/or both ears pointing towards the camera (acoustic contact) was used as an indication of apparent detection of the camera trap. As the observer cannot be completely sure if the animal has detected the camera or not, the term "apparent detection" is used. If apparent detection occurred, behavior response to camera trap was recorded. To quantify potential changes in orientation, the position of body and head relative to the camera was recorded by using a compass (Fig. 4). In cases where the animal was olfactory sensing or in physical contact with the camera, this was recorded separately. In these cases, the behavioral response was set to "observe" to ensure a response was not missed. If an animal was squinting in the photo, it was recorded even if it was not related to an apparent detection.

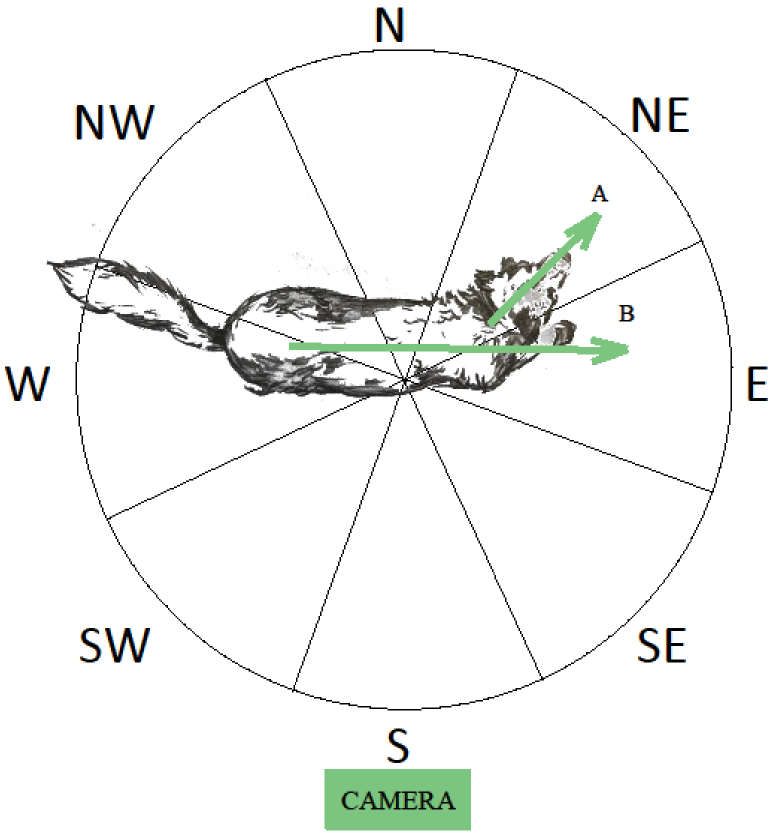

Figure.4: Seen from above, this picture is illustrating the use of compass courses to located body and head positions relative to the camera. The camera lens facing north, regardless of camera orientation in the field. Arrow B illustrates direction of animals' body (east), while arrow A illustrates animals head direction (northeast). (Illustration: Silje Marie Kristiansen).

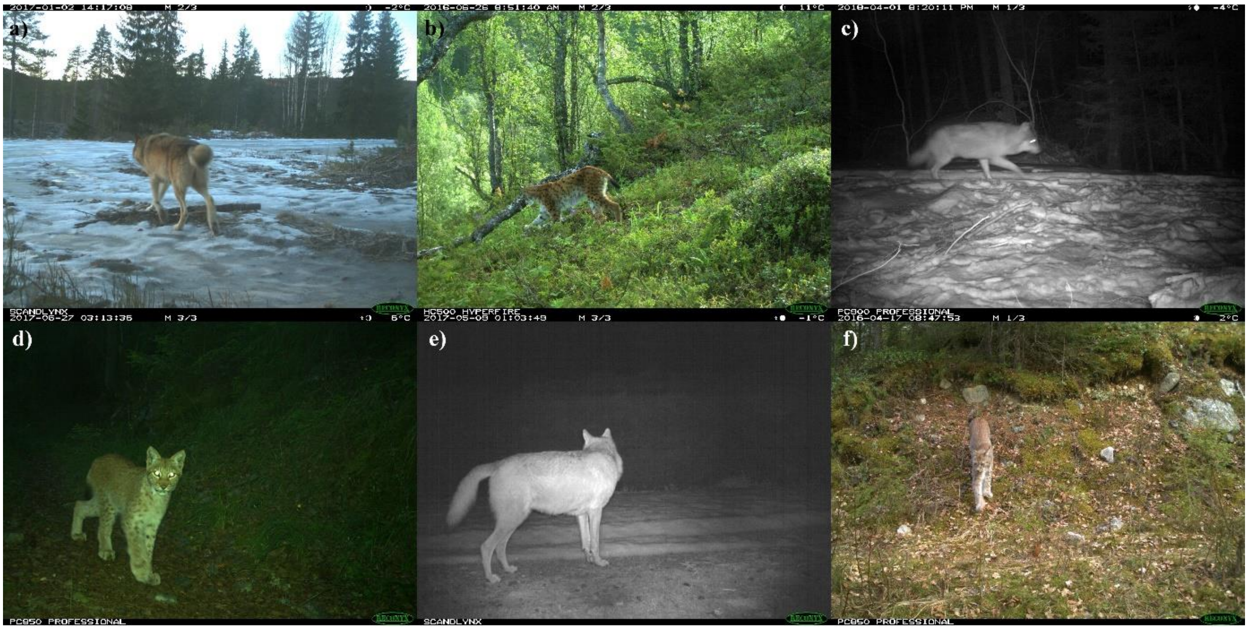

Figure 5: By using the compass in Fig. 4, with the camera lens facing north, courses were registered for body and head. a) body: Northwest (NW), head: Northwest (NW), b) body: West (W), head: West (W), c) body: East (E), head: east (E), d) body: Southeast (SE), head: South (S), e) body: East (E), head: Northwest (NW), f) body: South (S), head: Southwest (SW).

The recorded material was described by categorizing the behavior of the monitored animals as following:

Eye contact with the camera: “True” if the animal was looking directly at the camera trap and “false” otherwise (“NA” if head not visible) (Fig. 6 a).

Ears to the camera: Recorded as “0” if no ears pointing towards the camera,”1” if a single ear was turned towards the camera, and “2” if both ears were turned towards the camera (Fig. 6a).

Behavioral response to the camera: Recorded as a behavioral response to camera trap, after an apparent detection.

- Approach: Apparent movement towards the camera (Fig. 7b).
- Flight: Apparent flight response, running away from the camera (Fig. 6b)
- Observe: Apparent observation of the camera (Fig. 7b).
- Startle: Apparent startle response, lowering of the body and/or head, ears back, tail down or under the body (Fig. 7d).

Body angle relative to camera: Using a compass (Fig. 4B), with the camera lens facing north, the orientation (compass point) of the body relative to the camera was recorded. An imaginary anteroposterior axis through the body, looking in the anterior direction, marked the position.

- North
- Northeast
- Northwest (Fig. 5a)
- East (Fig. 5c, e)
- Southeast (Fig. 5d)
- Southwest
- South (Fig. 5f)
- West (Fig. 5b)

Head angle relative to the camera: Using the same compass as for body angle (above), I recorded the orientation of an imaginary line in the rostral direction through the head relative to the camera (Fig. 4A). Categorized as in “Body angle relative to camera trap”.

Olfactory sensing the camera: Recorded as “true” if an animal was facing the camera trap, tilting the nose slightly a towards the sky. If recorded as “true”, behavioral response to the camera was set to behavioral response “observe” (Fig. 7a).

Physical contact with camera: Apparent physical contact with the camera recorded as “true” if animal was so close to the lens only fur was visible, or any part of the body was clearly touching the camera. If recorded as “true”, behavioral response to the camera was set to observe (Fig. 7c).

Squinting: Recorded as “true” if an animal partly or fully closed its eyes, when flash was active (Fig. 7b).

Figure 6: Wolf expressing apparent detection of the camera trap with eyes and ears (a), followed by flight behavior (b, c).

Figure 7: Different behavioral responses to camera trap. a) Wolf olfactory sensing the camera trap, b) lynx to the left is observing the camera trap and the one to the right is approaching the trap while squinting, c) lynx in physical contact with camera trap and d) wolf to the left is showing a startle response, while wolf to the left is observing the trap.

2.5 Statistical analysis

All statistical analyses were performed in R Studio 1.1.463 (RStudio Team, 2016), R version 3.5.2 (R Core Team, 2018). After the image assessment, it was decided to only include visits with a single individual. All images with multiple animals was removed from the analysis, to limit the possibility of behavior change due to multiple animals in a visit. The visits were estimated with a buffer time set to 5 min (all photos within the buffer time were considered part of the same visit). A behavioral response to an apparent detection from an individual was quantified as a change in behavior before and after apparent detection. Level of significance $\alpha=0.05$.

In this study, the analysis consists of time-to-event and regression analysis. Model selection was performed for the time-to-event analysis and some of the regression analysis by assessing Akaike Information Criterion (AIC) (Akaike, 1974; Burnham & Anderson, 2002) (appendix A1/A2). The remaining regression models were selected by including predictors relevant and plausible for the respective response variable in question. The four predictor variables available to the analysis were: apparent detection, flash, flash type and species. Data used in the analysis were aggregated by visit, from the full dataset.

Time to apparent detecting of camera: To check for species-specific differences in time to apparent detection, a Cox proportional hazard regression model (CPH model) (Cox, 1972) was fitted by using R package *survival* and function *coxph* (Therneau, 2015). Time to event analysis has previously been used to analyze camera trap data (Bischof et al., 2014b). I used time elapsed between the first image in a visit and the apparent detection as the time to event. Visits without apparent detection were censored (event=0) at the time of the final image in the sequence. I considered flash type and species as predictor variables. Camera id was included as a strata (or cluster) variable to account for non-independence. The final model (predictors) was selected using AIC (appendix A1).

Apparent detection with flash/no flash: To detect if active flash effected the probability of apparent detection of camera traps, a generalized linear mixed-effect model (GLMM) was fitted by using the function *glmer*, with R package *lme4* (Bates et al., 2015). Response variable apparent detection was binomial and the family in the model was fitted to *Binomial*. Predictor variables included were flash and species (fixed effects). A mixed effect model was required to include fixed- and random effects, using camera id as random effect to account for non-independence.

Apparent detection with flash type: To estimate the probability of flash type influencing apparent detection, a GLMM was fitted by using the function *glmer*, with R package *lme4* (Bates et al., 2015). A mixed effect model was required to include fixed- and random effects. Response variable apparent detection was binomial and the family in the model was fitted to *Binomial*. Predictor variable included was flash type (fixed effect) and camera id included as random effect, to account for non-independence. The model was only fitted to data were flash was active and as wolves had no apparent detections including activated LED, LED was removed from the wolf data.

Behavioral response “approach”: To identify if flash types had an effect on behavioral response “approach” a GLMM model with the function *glmer* in R package *lme4 (Bates et al., 2015)* was used. A mixed effect model was required to include fixed- and random effects. The responses variable “approach response” was binomial and the model was fitted with family *Binomial*. Predictor variable included was flash type (fixed effect) and camera id included as random effect, to account for non-independence. The model was only fitted to data were flash was active. Only lynx was included as wolf did not have enough scores. A second GLMM model was fitted with the same response variable using function *glmer* in R package *lme4 (Bates et al., 2015)* to investigate if flash/no flash (flash as predictor variable) affected behavioral response “approach”.

Behavioral response “observe”: To identify if flash types had an effect on behavioral response “observe”, a GLMM model with the function *glmer* in R package *lme4 (Bates et al., 2015)* was used. A mixed effect model was required to include fixed- and random effects. The responses variable “observe response” was binomial and the model was fitted with family *Binomial*. Predictor variables included was flash type and species (fixed effect) and camera id included as random effect, to account for non-independence. The model was only fitted to data were flash was active. A second GLMM model was fitted with the same response variable using function *glmer* in R package *lme4* (Bates et al., 2015) to investigate if flash/no flash (flash as predictor variable) affected behavioral response “observe”. This was only done for lynx, as wolves had not enough scores where there was no flash.

Behavioral response “flight/startle”: To identify if flash types had an effect on behavioral response “observe” a GLMM model with the function *glmer* in R package *lme4 (Bates et al., 2015)* was used. The two responses “flight” and “startle” were merged together and used as a single response variable in the model, signifying an aversive reaction (hereafter called flight/startle response). A mixed effect model was required to include fixed- and random effects. The responses variable “flight/startle” was binomial and the model was fitted with family *Binomial*. Predictor variable included was flash type (fixed effect) and camera id included as random effect, to account for non-independence. The model was only fitted to data were flash was active. Only wolf was included as lynx did not have enough scores. A second GLMM model was fitted with the same response variable using function *glmer* in R package *lme4 (Bates et al., 2015)* to investigate if flash/no flash (flash as predictor variable) affected behavioral response “flight/startle”.

Physical contact with camera: To detect if flash type influenced physical contact with camera trap a GLMM model was fitted with function *glmer* in R package *lme4* (Bates et al., 2015). Response variable “physical contact” was binomial, hence family fitted as *Binomial.* A mixed effect model was required to include fixed- and random effects. Predictor variable included was flash type (fixed effect) and camera id included as random effect, to account for non-independence. The model was only fitted to data were flash was active. Lynx was the only species included, as wolves had no scores on physical contact. Flash type red-glow was removed from the lynx data, as no scores were detected. A second GLMM model was fitted with the same response variable using function *glmer* in R package *lme4* (Bates et al., 2015) to investigate if flash/no flash (flash as predictor variable) affected “physical contact”.

Olfactory sensing of camera: To detect if flash type influenced physical contact with camera trap a GLMM model was fitted with function *glmer* in R package *lme4* (Bates et al., 2015). Response variable “olfactory sensing” was binomial, hence family fitted as *Binomial.* A mixed effect model was required to include fixed- and random effects. Predictor variable included was flash type (fixed effect) and camera id included as random effect, to account for non-independence. The model included wolf only, as lynx did not have enough scores. Flash type

LED was removed from the wolf data, due to no scores. A second GLMM model was fitted with the same response variable using function *glmer* in R package *lme4* (Bates et al., 2015) to investigate if flash/no flash (flash as predictor variable) affected "olfactory sensing".

Squinting: There were not enough scores to run analysis on squinting to the camera. The number of visits including squinting is reported.

Time to departure: To explored if the time to departure from the camera trap was influenced by apparent detection, a CPH model was fitted (Cox, 1972) by using R package *survival* and function *coxph* (Therneau, 2015). Time to event analysis has previously been used to analyze camera trap data (Bischof et al. (2014b)). I used time elapsed between the first image in a visit and the last image as the time to event. I considered apparent detection and species as predictor variables. Camera id was included as a clustering variable to account for non-independence between observations at the same camera. The final model (predictors) was selected using AIC (appendix A2).

Drastic change of orientation: To quantify if a behavioral response to apparent detection changed the direction of travel, a GLMM model was fitted with function *glmer* in R package *lme4* (Bates et al., 2015). I tested whether individuals "drastically" changed their orientation following apparent detection. A drastic change of orientation was defined as a change in body orientation over 90^o within a visit (a change in orientation overstepping two compass directions (e.g. a change in body angle from west to northeast within a visit.). A mixed effect model was required to include fixed- and random effects. Predictor variable as fixed effects and camera id included as random effect, to account for non-independence. Response variable "rotation angle >90" was used to perform three GLMMs. 1) Predictor variables "approach response" and flash type, was used with lynx data, as wolves did not have enough scores. 2) Predictor variables "observe response", flash type and species. 3) Predictor variable "flight/startle response" with data on wolves, as lynx did not have enough scores. All three models used data not distinguishing between inactive and active flash and they were selected after assessing ACI output (appendix A2).

3. Results

3.1 General results

I used a total of 3696 registered observations of lynx and 2449 registries observations of wolves. Of these, 1605 observations were removed, to include visits containing only one individual. This corresponded to 944 visits (lynx 524, wolves 420) from single individuals. Lynx was photographed at 136 unique camera traps and wolves at 67, with species overlapp at 21 camera traps. The mean number of photos in a visit was 5.4 for lynx and 4.0 for wolf. Both species expressed apparent detection of camera traps (Fig. 8) which occurred in 10.9% and 11.1% of the visits from lynx and wolf, respectively. No significant difference was detected in the prevalence of apparent detection between the target species (p-value= 0.95). Most visits happened during dark (Fig. 9), hence flash was triggered in 82% of lynx visits and 75% of wolf visits.

Figure 8: The two target species expressing apparent detection (eyes and ears). The wolf (left) is photographed with red-glow flash and responding with behavioral response "observe". The body position is east and head south. The lynx (right) is responding with "observe" to a LED flash. Body position is west, while head is south.

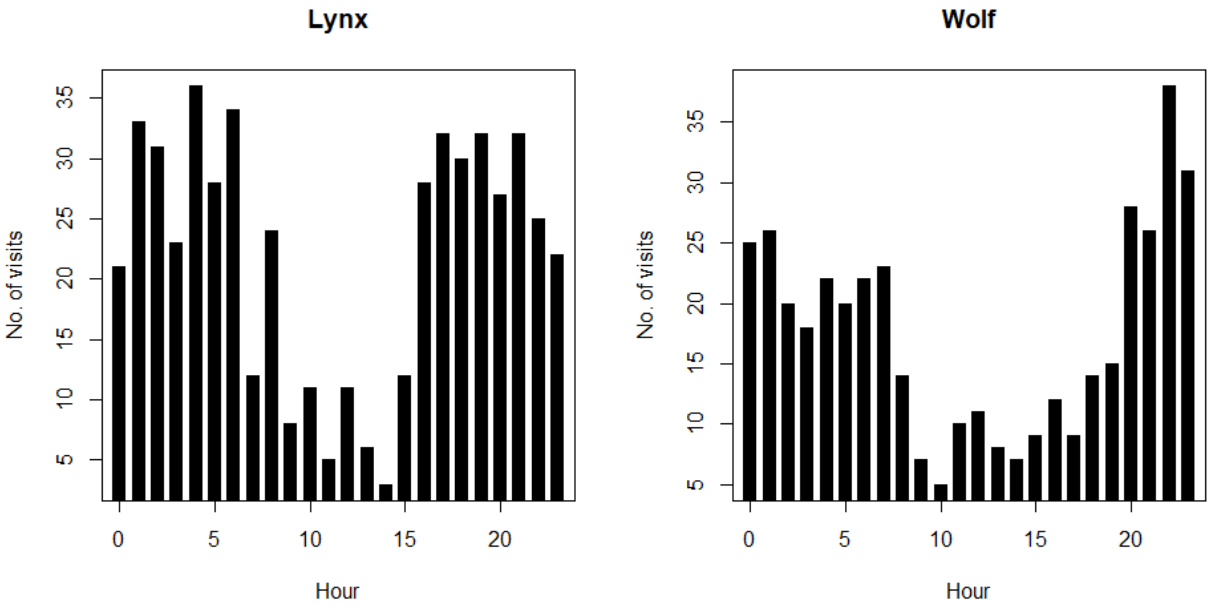

Figure 9: 24-hour activity pattern for the target species during the study period. X-axis shows hours of the day, and y-axis the frequency of visits. Times do not account for day-light saving.

3.2 Time to apparent detection of camera trap

The time-to-event analysis revealed no significant difference between lynx and wolf in time to apparent detection of camera traps (p-value= 0.71). Positive coefficient values indicate higher risk of apparent detection and shorter times to event occurrence compared to intercept. Lynx exhibited a significant positive effect on time to apparent detection with LED (coef = 0.72, exp(coef) = 2.06, se(coef) = 0.30, robust SE = 0.31, z-value = 2.30, p-value = 0.02) compared to no-glow (intercept do not show in CHP output). Wolves showed no significant effect on time to departure (Table 2). When including data from cameras with active flash only, only wolf showed a trend for red-glow (coef = 0.89, exp(coef) = 2.44, se(coef) = 0.50, robust SE = 0.53, z-value = 1.68, p-value = 0.09. Within the first two seconds of the visit, 50% of lynx and 70% of wolves expressed apparent detection of the camera trap. Before 20 seconds had pasted over 90% of lynx had detected the camera, while 90% of wolves had detected the camera after 12 seconds had passed. With the predicted hazard ratio (Fig.10), values above one will indicate a negative impact of the survival, meaning time to event will be shorter. Opposite if value is lower than one, the risk of survival will express time to event will be longer.

*Table 2: The result from the CPH model (Surv (time, event) ~ flash. type * species + cluster (camera.id)), with the effect of flash types on time to apparent detection of the camera traps, for lynx and wolf.*

Time spent at camera trap	Coef	Exp(coef)	SE (coef)	Robust SE	z-value	p-value
Lynx						
LED	0.72	2.06	0.30	0.31	2.30	**0.02**
Red-glow	0.14	1.15	0.32	0.11	0.44	0.66
Wolf	0.15	1.17	0.29	0.41	0.37	0.71
LED	0.12	1.13	0.56	0.94	0.13	0.89
Red-glow	0.64	1.89	0.46	0.50	1.29	0.21

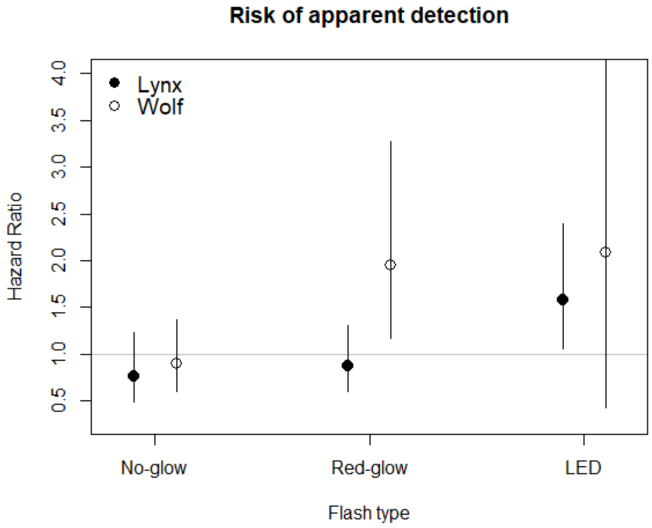

*Figure 10: Plotted predictions to the CHP model (Surv (time, event) ~ flash. type * species + cluster(camera.id)). Predicted hazard ration, gives the ratio of survival risk. The filled symbols represent lynx, and the open symbols represent wolves. Values above 1 indicates shorter time to apparent detection compared to lynx no-glow. The vertical lines mark the 95% CI, and for wolves LED it goes up to 10.5 on the y-axis.*

3.3 Apparent detection with flash/no flash

I detected a significant positive effect of flash on apparent detection for lynx and wolves (Table 3). With flash triggered (estimate = 2.55, SE = 1.02, z-value = 2.51, p-value = 0.01) the probability of apparent detection was predicted to be 14.7% with active flash, compared to the probability of 1.2% without flash. Wolf expressed a significant positive effect with inactive flash (estimate = 2.33, SE = 1.06, z-value = 2.20, p-value = 0.03) with 11% probability of apparent detection. When flash was activated the chance of apparent detection went up to 14% (estimate = -2.40, SE = 1.09, z-value = -2.20, p-value = 0.03) (Fig. 11). I recorded lynx with apparent detection without flash once, compared to 53 times with flash. Wolf showed apparent detection in ten visits without flash and in 33 visits with flash.

*Table 3: Output from the GLMM (apparent.det ~ flash * species + (1|camera.id)). The effect on apparent detection, with the presence or absent of flash. The numbers specify the estimate, standard error, z-value and p-value. The numbers are rounded up to two decimals. Significant p-value are bold.*

Flash per species	Estimate	SE	z-value	p-value
Lynx				
(Intercept) No flash	-4.38	1.00	-4.36	**<0.01**
Flash	2.55	1.02	2.51	**0.01**
Wolf				
No flash	2.33	1.06	2.20	**0.03**
Flash	-2.40	1.09	-2.20	**0.03**

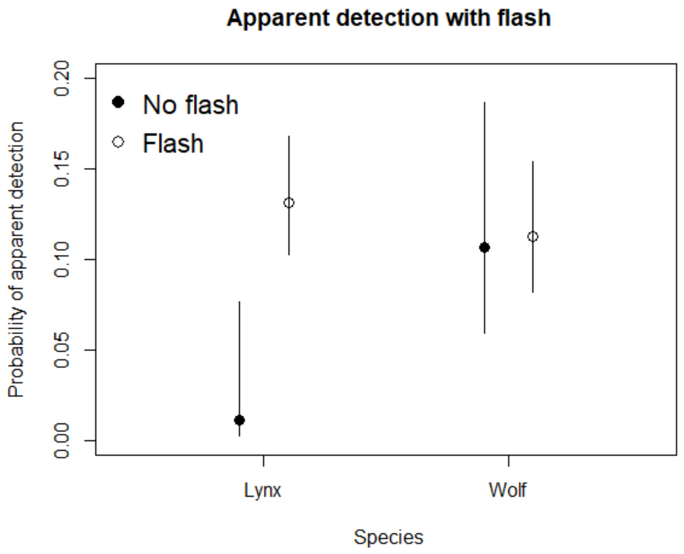

*Figure 11: Predicted effect of apparent detection, with and without flash present (apparent.det ~ flash * species + (1|camera.id)). Filled symbols represent inactive flash, while open symbols represent flash. Lynx is on the left of the x-axis and wolf to the right. Probability of apparent detection of the camera is on the y-axis. The vertical lines mark the 95%.CI.*

3.4 Apparent detection with flash types

Flash type LED expressed a positive significant effect on lynx (estimate = 1.00, SE = 0.44, z-value = 2.28, p-value = 0.02) with a 17.5% chance of apparent detection, compared to 7% with no-glow (estimate = -2.54, SE = 0.35, z-value = -7.20, p-value = <0.01). Lynx was also detected with a trend on red-glow (p-value = 0.06), having a probability of apparent detection twice as high as no-glow (Fig. 12). Flash types had no significant effect on apparent detection by wolves (Table 4).

Table 4: Output from the GLMM (apparent.det ~ flash. type + (1|camera.id)). Expressing the effect from the different flash types on apparent detection. The numbers specify the estimate, standard error, z-value and p-value.

Flash type per species	Estimate	SE	z-value	p-value
Lynx				
(Intercept) No-glow	-2.54	0.35	-7.20	**<0.01**
LED	1.00	0.44	2.28	**0.02**
Red-glow	0.83	0.44	1.91	0.06
Wolf				
(Intercept) No-glow	-1.99	0.20	-10.05	**<0.01**
Red-glow	-0.23	0.56	-0.42	0.67

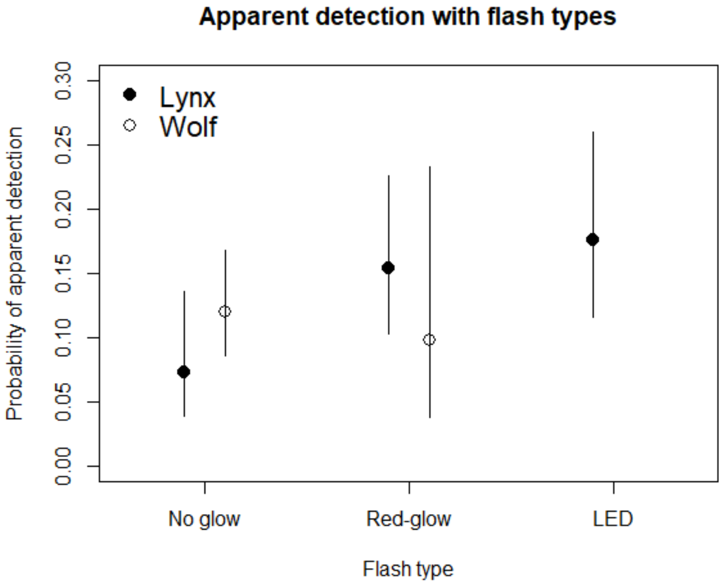

Figure 12: Predictions on the probability of apparent detection by flash type, for each species. Lynx to the left and wolf to the right the filled symbols represent the predicted probability and the vertical lines mark the 95% CI. Wolf did not have enough scores to run statistics on LED flash.

3.5 Behavioral responses

The target species expressed behavioral responses in relation to apparent detections. Lynx displayed three different responses. The most frequent scored response in images were “observe”, followed by “approach” and “flight”. Wolf expressed four types of responses. As for the lynx, “observe” was scored most frequently, before “flight”, “startle” and “approach” (Fig. 13).

In addition to the behavioral responses following a registered apparent detection, I found behavior responses not necessarily followed by an apparent detection, but rather due to the presence of camera traps. Lynx was observed in physical contact with the camera and olfactory sensing of the camera, as well as reacting to flash by squinting. Wolf was found only olfactory sensing the camera, in comparison to lynx.

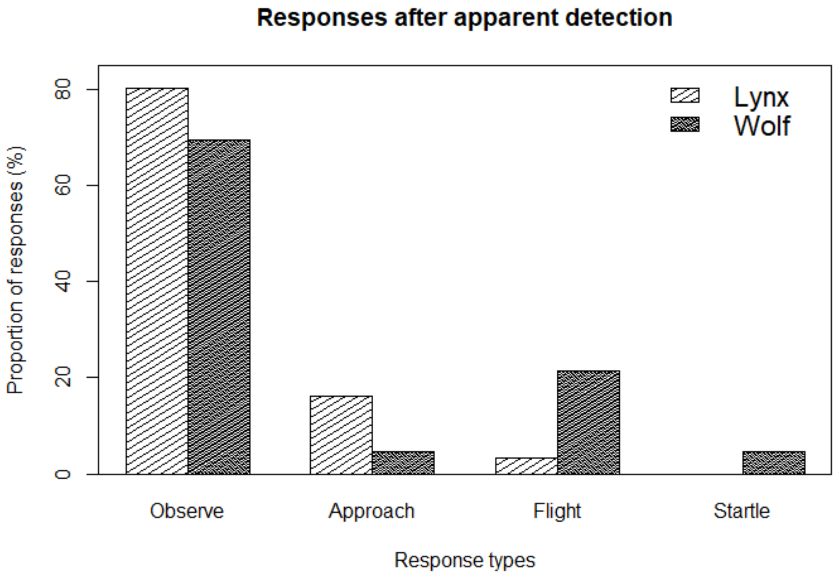

Figure 13: The proportion of behavioral responses to camera traps in images following an apparent detection. Lynx in light shaded bars and wolf in dark shaded bars.

Approach response

Flash/no flash had no significant differences on the probability of lynx approaching the camera (p-value = 0.83), nor any significant effect from the flash types with data on active flash (Table 5). Lynx approach response occurred in four visits without flash and in eleven visits with flash (three no-glow, four LED and four red-glow). Wolf expressed approach response once, when flash was inactive (Table 6).

Table 5: Output from the GLMM (approach. response ~ flash. type + (1|camera.id)). The effect from flash type on the behavioral response "approach". The numbers specify the estimate, standard error, z-value and p-value.

Flash type	Estimate	SE	z-value	p-value
Lynx				
(Intercept) No-glow	-3.92	0.58	-6.72	**<0.01**
LED	0.54	0.77	0.70	0.48
Red-glow	0.28	0.77	0.36	0.72

Table 6: Number of scored visits of lynx and wolf approaching the camera. Divided between flash types no-glow, LED and red-glow and with flash active or inactive.

Species/	Lynx		Wolf	
Approach response	Flash	No flash	Flash	No flash
No-glow	3	0	0	1
LED	4	2	0	0
Red-glow	4	2	0	0

Observe response

The analysis revealed no significant differences between flash/no flash for lynx on observe response (p-value= 0.70). Wolf expressed a significant higher chance of observe response than lynx (estimate = 0.66, SE = 0.32, z-value = 2.05, p-value = 0.04) (Table 7). Compared to no-glow (estimate = -2.37, SE = 0.28, z-value = -8.35, p-value = <0.01) lynx showed a positive significant effect on flash type LED (estimate = 1.19, SE = 0.36, z-value = 3.28, p-value = <0.01). For lynx to express observe the probability was 8.5% by no-glow and 23.5% for LED. Wolf was significantly different to lynx no-glow (Fig 14). No significant difference between red glow and no-glow was detected in terms of the probability of an observe response. The number of visits with observe response is in Table 8.

Table 7: Output from the GLMM (observe. response ~ flash. type + species + (1|camera.id)). The effect from flash type on the behavioral response "observe". The numbers specify the coefficient estimate, standard error (SE), z-value, and p-value.

Flash type per species	Estimate	SE	z-value	p-value
(Intercept) No-glow	-2.37	0.28	-8.35	**<0.01**
LED	1.19	0.36	3.28	**<0.01**
Red-glow	0.39	0.35	1.09	0.27
Species wolf	0.66	0.32	2.05	**0.04**

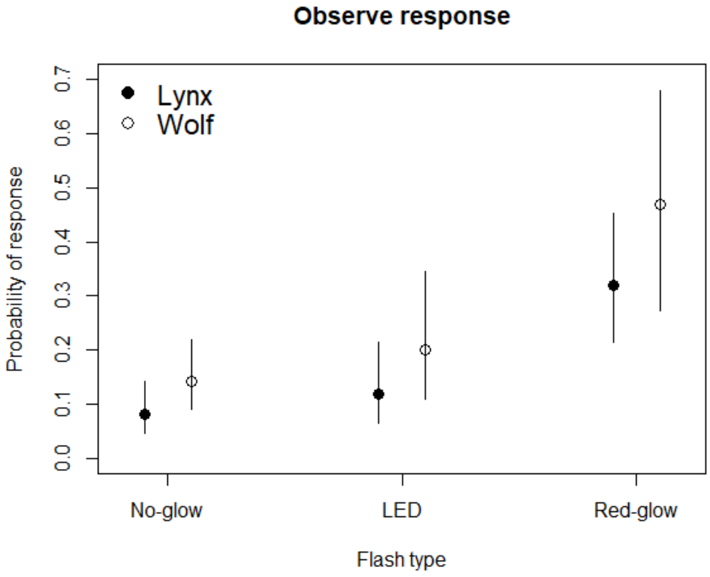

Figure 14: Predicted probability of responding with behavior response "observe", when there is flash. X-axis show three different flash types, y-axis the predicted probability. Lynx is represented with filled symbol, while wolf is represented with open symbol. The vertical lines mark the 95% CI.

Table 8: Number of scored visits of lynx and wolf observing the camera after apparent detection. Divided between flash types no-glow, LED and red-glow and with flash active or inactive.

Species/	Lynx		Wolf	
Observe response	Flash	No flash	Flash	No flash
No-glow	13	3	35	7
LED	28	4	3	0
Red-glow	18	7	12	0

Flight/startle response

I detected no significant differences between flash/ no flash on flight/startle response by wolf (p= 0.24). Compared to no-glow (estimate = -2.94, SE = 0.28, z-value = -10.33, p-value = <0.01) a positive significant effect was found for both LED (estimate = 2.13, SE = 0.66, z-value = 3.20, p-value = <0.01) and red-glow (estimate = 1.61, SE = 0.47, z-value = 3.42, p-value = <0.01) (Table 9). No-glow showed a predicted probability of 5.0% to cause flight/startle response in wolves, with red-glow on 20.9% and 30.7% for LED (Fig. 15). Lynx responded with flight/startle in five visits (four with flash, one without), while wolves reacted with flight/startle in 30 visits (four without flash, 26 visits with flash) (Table 10).

Table 9: Output from the GLMM (flight. startle. response ~ flash. type + (1|camera.id)). The effect from flash type on the behavioral response "flight" and "startle". The numbers specify the estimate, standard error, z-value and p-value.

Flash type	Estimate	SE	z-value	p-value
Wolf				
(Intercept) No-glow	-2.94	0.28	-10.33	**<0.01**
LED	2.13	0.66	3.20	**<0.01**
Red-glow	1.61	0.47	3.42	**<0.01**

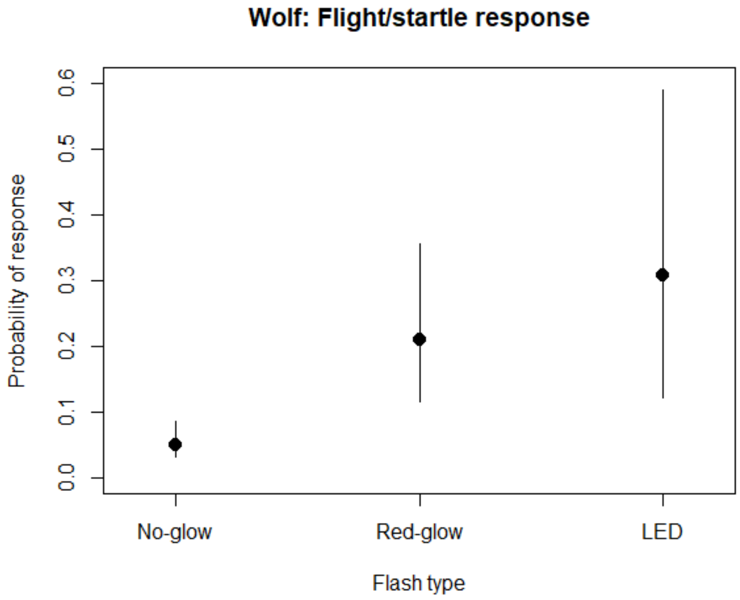

Figure 15: Predicted probability of responding with flight/startle response, with active flash. X-axis show the three different flash types used in the study, y-axis the predicted probability of response. The vertical lines mark the 95% CI.

Table 10: Number of scored visits of wolf and lynx with flight/startle response to camera. Divided between flash types no-glow, LED and red-glow and into flash active or inactive.

Species/ Flight/startle response	Lynx Flash	 No flash	Wolf Flash	 No flash
No-glow	0	0	13	4
LED	3	0	4	0
Red-glow	1	1	9	0

Physical contact with camera

The analysis revealed no significant effect on physical contact between flash/no flash for lynx (p-value= 0.38), nor any significant differences was detected from flash types on physical response to the camera (Table 11). No-glow scored physical response in two visits and LED in seven visits (five with flash active), while red-glow had zero scores on physical contact. Wolves never expressed any physical contact with camera traps (Table 12).

Table 11: Output from the GLMM (physical. response ~ flash. type + (1|camera.id)). The effect from flash type on physical contact with the camera trap. The numbers specify the estimate, standard error, z-value and p-value.

Flash type	Estimate	SE	z-value	p-value
Lynx				
(Intercept)No-glow	-8.76	2.38	-3.67	**<0.01**
LED	0.77	2.07	0.37	0.71

Table 12: Number of scored lynx and wolf in physical contact with the camera. Divided between flash types no-glow, LED and red-glow, and flash active or inactive.

Species/ Physical contact with camera	Lynx Flash	 No flash	Wolf Flash	 No flash
No-glow	2	0	0	0
LED	5	2	0	0
Red-glow	0	0	0	0

Olfactory sensing of camera

The analysis revealed no significant effect from flash/no flash, for neither of the species (p-value flash = 0.43, p-value species = 0.58), nor any significant differences on flash types (Table 13). Wolf scored an olfactory sense response at eight occasions for no-glow (seven without flash and one with flash) and once for red-glow (with flash). Lynx scored an olfactory sense response in six visits (five with LED and once with red-glow, all included flash, Table 14).

Table 13: Output from the GLMM (olfactory sensing ~ flash. type + (1|camera.id). The effect from flash type on olfactory sense response to camera trap. The numbers specify the estimate, standard error, z-value and p-value. The numbers are rounded up to two decimals. Significant p-value are bold.

Flash type	Estimate	SD	z-value	p-value
Wolf				
(Intercept) No-glow	-4.42	0.50	-8.78	**<0.01**
Red-glow	0.57	1.13	0.50	0.61

Table 14: Number of scored lynx and wolf olfactory sensing the camera. Divided between flash types no-glow, LED and red-glow and into flash active or inactive.

Species/	Lynx		Wolf	
Olfactory sensing of camera	Flash	No flash	Flash	No flash
No-glow	0	0	1	7
LED	5	0	0	0
Red-glow	1	0	1	0

Squinting

Lynx was the only species expressing squinting response to camera traps. LED flash provoked a squinting response in 25 visits, whereas no-glow and red-glow did not have any scores on squinting (Table 15).

Table 15: Number of scored visits where lynx squinting due to the camera. Divided between flash types no-glow, LED and red-glow and into flash active or inactive.

Squinting	Flash	No flash
No-glow	0	0
LED	25	0
Red-glow	0	0

3.6 Time to departure

I detected no significant differences on departure time with and without apparent detection, nor any differences between species (Table 16). Predicted hazard ration expressed animals to leave the camera trap sooner if no apparent detection occurred (Fig. 16). The median time to departure with apparent detection was four seconds for lynx and three seconds for wolves, while with no apparent detection mean time was 3.5 seconds for lynx and three for wolf.

Table 16: The result from the CPH model (Surv (time, event) ~ apparent.det + species + cluster (camera.id)). The effect of apparent detection on time to departure at the camera traps, for lynx and wolf.

Time spent at camera trap	Coef	Exp(coef)	SE (coef)	Robust SE	z-value	p-value
Apparent detection	-0.20	0.82	0.33	0.27	-0.72	0.47
Wolf	-0.08	0.92	0.18	0.29	-0.30	0.76

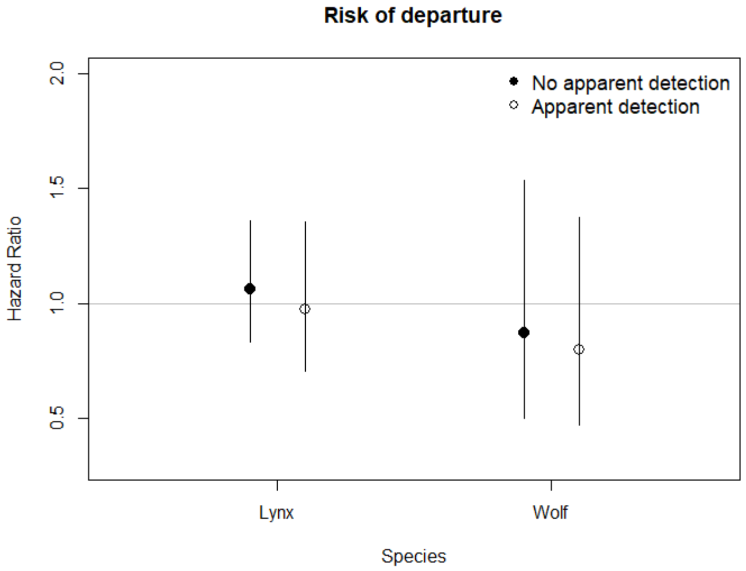

Figure 16: Predictions of hazard ratio with the risk of departure. Hazard ratios above 1, indicate the risk of event to increase and time to event will decrease, 1 = no effect, values below 1 indicates time to event to increase. Filled symbols are events with no apparent detection, open symbols are events with apparent detection. Lynx to the left and wolf to the right in the graph. The vertical lines mark the 95% CI.

3.7 Drastic change of orientation

The analysis for model one revealed a significant positive difference (estimate = 2.28, SE = 0.70, z-value = 3.27, p-value = <0.01) between no response and response (Table 17a), indicating a 6.5 % higher chance of a drastic change in orientation when an approach response occurred. LED (estimate = 1.28, SE = 0.61, z-value = 2.10, p-value = 0.03) expressed a probability of 32% to respond with a drastic change in orientation (Fig. 18). The second model looked at a drastic change of orientation following the behavioral response observe of the camera trap (true or false) (Table 17b). It was detected a positive significant effect for lynx (estimate = 1.44, SE = 0.40, z-value = 3.63, p-value = <0.01) with 2.5% chance of drastic change in orientation with no observe response, up to 9.6% with response. LED (estimate = 0.99, SE = 0.47, z-value = 2.10 p-value = 0.03) expressed a positive significant effect for both species, increasing the probability of drastic change by 6% (Fig. 17). No significant effect was detected for wolves with or without response, nor between lynx and wolf. In the third model I detected a significant positive effect when flight/startle response was expressed (estimate = 2.13, SE = 0.43, z-value = 4.91, p-value = >0.01) (Table 17c). The probability of flight/startle response increase from 8% with no response to 41% with response (Fig. 18).

*Table 17: Output from the GLMM on the three different models looking at "drastic" change of orientation. Approach response model: lynx with the effect of flash type and approach response (I (max. rotation. angle>90 ~ flash. type + approach. response + (1|camera.id)). Observe model: For lynx and wolf with the effect from observe response and flash type with the interaction of species (I (max. rotation. angle>90 ~ flash. type + observe. response *species + (1|camera.id)). Flight/startle response: For wolf with the effect from the response on "drastic" change of orientation. The numbers specify the estimate, standard error, z-value and p-value.*

a) Approach response	Estimate	SE	z-value	p-value
Lynx				
(Intercept) No-glow	-3.75	0.55	-6.75	**<0.01**
LED	1.28	0.61	2.10	**0.03**
Red-glow	0.44	0.63	0.70	0.48
Response	2.28	0.70	3.27	**<0.01**

b) Observe response	Estimate	SE	z-value	p-value
(Intercept) No-glow/Lynx no response	-3.67	0.43	-8.55	**<0.01**
LED	0.99	0.47	2.10	**0.03**
Red-glow	0.29	0.44	0.66	0.51
Lynx response	1.44	0.40	3.63	**<0.01**
Wolf response	0.42	0.57	0.75	0.45
Wolf	0.63	0.44	1.42	0.16

c) Flight/startle response	Estimate	SE	z-value	p-value
Wolf				
(Intercept) No response	-2.47	0.21	-11.64	**<0.01**
Response	2.13	0.43	4.91	**<0.01**

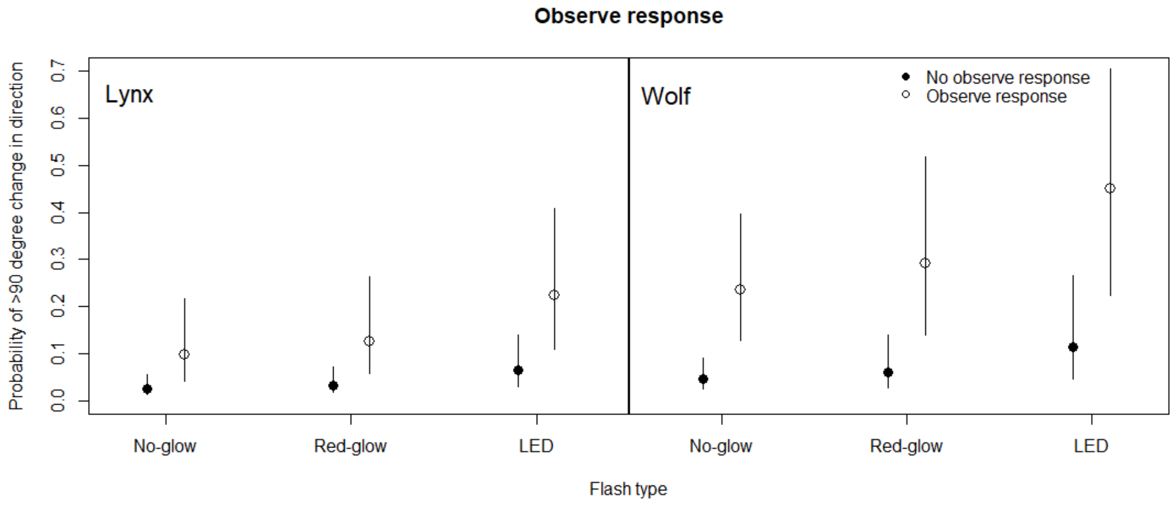

Figure 17: Predicted probability of observer response causing an individual (lynx and wolf) to change their orientation more than 90 degrees. Y-axis is the predicted values and x-axis show the different flash types. Filled symbols represent visits with no scored response, open symbols visits with observe response occurrence. Lynx to the left window and wolf to the right. The vertical lines mark the 95% CI.

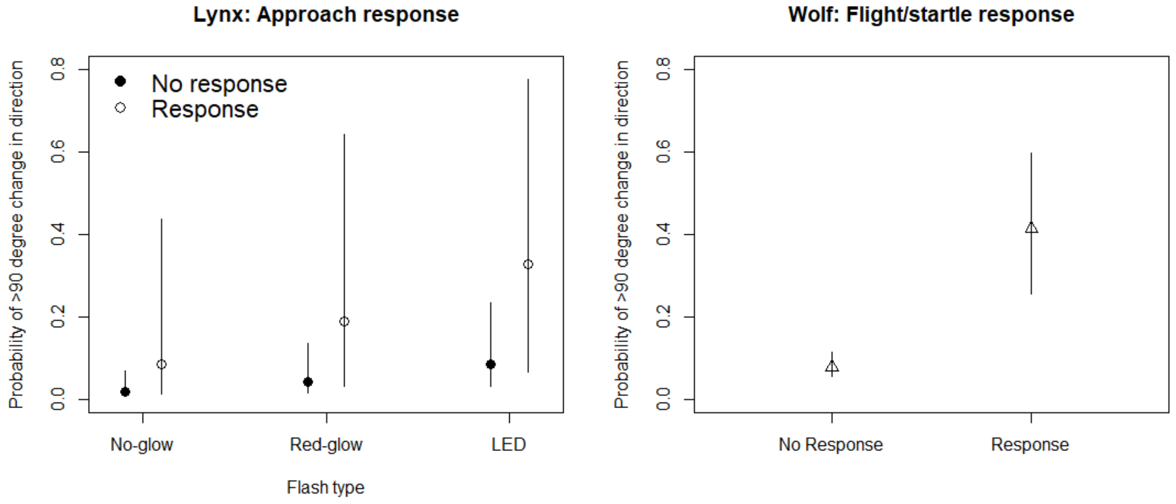

Figure 18: Graph to the left: Predicted probability of approach response causing lynx to change their orientation more than 90 degrees. Y-axis is the predicted values and x-axis show the different flash types. Filled symbols represent visits with no observe response, open symbols visits with approach response occurrence. Graph to the right: Predicted probabilities for a flight/startle response making wolf change their orientation more than 90 degrees. Y-axis is the predicted values and x-axis show no response and response. The vertical lines mark the 95% CI.

4. Discussion

This study revealed clear evidence that camera traps are low-invasive but not non-invasive wildlife monitoring tools. Both lynx and wolves expressed apparent detection (eyes and/or ears pointed directly at the camera) of the camera trap and altered their behavior in response. It was found species-specific and camera-specific differences in type of responses.

4.1 Apparent detection and time to apparent detection

Both species expressed apparent detection to camera traps in approximately 11% of the visits. I predicted species-specific differences in the time from entering the camera trap site until apparent detection of the camera. This pattern was not found in this study. An explanation could be the limitation in the definition of an apparent detection. This will not always reflect the actual time an animal has indeed noticed the camera. In my study, wolves have been registered running off from the camera trap site without being photographed looking at the camera. This could be one of the reasons wolves never scored an apparent detection on LED cameras, in the few cases wolf and LED had an encounter. Also, both species claim territories and will be aware of their surroundings, which probably makes them conscious about foreign objects.

4.2 Flash and flash type

The activity pattern revealed by my camera trap data suggests that visits occur most frequently during dark hours, when flash is activated. The probability of apparent detection of cameras by both target species was found to be greater with active flash. My findings are consistent with Meek et al. (2016) who found most camera captures by the felid (*Felis catus*) and the two canid species (*Canis familiaris* and *Vulpes vulpes*) to happen during the night. In my study, lynx showed a greater probability/prevalence of apparent detection if there was LED flash. The reason may be the white light emitted. Glen et al. (2013) reported three out of the six feral cats who expressed detection of camera traps, reacted with startle response to white flash in New Zealand. They suggested white flash made cats react more often than infrared flash. Overall, wolves seemed to have a higher probability of apparent detection, without a noticeable difference between visits during which flash was triggered vs. visits without flash. The differences between lynx and wolf might originate from the different use of visual and acoustic senses (Boitani & Mech, 2006; Kitchener A, 1998).

Felids have one of the most developed binocular visons off all carnivores, as they depend on night vision to stalk their prey. They use their vision and tactile information to interpret their surroundings, more than they will use acoustic sensing (Kitchener A, 1998). During the day, when the flash is inactive, lynx may not discover the camera trap, as it gives no visual signals. The absence of apparent detection without flash may also result from fewer encounters, due to the more nocturnal activity pattern. In my study, no-glow cameras (HC600 and PC900) caused the least apparent detections, which substantiates the fact that lynx use their eyes, more than their ears. As wolves seemingly detects the camera close to equally with and without flash, it can originate from the active use of their ears. Wolf as a pack-living animal, have developed an extraordinary acoustic- and olfactory sense for communication and to locate prey (Boitani & Mech, 2006). From the predicted probabilities on apparent detection with flash types, wolves detect no-glow cameras with greater probability than lynx. This could derive from noise coming from the camera shutter. As described in Meek et al. (2014), animals can potentially hear camera traps. Except from Reconyx model HC600 (no-glow model), which proved to be within the hearing range of most animals (Meek et al., 2014), there is no record in which the remaining Reconyx models emits audible noise. Nevertheless, there are reasons to believe both the shutter and flash from other models will emit sound in the range of animals hearing. Other models from different camera manufacturers were found to be within animals hearing range (Meek et al., 2014).

The use of infrared flash has been recommended as a method to avoid animals detecting and ultimately avoiding the camera traps (Claridge et al., 2004; Kays et al., 2009; O’Brien, 2011p.38; Weingarth et al., 2013), although I have found no studies quantifying if this assumption is accurate. The results from this study indicated that both species in question reacted to all three flash types, though to a varying degree. Studies on lynx could benefit from the use of camera traps with infrared flash, as this was associated with reduced apparent detection, while wolves will presumably not gain the same reduction, as the predicted difference between inactive and active flash were not significant. Having said that, LED is commonly used to enable accurate identification of individuals (e.g. felids) based on coat patterns, and density estimation with capture-recapture methods (Karanth & Nichols, 1998; Karanth et al., 2006; Zimmermann et al., 2013). In circumstances that require individual identification, LED may be the preferred flash type.

4.3 Behavioral responses

I detected differences in types of responses “caused by camera traps”, and responses “related to camera traps”. After an apparent detection, responses were assumed to have been caused by camera traps. During the study, both species responded with approach, flight and observe. Wolves showed in addition to this, startle as a response. These findings are consistent with Meek et al. (2016), who found approach- and observe response to be more pronounced in their felid species, with flight (repel/retreat) and startle more pronounced in the canid species. Approach response appeared in a single visit for wolves, and it was without flash triggered. This visit consisted of a photo sequence showing a wolf walking past the camera (camera model PC900; no-glow), before turning around and approaching the camera trap. The fact that the wolf stopped after passing the camera, may suggest that the camera may have made sufficient noise to alert the animal. Lynx expressed more attraction towards the camera, compared to wolves. Lynx approached the camera in 11 visits with active flash, compared to four visits without flash. LED and red-glow was more pronounced, but also no-glow attracted lynx. No-glow flash is reputed to be invisible, which is confirmed to be correct for humans vision, but proven to not be true for all animals (Meek et al., 2014). Based on my findings, there could be an indication of no-glow flash emitting light in the visual range of lynx. Lynx exhibited approach response to no-glow cameras in only three visits, where all three had active flash.

Observe response was the most prominent behavioral response scored for both species. One reason is that for every apparent detection the animal's first response is observe, as they just discovered the camera. Some animals observed the camera over a few seconds (images), before responding with either a second reaction (approach, flight, startle, physical contact or olfactory sensing) or leaving the camera trap site. As expected, flight/startle response was more pronounced for wolves, than lynx. When hunting, wolves often hunt prey bigger than themselves. So, if they do not act carefully and cautious, prey can attack them (Boitani & Mech, 2006). This can be one of the reasons wolves tend to exhibit wary and "on alert" behavior and predominantly act with caution around camera traps. This behavior towards camera traps has also been found in coyotes (*Canis latrans*) (Séquin et al., 2003). Lynx only expressed flight/startle in five visits, while wolves in 30. From the predictions on response probability due to flash type, LED flash was most likely to spook wolves. The red-glow came out as second, with no-glow at the lowest probability. This finding supports the assumptions of reduced startle response, in some carnivores when using camera models with no-glow (Gibeau & McTavish, 2009; McCarthy et al., 2010).

Physical contact, olfactory sensing and squinting as behavioral responses to camera trap, turned out to not necessarily be followed by an apparent detection, but rather to be a behavioral response related to the presence of camera trap. In some cases, the initial of a visit showed the animal in physical contact with the camera, without the approach having been captured. Olfactory sensing could appear if an individual did not see the device but could sense it. Same as for squinting, this could also be a response, without an animal expressing apparent detection.

Physical contact was only observed in visits by lynx. This response was scored in nine visits, with no significant effect on flash type. Why lynx is carrying out this type of behavior, and wolves do not, might be explained by the differences in territorial marking behavior. Lynx often use their scent glands on their face and body, rubbing against objects (Kitchener A, 1998; Vogt et al., 2014), while wolves generally scent mark territories by urine spray and feces (Boitani & Mech, 2006; Vilà et al., 1994).

Wolves expressed an olfactory sensing response to camera in nine visits, whereas lynx did so in six. Wolves are dependent on a good nose to examine the surroundings and will use their nose more active than lynx (Boitani & Mech, 2006; Kitchener A, 1998). The low number of observations for wolf is therefore surprising. A reason for not detecting more olfactory sensing in wolves could be that behavioral responses are missed if they occur outside the cameras field of view. Another possibility is that subtle responses and short-lived behaviors which falls between photos, will go undetected by the observer. Wolves might olfactory sense and/or hear the camera without locating the device, as seven out of nine visits occurred without flash triggered. For lynx, the low number of scores is more expected. Not only do felids have less developed olfactory sense, they seldom use their nose for hunting, but rather to communicate (Kitchener A, 1998). Squinting was found in 25 visits by lynx and only with LED flash. The need for great vision during the night, calls for the ability to greatly enlarge the pupils. During the day the pupils retract to handle daylight (Kitchener A, 1998). As a reaction to the instant white flash in camera model PC850 lynx will squint. This may explain why I detected no squinting for either of the infrared flashes, nor by wolves.

4.4 Time to departure

Surprisingly, despite the dissimilarities in apparent detection probabilities, no differences between or within species in their expected departure time, after apparent detection was found. The cautious behavior of wolves was thought to create shorter visits, whereas lynx exhibit more inquisitive behavior, and was thought to create longer visits. Predicted hazard ration expressed that animals would leave the camera trap quicker if no apparent detection occurred. Which can be explained by the short time it takes for an individual to pass the camera undisturbed. With an apparent detection, they often stop, keeping them in front of the camera for longer.

The use of time-to-event analysis had some limitations, which may be explained by the utilization of the available data. Various response types could be a reason for not detecting any significant differences. All visits were included, leading to visits of short time (e.g. flight and startle) being paired up with visits of longer time (e.g. observe or approach). To deal with this, response types could have been divided into sub-groups to distinguish between responses expected to generate longer stays and those expected to generate shorter stays, to run them separately. Furthermore, even with pictures taken every second (in some cases two pictures are within the same second), the fact is, this might not be detailed enough to detect time differences. Considering 50% of lynx and 70% of wolves express apparent detection in the first two seconds, with the median time to departure being 3-4 seconds (for both species and with and without apparent detection), time differences could be in the order of seconds or less. In addition, the time it takes for an animal to arrive, express apparent detection, respond and leave, could potentially be the same amount of time it takes for an animal to pass the camera trap without apparent detection. This could especially be the case in visits containing flight- or startle responses. Additionally, the purpose of passing the camera could also influence the time spent, depending on traveling speed, the intention of travel (hunting, transport, territorial round), disturbance of olfactory senses or other animals.

The analysis does not distinguish between whether an animal stayed longer at the camera trap because it detected the camera, or if it stayed a certain time period before it noticed the camera. To deal with this matter, a comparison of time from apparent detection to departure could have been executed.

4.5 Change in orientation

I tested whether individuals passing the camera trap change their initial orientation, due to a behavioral response to camera. If no behavioral response of the camera occurred, the predicted probability of a drastic change in orientation was below 10% for all three behavior response types tested. Lynx was more likely to change its orientation when it was a LED camera (PC850). This model did not consider if the probability of orientation change differed between inactive and active flash. However, based on other results from my study, lynx do have a greater probability of apparent detection of camera traps when flash is active, and particularly when it is LED. A reason for getting an effect on drastic change from approach response is that the majority of cameras are installed with the intention of making animals pass from east to west or opposite (referring to Fig. 4). To approach the camera trap e.g. with the body-oriented east, the individual will need to turn its body towards the camera to approach it. This finding supports the idea about lynx get attracted to active camera flash, acting trap-happy. As for approach response, observe response was also associated with drastic change in orientation at a higher predicted probability with LED flash than no-glow and red-glow.

As mentioned earlier, for each behavioral response there is generally an observe response as the first response. It is unlikely that observe response alone make animals drastically change their orientation, as they mostly turn their head towards the camera when observing (Fig. 8), keeping their body in the same orientation as when they entered the camera trap site. But, after observing the camera, an animal could obtain a second response which will increase the probability of changing movement direction. This applies for both species with observe response, with wolves having a higher probability of drastic change, as they show more aversive behavior as a second response. Aversive behavior response had a predicted probability on 41% of causing a wolf to drastically change orientation. This contrasts with lynx, which oriented its body towards the camera to inspect it. Wolves predominately turned away from the camera, making a U-turn. When travelling, wolves tend to travel in a more or less straight line (Musiani et al., 1998), making these drastic changes unnatural, and might disturb the intention of the travel. Lynxes moving pattern is slower than wolves, even slower than other felids, and they do not travel as straight as wolves neither (Jędrzejewski et al., 2002). These differences in moving patterns might make wolves more vulnerable to disturbance, as lynx often take time to investigate and can carry on afterward. To minimize disturbance for wolves, a solution could be choosing the right camera model. In this study, no-glow models created the least flight/startle responses of the three flashes resulting in fewer responses, although wolf apparent detected them just as often as re-glow. Camera trap data has been used as a method to estimate to what extent an animal turns while moving, to calibrate data on traveling distance obtain by fine-scale telemetry (Rowcliffe et al., 2012). If individuals react to the camera like in this study, this needs to be accounted for. Animals sensing the camera trap may have change their movement speed or direction.

4.6 Implications

To my knowledge, no previous studies have quantified behavior responses to camera traps to the extent of this study. The potential pitfalls and errors caused by ignoring this topic have already been acknowledged in the literature, but still not extensively considered among researchers. This study has found camera traps potentially creates detection error for some analysis, which should not be overlooked. The challenge with this kind of behavior study is to quantify the extent of the bias generated by each behavior response to an apparent detection, or responses related to the camera. The bias will vary, depending on how the data are being utilized. Though it is important to keep in mind that some of the behavior changes alone might not create noticeable bias, but the total effect may create unknown errors in a study. The assumption of equal detectability in e.g. closed and open capture-recapture models (Larrucea et al., 2007; O'Brien, 2011; Weingarth et al., 2013) may experience bias causing estimation errors, caused by behavior modifications. This will especially apply if animals respond with aversion, as wolves in this study or avoid camera traps like coyotes were reported to do in California (Larrucea et al., 2007). All research which requires target species behaving undisturbed will incur bias if such impacts are ignored. O'Brien (2011) discusses the problem tied to camera traps, with the assumption on equal detectability in models. He explains how covariates which influence detection probability must be identified, and that there is a need for understanding how detection probability varies under different conditions. Additionally, Hofmeester et al. (2019) has recently made a framework to try an address the factors which can influence camera trap data, with unequal detectability of animals.

Together with Meek et al. (2016), my study addresses the importance of this topic. My study shows differences in response between a felid and a canid species, which amplify the importance of taking it into account, particularly when dealing with surveys including multiple species (Larrucea et al., 2007). Furthermore, this study has demonstrated that the use of infrared (no-glow and red-glow) is not an easy fix to avoid behavioral response to camera traps for all species and researcher cannot refer to camera trapping as a non-invasive method. The result of this study highlights the importance of considering behavioral effects on wildlife, caused by camera traps. It suggests that flash type must be carefully chosen, to try and minimise the impact cameras can have on animals. No-glow flash will most likely generate less disturbance to wildlife, especially if compared to LED, which appeared to cause the most frequent change in behavior for both species. Along with active flash and flash types, noise emission from cameras are recommended to be considered if implemented in areas with cautious species, like wolves.

4.7 Limitation and suggestions for future studies

Apparent detections and behavior responses could be missed by the observer during the assessment which may lead to an underestimation of behavioral effects caused by camera traps. Camera traps only allows observers to assess captured information and everything outside the field of view will go unnoticed. This can contribute to an underestimation of the impact from cameras, implying my studies estimate is a minimum level of camera. Also, we are using the same device which is causing the impact to quantify the impacts. To ensure all visits were identified as unique visits, rather than estimating visitant post data preparation, visits could have been labeled while assessing images. To access context-dependence of camera impacts, site specific covariates, such as human traffic and density/level of infrastructure around camera sites, could have been included. Séquin et al. (2003) reported coyotes to be less wary around camera traps when they were close to urban settings. Another interesting aspect not addressed in this study, is how human scent on the camera device could influence the proportion of apparent detections by adding days since last human handle of the camera trap.

For further studies on this topic, I recommend including multiple-individual photos. In the case of visits with more than one animal, the detection probability of the camera might differ from single individual visits, which may impact solitary and pack-living species differently. To increase observer's detection of behavior response, the assessment of the data might benefit from multiple independent observers, to assess variation in scoring between observers and potential observer bias. As it was not investigated to what extent these findings influence detection rate of the species or if lynx and wolves get attracted from distance or avoid camera traps, this is recommended for further studies.

5. Conclusion

Camera trapping is an efficient and popular research method, used for recreational and wildlife monitoring purposes worldwide, as it is often deployed with the assumption of being non-invasive. Behavioral responses caused by the presence of camera traps are not well studied but can have a great impact on estimation if behavior modification influences the study organism and thus the resulting data and inferences. My study quantified behavioral responses to camera trap in two of Norway's large carnivore's, lynx and wolf. Both species expressed apparent detection to camera traps and responded with changes in their behavior. I detected differences in the magnitude and patterns of impacts between species and between camera flash types. Lynx was found to most likely use its vision and acting more inquisitive towards the camera. Active flash caused most responses in lynx, with LED causing the greatest impact. Wolf with its more cautious behavior seemed to rely on acoustic information more than lynx, acting more aversively towards the camera traps. Wolves expressed awareness of the camera regardless if flash was active or not. However, camera-specific factors suggested no-glow to cause fewer incidence of behavior changes than red-glow and LED. With the results from this thesis, I hope to bring attention to the importance of this topic, and to the lack of research on this field. Camera traps are not entirely "non-invasive", and this aspect should not be ignored in studies using them for collection of observation data and should not be overlooked in studies.

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Appendix

Table A1: Model selection done by Akaike Information Criterion (AIC). The numbers are the AICc, the differences between models (ΔAICc), the Akaike Weight (Wi) and the estimated numbers of parameters in the model (K). Selected model is bold.

Model ID	Model	AICc	ΔAICc	Wi	K
Time to apparent detection					
TAD-1	Surv(time,event) ~ flash + flash.type * species + cluster(camera.id)	1624.18	1.09	0.35	6
TAD-2	Surv(time,event) ~ flash * species + cluster(camera.id)	1630.15	7.06	0.02	3
TAD-3	**Surv(time,event) ~ flash.type * species + cluster(camera.id)**	**1623.09**	**0.00**	**0.60**	**5**
TAD-4	Surv(time,event) ~ species + cluster(camera.id)	1629.24	6.16	0.03	1
Time to departure					
TD-1	**Surv(time,event) ~ apparent.det + species + cluster(camera.id)**	**1352.48**	**0.00**	**0.41**	**2**
TD-2	Surv(time,event) ~ apparent.det + flash.type + species + cluster(camera.id)	1353.42	0.94	0.26	4
TD-3	Surv(time,event) ~ apparent.det + flash+ species + cluster(camera.id)	1354.00	1.52	0.19	3
TD-4	Surv(time,event) ~ apparent.det + flash.type * species + cluster(camera.id)	1354.56	2.08	0.14	6

Table A2: Model selection done by Akaike Information Criterion (AIC). The numbers are the AICc, the differences between models (ΔAICc), the Akaike Weight (Wi) and the estimated numbers of parameters in the model (K). Selected model is bold.

Model ID	Model	AIC	AICc	Wi	K
Approach response					
A-1	I (max. rotation.angle>90) ~ appraoch.response + flash + flash.type + (1|camera.id)	177.58	0.04	0.26	4
A-2	**I (max. rotation.angle>90) ~ appraoch.response + flash.type + (1|camera.id)**	**177.51**	**0.00**	**0.27**	**5**
A-3	I (max.rotation.angle>90) ~ appraoch.response + (1|camera.id)	178.10	0.60	0.20	3
A-4	I (max.rotation.angle>90) ~ appraoch.response + flash + (1|camera.id)	177.63	0.12	0.26	6
Oberve.response					
O-1	I (max.rotation.angle>90) ~ observe.response *species+ flash + flash.type + (1|camera.id)	468.08	1.93	0.89	8
O-2	**I (max.rotation.angle>90) ~ observe.response *species + flash.type + (1|camera.id)**	**466.14**	**0.00**	**0.37**	**7**
O-3	I (max.rotation.angle>90) ~ observe.response* species + (1|camera.id)	466.16	0.02	0.37	5
O-4	I (max.rotation.angle>90) ~ observe.response + flash.type * species + (1|camera.id)	468.50	2.36	0.11	8
Flight/startle response					
FS-1	I (max.rotation.angle>90) ~ flight/startle.response + flash + flash.type + (1|camera.id)	219.63	5.48	0.04	6
FS-2	I (max.rotation.angle>90) ~ flight/startle.response + flash.type + (1|camera.id)	217.56	3.41	0.11	5
FS-3	**I (max.rotation.angle>90) ~ flight/startle.response + (1|camera.id)**	**214.15**	**0.00**	**0.62**	**3**
FS-4	I (max.rotation.angle>90) ~ flight/startle.response + flash + (1|camera.id)	216.19	2.04	0.22	4

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