



Preface

This master thesis was written at the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences. It covers 30 credits of my master's degree in natural resource management. My field work was conducted within the frames of the Scandinavian Lynx Project and was funded by the "Norwegian Directorate for Nature Management", the Research Council of Norway, the County administrations in Oslo & Akershus and Østfold Counties as well as the Carnivore management board in region 4.

I would like to express my sincere gratitude to my supervisors Leif Egil Loe (NMBU), John Odden (NINA) and Richard Bischof (NMBU). I'm grateful to Leif Egil for helping me with statistical analysis and the writing process and for finding time to answer my never-ending questions. Thanks to John for organizing the fieldwork, collecting and organizing the data and for answering questions, and to Richard for his invaluable knowledge of statistics, for helping me build models and analyze the data. To them all for constructive commentaries on my manuscript.

I am also very grateful to Kjartan Sjulstad for finding suitable locations for the camera traps and for placing many of them. I would also like to thank the countless volunteers who have contributed with their knowledge of good camera trap locations and for collecting data from the trap sites. Thanks also to John Linnell, my friend Morten Meland, my girlfriend, and my mom and dad for valuable comments on the manuscript.



Ås 09.05.2014.

Are Endal Rognes

Abstract

Predators are one of the key elements in shaping the behavior of prey species. Through constructing a landscape of fear they make their prey modify their behavior regarding both habitat and space use, but also activity patterns. Activity patterns may also be affected by a number of other factors such as seasonality. The animal predators pose a threat to their prey throughout the year while humans are bound by hunting seasons. During the day visibility is high and it is a lot easier for the prey to spot predators at greater distances. This makes it difficult and less attractive for predators to hunt in daylight. In the night time conditions are the opposite, low visibility makes it easier for predators to sneak up on their prey. Moonlight changes the night time conditions, giving higher visibility, and is expected to affect the activity patterns of both predators and prey.

In this study I have investigated the circadian activity patterns of lynx (*Lynx lynx*), fox (*Vulpes vulpes*), roe deer (*Capreolus capreolus*), and humans (*Homo sapiens*) using automatic camera traps. I tested the effects of season, moonlight, habitat, and vicinity of roads on the activity patterns and compared activity patterns of the different animals to see if prey avoid predators in time. In contradiction to what I expected, roe deer - the prey - increased activity levels most in moonlit nights. This might be indicative of a benefit due to moonlight making it easier for the roe deer to detect the predators rather than improving the hunting success of lynx. Still, although they responded less than roe deer, the lynx and fox were also most active in nights with moonlight in compliance with my predictions. The roe deer displayed a crepuscular activity pattern throughout the year with a higher daytime activity level than I expected. The lynx proved to be crepuscular while the fox was nocturnal. Humans were as predicted diurnal. Given these patterns there was some indication that the roe deer avoided both its animal predators by maintaining a relatively high activity level also during the day. It might also be that the lynx attempts to synchronize its activity with that of the roe deer. The fox seemed to avoid its predator, the lynx, by being active during parts of the night when the lynx was less active. The roe deer was more active during summer than during winter while for lynx and fox the results were the opposite. Fox was the only species which seemed to prefer camera trap locations that were close to roads, indicating that it benefits from travelling and searching for food along them.

In this study I have by the use of automatic camera traps documented the circadian activity patterns of lynx, roe deer, fox, and humans. I have evaluated the effects environmental factors such as season and moonlight have on the activity patterns of the studied species. In addition I have also documented adaptations in activity patterns in prey and predators. To my knowledge this study is the first of its kind to document the circadian activity patterns of the studied species in a northern boreal ecosystem. It is also unique by its size and duration and I believe that it will be a good contribution to science and an inspiration for researchers worldwide.

Sammendrag

Predatorer er nøkkelarter i økosystemer og påvirker aktivitetsmønstre hos sine byttedyr. De skaper et «fryktens landskap» som tvinger byttedyrene til å endre både habitat og områdebruk, men også aktivitetsmønstre. Aktivitetsmønstre påvirkes også av en rekke andre faktorer som for eksempel sesong. Dyrepredatorene utgjør en trussel for byttedyr hele året, mens mennesker er begrenset av jakt sesong. Midt på dagen er det god sikt og mye enklere for byttedyr å få øye på predatorer på lengre avstand. Dette gjør det mindre attraktivt for predatorene å jakte i dagslys. Om natta er forholdene motsatt. Kort sikt gjør det lettere for predatorene å snike seg inn på byttet sitt. Månelys endrer forutsetningene for jakt på natta og de bedre lysforholdene forventes å påvirke både predatorer og byttedyr.

I dette studiet har jeg undersøkt døgnaktiviteten til gaupe (*Lynx lynx*), rev (*Vulpes vulpes*), rådyr (*Capreolus capreolus*) og mennesker (*Homo sapiens*) ved bruk av viltkamera. Jeg har også testet effektene av sesong, månelys, habitat og nærhet til vei og sammenlignet aktivitetsmønstrene til de ulike artene for å se om byttedyr unngår de mest aktive periodene til sine predatorer. I motsetning til hva jeg ventet viste rådyret størst respons på månelys. Dette indikerer at rådyret kan ha fordel av månelys siden det da er enklere for rådyret å se predatorene enn omvendt. Selv om predatorene ikke viste like kraftig respons på månelys som rådyret, så var både gaupe og rev mer aktive i månelyse netter i samsvar med mine prediksjoner. Rådyret var skumringsaktivt gjennom hele året og hadde et høyere aktivitetsnivå på dagtid enn forventet. Gaupa var også skumringsaktiv, reven nattaktiv og mennesker var som forventet dagaktive. Disse aktivitetsmønstrene antyder at rådyret til en viss grad unngår begge sine dyrepredatorer ved å opprettholde et relativt høyt aktivitetsnivå på dagtid. Det kan også virke som om gaupa prøver å synkronisere sine aktivitetstopper med rådyrets. Reven synes å unngå predasjon fra gaupa ved å være mest aktiv på den tiden på natta da gaupa er minst aktiv. Rådyret var mer aktivt om sommeren enn om vinteren, mens for gaupe og rev var resultatene motsatt. Reven ble mest hyppig fotografert av de kamerafellene som stod nærmest vei. Dette kan indikere at den drar fordel av å forflytte seg langs veier og lete etter mat langs dem.

I dette arbeidet har jeg dokumentert døgnaktiviteten til gaupe, rev, rådyr og mennesker ved bruk av viltkamera. Jeg har vurdert betydningen miljøfaktorer som sesong og månelys har på aktiviteten til artene. Resultatene viser tilpasninger i aktivitetsmønstre hos både predatorer og

byttedyr. Så vidt meg bekjent er dette studiet det første som dokumenterer døgnaktiviteten til disse artene i et borealt økosystem ved bruk av viltkamera. Det er også unikt på grunn av dets størrelse, omfang og varighet, og studiet vil bidra med viktig kunnskap og fungere som en inspirasjon for forskere verden over.

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1.0 Introduction

Top predators can shape their communities through intraguild predation and interaction with their prey. Predators and prey interact in an arms race, where the predators will seek to track down their prey during their most vulnerable period, while the prey will counter with anti-predator behavior (Caro 2005). As shown by Laundré et al. (2001) and Altendorf et al. (2001) predation risk can make prey species alter their habitat use described as the “landscape of fear”. Predators may also make their prey species alter their activity levels and activity patterns (Bischof et al. 2013; Penteriani et al. 2013).

The animals are mainly active when searching for and catching food, except for the mating season when they move a lot due to reproductional purposes (Schmidt 1999). Especially herbivores use a lot of time feeding since they live on low energy food (Mysterud et al. 1997). When the animals are not active they are mostly resting. Prey species will benefit from being active when it is safest to forage, which will be the time when predators are less active or when conditions allow them to discover the predator in time to flee. Predators need to adjust their activity patterns to when the prey is active and hunting conditions are good.

Several factors influence the circadian activity patterns of animals. The mating season often means an increase in activity especially among males (Schmidt 1999), related to finding and watching over a mate and for some species protection of territories (Andersen et al. 2005). Spring and summer mean rearing of offspring associated with increased activity levels (Schmidt 1999). Winter means snow, harsh conditions and less available food, in particular for ungulates (Ratikainen et al. 2007), which may increase or decrease activity depending on the setting. Activity patterns may also vary with photoperiod, i.e. season (Beltrán & Delibes 1994; Daan & Aschoff 1975), weather, barometric pressure, availability of prey, sex, reproductive status, temperature, and other environmental factors (Beltrán & Delibes 1994; Pagon et al. 2013; Podolski et al. 2013; Schmidt 1999). One of the most striking features is the diurnal variation in activity patterns. Animals are often described as nocturnal, such as fox (Ables 1969; Weber et al. 1994), diurnal (Shkolnik 1971) or crepuscular (Podolski et al. 2013). Pagon et al. (2013) found bimodal activity patterns in roe deer all year around with peaks around dusk and dawn and with variations in activity related to summer. They also documented differences in activity levels between males and females in the territorial period (early spring to late summer). There can be large variations in activity patterns between

populations of the same species and individuals of the same population. Exemplified by lynx by Schmidt (1999) who found nocturnal activity patterns with peaks between 15:00 and 07:00, while Podolski, Belotti et al. (2013) documented crepuscular activity patterns in lynx. Reinhardt and Halle (1999) also found high activity in crepuscular periods, but also reported a higher activity level in lynx during the day than during the night, in contrast to the findings of Schmidt (1999). This illustrates the animal's flexibility in adapting to environmental factors and different life history events.

One particularly intriguing factor affecting nocturnal activity is variation in moonlight. Moonlight is thought to offer favorable hunting conditions for predators, making prey more vulnerable. Penteriani et al. (2013) who studied the Iberian lynx (*Lynx pardinus*), red fox, and their shared prey, the rabbit (*Oryctolagus cuniculus*) found modified behavior in prey as a response to increased predation risk on moonlit nights. Most of the research on effects of moonlight on predator and prey activity patterns has so far been carried out in areas with a mild climate (Kotler et al. 2010; Penteriani et al. 2011; Penteriani et al. 2013). To my knowledge this is the first study to document effects of moonlight on species of predators and prey in a northern boreal ecosystem. The effects of moon illumination could be expected to be of a bigger influence in areas with snow-covered ground reflecting the moonlight.

The traditional way to study activity patterns in wild animals has been by radio telemetry or GPS tracking. With the introduction of automatic camera traps new possibilities for non-invasive field research have opened. They have mainly been used to study rare and cryptic species appearing at low densities and leading a hidden lifestyle, such as jaguars (*Panthera onca*) (Sollmann et al. 2011), puma (*Puma concolor*) (Negrões et al. 2010), Iberian lynx (*Lynx pardinus*) (Gil-Sánchez et al. 2011), bobcat (*Lynx rufus*), and the Altai mountain weasel (*Mustela altaica*) (Bischof et al. 2013). Solitary predators such as large felids have been extensively studied in order to reveal geographic occurrence and to make population estimates (Balme et al. 2009; Heilbrun et al. 2006; Karanth & Nichols 1998) and the focus has mainly been on one species at a time. However, some studies on activity patterns of ocelots (*Leopardus pardinus*) (Kolowski & Alonso 2010), jaguars and pumas (Harmsen et al. 2011) have been conducted using automatic camera traps. Especially large solitary carnivores have been subject to these methods because of the conflicts associated with them (Linnell et al. 1998b) and their hidden lifestyle making them difficult to study (Sollmann et al. 2011). Being active 24 hours a day during the study period, catching every movement in its sector, the

automatic camera traps are, if used correctly, a cost-efficient and precise tool for studying a variety of species.

Humans posing a potential threat to all studied species are thought to modify the animals' activity patterns. Especially during the hunting season human activity should influence the activity patterns of animals, but also throughout the rest of the year. Sönnichsen et al. (2012) reported higher levels of vigilance behavior in roe deer during the hunting season than during the non-hunting season, implying that they modify their behavior as a result of human activity. Also results by Bonnot et al. (2013) indicate a differentiation in habitat use related to predation risk by humans. It is a common assumption that humans are mainly active during the day. In this study I will be able to document the activity patterns of humans accurately for my study area.

In 2010 the Norwegian Institute of Nature research (NINA) placed automatic camera traps in an area in southern Norway to monitor the Eurasian lynx in order to make population estimates or at least to aid and improve the accuracy of population estimates made with traditional monitoring methods (Odden et al. 2011). The area used in this study is a varied multiuse landscape with densely populated areas, rural agricultural areas and forests of varying size and degree of human influence. A study of this magnitude and duration is the only one of its kind in the world and one of few carried out in a boreal forest ecosystem. In this project data on all species of mammals and birds have been registered and processed. This has yielded a large amount of data on several species such as the roe deer, which is the preferred prey for lynx in Norway, and the meso predator the red fox. The red fox is both a prey for lynx, but also a competitor for food (Helldin et al. 2006; Kvam et al. 1998; Linnell et al. 1998a; Odden et al. 2006). In addition also records of human activity have been registered as this might affect animal behavior and activity patterns. Photos of humans and animals taken at different times during the day and night will reflect the activity patterns of the studied species.

In this study I will investigate the activity patterns of animals and humans using these automatic camera traps. I predict that:

P1: Both lynx, fox and roe deer are nocturnal and/or crepuscular, while I expect humans to be diurnal.

Moonlight offering increased illumination should yield favorable hunting conditions for predators such as the lynx and fox. However, the alternative might also occur – that the predators might be more visible enabling detection at longer distances. I predict that:

P2: Due to increased predator success, the lynx and fox are more active, while roe deer is less active on moonlit nights compared to dark nights.

Winter is a tough time for both predators and prey with food restrictions (in particular for roe deer) and high locomotion costs due to movement in snow (Parker et al. 1984). Presence of snow will also increase the vulnerability of roe deer to lynx predation. Therefore I want to test if there is a difference in activity levels between the seasons of summer and winter. I predict that:

P3: a) Lynx and fox are more active during the winter than during the summer.
 b) Roe deer are more active during the summer.
 c) Humans are more active during the summer.

Human installations and activity might affect the activity of animals. Therefore I want to test if there is an effect of the distance from the camera trap locations to the nearest main road on the activity of the animals.

P4: I predict that the lynx avoid main roads because they are associated with human presence, hence I expect there to be more pictures of lynx on cameras that are further from main roads. For roe deer and fox I expect the results to be the opposite.

The different species might prefer different habitats and I want to see if there is any effect of the habitat at the trap site on the number of visits by the different species.

2.0 Materials and methods

2.1 Study area

This study was conducted in two separate study sites in southern Norway (Fig. 1). The eastern study site covers 1850 km² and is located in the counties of Oslo, Akershus and Østfold. The western study site is about 4000 km² and situated in the counties of Vestfold, Buskerud and Telemark. The Oslo fjord divides the two study sites.

The study area is a multi-use landscape with both densely populated and more rural agricultural areas with scattered towns and farms. It is located in the transition between the southern boreal vegetation zone and the boreonemoral vegetation zone (Andersen et al. 2005). Oslo is the biggest city in the study area. The dominating tree species in the area are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and Birch (*Betula Spp.*). The climate is continental with cold winters and hot summers. The annual temperature the last ten years has averaged about 5.3 C° and the mean annual precipitation about 900 mm per year (<http://eklima.met.no>). The temperature in January has in the same period averaged -4.4 C° and in July 16 C° (<http://eklima.met.no>). Snow cover usually lies from December through March and the snow depth in January averages about 33 cm (<http://eklima.met.no>). There is a big difference in light conditions between day and night and this differs a lot between seasons. In January there is usually daylight for about eight hours and in July for about 20 hours. In the eastern study site there were 103 camera trap locations which give a density of one camera per 18 km². In the western study site there were 77 camera trap locations which give a density of one camera trap per 52 km².

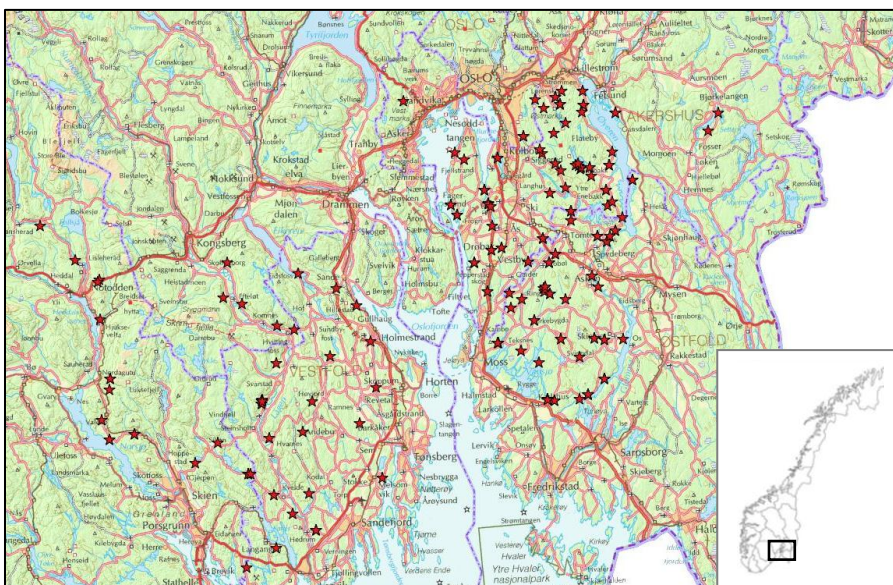


Figure 1. Map of the study area with stars marking the camera trap locations.

2.2 Hunting season

The hunting season for roe deer is divided in two. From the 10th of August until the 25th of September only adult roe deer bucks can be hunted (Klima- og miljødepartementet 2012). The only hunting techniques allowed in this period are stalking and calling. At this time the bucks can easily be distinguished from females and juveniles by their antlers. From the 25th of September until the 23rd of December both sexes, and both juveniles and adults can be hunted. From this date on dogs can also be used during hunting (Klima- og miljødepartementet 2012). The red fox hunt lasts from the 15th of July until the 15th of April (Klima- og miljødepartementet 2012). The most popular ways to hunt fox is by using dogs, bait or by calling. The Lynx hunting season lasts from the 1st of February until the 31st of March (Klima- og miljødepartementet 2012), although as a result of low quotas in many areas the hunt is usually over after a few days. Lynx is almost exclusively hunted by large hunting parties and by the use of dogs.

2.3 Field method

A total of 422 cameras were placed at 180 locations over a period of four years. The camera types used in this study are Cuddeback “Capture” (201 cameras), Reconyx (“HC600 HyperFire High Output Covert IR”, “PC900 HyperFire Professional High Output Covert IR”, “PC800 HyperFire Professional Semi-Covert IR”) in all 154 of these three types, and 21 of the Reconyx “HC850 HyperFire White Flash LED”, Acorn (4 cameras) and Scoutguard (42 cameras). The cameras were set to take a series of three pictures per trigger with one second delay between pictures, but no delay between series. The resolution was set at 3.1 megapixels. The Cuddeback camera and the Reconyx HC850 HyperFire White Flash Led take color pictures both during the day and night (using flash). The rest of the camera types take color pictures during the day and at night they take black and white pictures using an IR-flash.



Collared lynx photographed at night using IR-flash.



Roe deer photographed in daylight.

Being a part of the Scandinavian lynx project (<http://scandlynx.nina.no/>) the cameras were placed at known or suspected passages for lynx. The lynx often follows the same paths as moose, roe deer and other animals and these can be identified in the field (John Odden pers. comm.). The locations were found by NINA personnel and local people who have seen lynx or lynx tracks. Also data on collared lynx were used along with knowledge of preferred habitat among lynx. Most of the cameras were placed in the forest (89%). Some were placed on gravel roads known to be good lynx passages. In order to make lynx stop in front of the cameras to get a good picture of the coat pattern synthetic Lynx urine, catnip-oil, beaver castorium or valerian oil (Snareshop.com) were used to some extent. This is important for making individual recognition possible. The cameras were visited only once a month, and a cloth soaked with lures were put in front of the camera.



Lynx smelling and tasting a cloth with synthetic lynx urine.

Trails were trampled in deep snow and branches and dead trees were placed strategically to make the animals walk in front of the cameras. Vegetation was removed in front of the cameras to get good pictures in order to ease identification of animals caught. Having the area in front of the camera as “clean” as possible also reduces the risk of moving branches and similar objects triggering the camera and draining the batteries. Each camera was protected inside a metal security enclosure which was mounted to a tree and locked. The cameras also had a plastic “roof” in order to protect them from rain and snow. They were placed at a height of 50-90 cm above the ground.

The cameras were checked once a month from the 1st of October to the 1st of April. In this period low temperatures drain the batteries for power faster than in the rest of the year. From the 1st of April the cameras were usually checked every second month until the beginning of October. Each time the cameras were checked the batteries were changed if necessary and all pictures collected. Once collected the pictures were marked with an ID containing the grid

number, date, and number of the specific camera trap location and camera. Photos of people were deleted immediately in compliance with Norwegian privacy protection legislation. The date and time of the visit and numbers of individuals, however, was noted for humans, dogs, and vehicles. One or more animals passing in front of the camera within a five minute interval was defined as one visit. The number of photos kept per visit matches the number of animals passing. This was done to ease the data processing. The Central European Time (CET=UTC+1) was used in all analysis. Data on sunrise/sunset, moonrise/moonset and percentage of the moon disk illuminated was collected from <http://aa.usno.navy.mil/data/>. The seasons were divided by the vernal equinox and the autumnal equinox, being on the 21st of March and the 21st of September respectively for the year 2010 which was used as a reference year. Photos of all species ranging in size from rodents to moose (*Alces alces*) were registered. Sorted photos were uploaded to an online database resulting in a publicly accessible website <http://viltkamera.nina.no> where everyone can follow the project.

2.4 Statistical analysis

All statistical analyses were conducted using R 3.0.2 (R Development Core Team 2013) .

The circadian activity patterns of the three studied species were estimated using generalized additive mixed-effect models (GAMMs) with a Poisson link (gamm function in the R package mgcv) (Wood 2011). As a response variable I used the number of visits (captures with minimum 5 minutes apart), aggregated by hour of the day (0-23) at each location. The predictor variable was hour of the day and location ID as a random effect on the intercept. This was done to account for non-independence of multiple visits at the same location. Comparisons of circadian activity patterns were made using plots of GAMM-predicted relative activity for each species.

I also ran generalized linear mixed models using the number of visits as the response variable (function glmer in package lme4 in R) to test for significance of seasons (summer and winter), time of day (day, night, twilight), distance to roads (continuous variable), habitat (agricultural areas, forests, barren areas, marshes/peats/bogs and fresh water/lakes), sunrise/sunset, moonrise/moonset, and fraction of the moon disk illuminated. For comparisons with fraction of the moon disk illuminated I made two categories, < 50 % illuminated (no moon) and > 50

% illuminated (with moon).

3.0 Results

A total of 64 989 trap nights yielded 20 667 visits. Of these 284 were visits of lynx, 2 877 visits of fox, 3 570 visits of roe deer, 905 of vehicles, and 1 475 of humans. Of the 422 cameras that were used I have complete data from 356 cameras and these are the basis of my analysis. The other cameras were either stolen (2), or data was missing because of camera failure or human error.

3.1 Circadian activity patterns

Roe deer was most active during the morning, having a peak in activity between 04:00 and 08:00, with a smaller but less significant peak during evening (Fig. 2). This is in compliance with my prediction P1, although the general activity level throughout the day was higher than I expected and higher than for lynx and fox. As predicted (P1) the lynx was predominantly crepuscular with two similar peaks of activity from 02:00 to 04:00 and from 18:00 to 20:00 but also with a high nocturnal activity level (Fig. 3). The period of least activity in lynx was from 10:00 to 16:00 (Fig. 3). The fox was mainly nocturnal, being most active from 17:00 to 08:00 (Fig. 4) in compliance with P1. Humans, represented by visits of humans and vehicles, were as predicted in P1 active during the day primarily between 08:00 and 20:00 (Fig. 5 and 6).

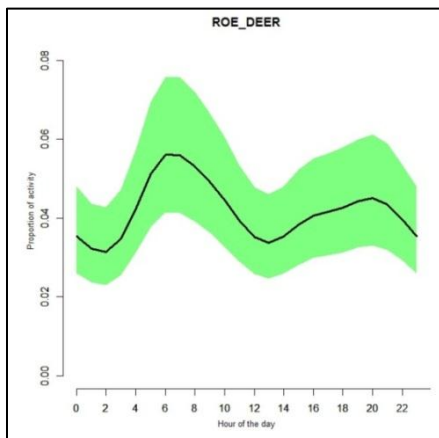


Figure 2. Circadian activity pattern of roe deer.

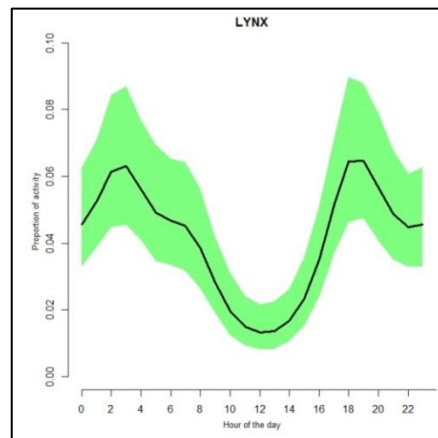


Figure 3. Circadian activity pattern of lynx.

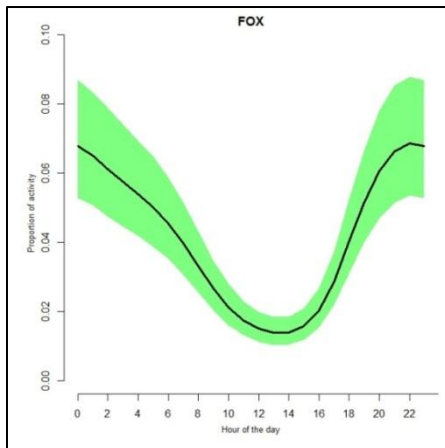


Figure 4. Circadian activity pattern of fox.

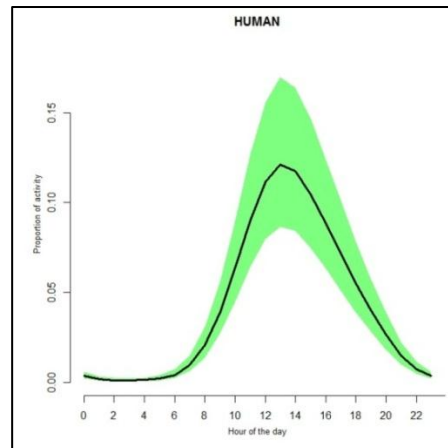


Figure 5. Circadian activity pattern of humans.

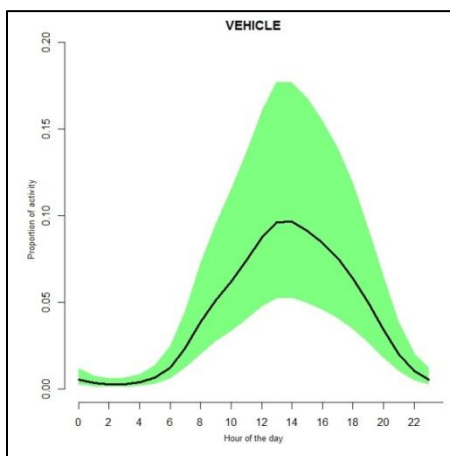


Figure 6. Circadian activity pattern of vehicles.

3.2 Effect of moonlight

The roe deer was more active on nights with moonlight than on nights with little or no moonlight (GLMM; $z = 17.76$, $p < 0.001$) differing from my prediction P2. As predicted for predators (P2) the general activity level of the lynx and fox was higher in nights with moonlight than nights with no moonlight (GLMM; $z = 3.51$, $p < 0.001$) and (GLMM; $z = 11$, $p < 0.001$) respectively, but they did not respond as much as the roe deer.

During winter with moon the fox displayed a crepuscular activity pattern (Fig. 8). The lynx proved to be less active from 15:00 to 21:00 than the average for the rest of the year (Fig. 9). There was little variation in the roe deer's activity throughout the day, but with a slightly higher activity level during early evening and night between 16:00 and 02:00 (Fig. 7).

On winter days with no moon the lynx was less active between midnight and 08:00 than on moonlit nights (Fig. 9). The fox was under the same conditions less active between 00:00 and 07:00 than in winter with moon and the average for the rest of the year (Fig. 8). The roe deer, however, was more active during the day with a peak in activity from 08:00 to 12:00 and a smaller peak from 14:00 to 17:00 (Fig. 7). This activity pattern for roe deer resembles the average for the entire year.

In summer with moon the roe deer showed crepuscular activity patterns, with a period of very low activity at midday (Fig. 7). In summer with no moon it displayed a similar activity pattern as in winter with no moon, but with a displacement in the activity peak which in summer was from 03:00 to 10:00 (Fig. 7). Generally the animals shifted to a nocturnal activity level on nights with moonlight.

Roe deer

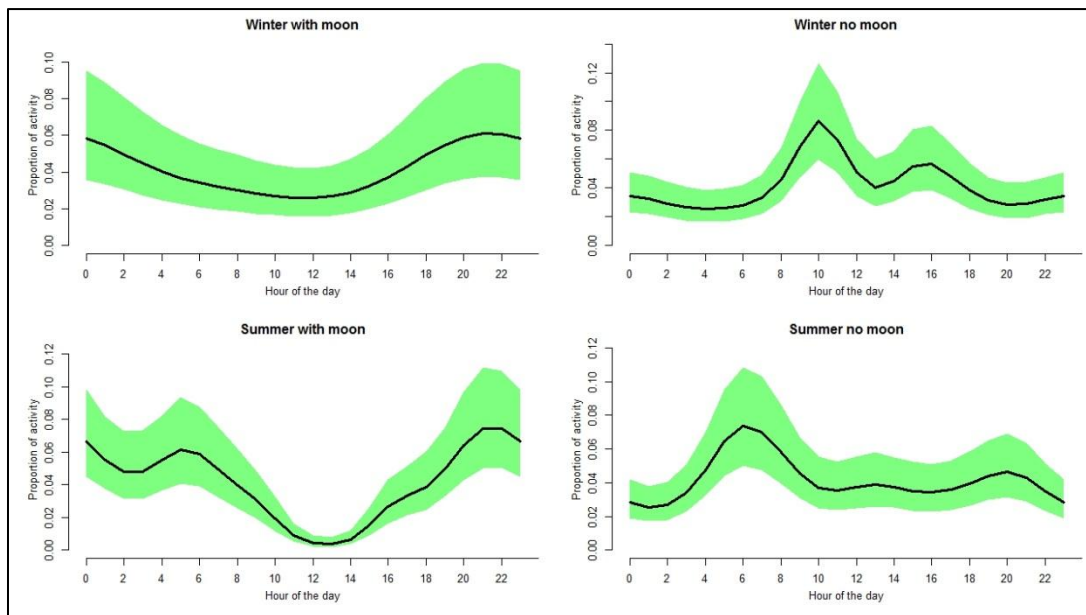


Figure 7. Circadian activity pattern of roe deer at different seasons with and without moonlight.

Fox

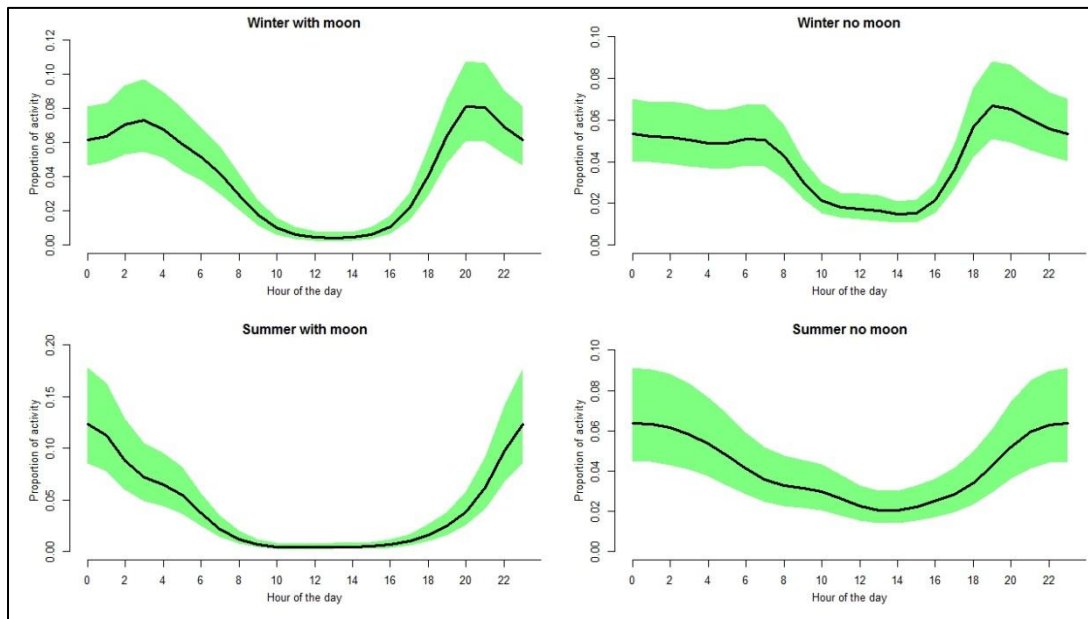


Figure 8. Circadian activity pattern of fox at different seasons with and without moonlight.

Lynx

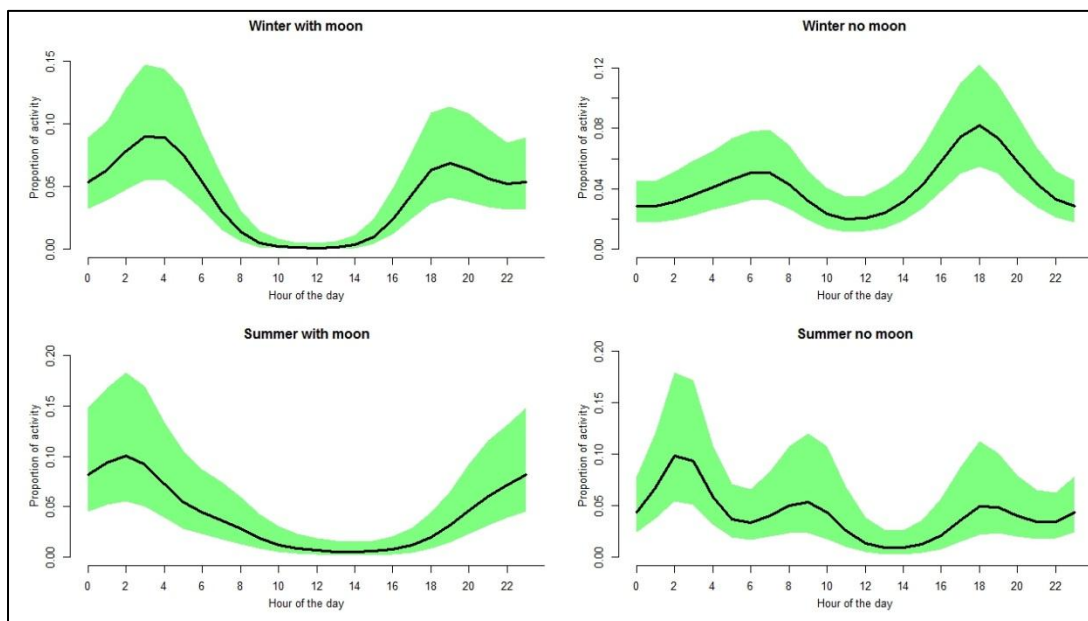


Figure 9. Circadian activity pattern of lynx at different seasons with and without moonlight.

3.3 Seasonal variation in activity patterns

The lynx proved to be more active in winter than in summer (GLMM; $z = -4.5$, $p < 0.001$). For fox the results were similar although marginally non-significant ($p = 0.08$). Both roe deer (GLMM; $z = 13.04$, $p < 0.001$) and humans (GLMM; $z = 3.63$, $p < 0.001$) were more active during the summer than during the winter (all in compliance with prediction P3 a), P3 b) and P3 c). Vehicles, surprisingly, were more frequently photographed during winter (GLMM; $z = -8.73$, $p < 0.001$) opposite of P3 c).

3.4 Effects of roads and habitat

For fox activity there was a negative correlation with distance to roads (GLMM; $z = -3.1$, $p < 0.001$) implying that there were more fox caught on cameras close to roads. There was a strong tendency (GLMM; $z = 1.831$, $p = 0.07$) for humans preferring forest habitats (Fig. 10), which was also the habitat where most cameras were placed. The habitat at the camera trap site did not have any effect on the activity pattern of lynx (GLMM; $z = 0.63$, $p = 0.52$), fox (GLMM; $z = 1.64$, $p = 0.1$) or roe deer (GLMM; $z = -0.43$, $p = 0.66$). Neither was there any significant correlation between the activity of lynx and roe deer and the distance from the camera trap to the nearest main road (GLMM; $z = -0.23$, $p = 0.82$) and (GLMM; $z = -1.05$, $p = 0.3$) respectively. Hereby confirming prediction P4 for lynx, and disproving it for roe deer.

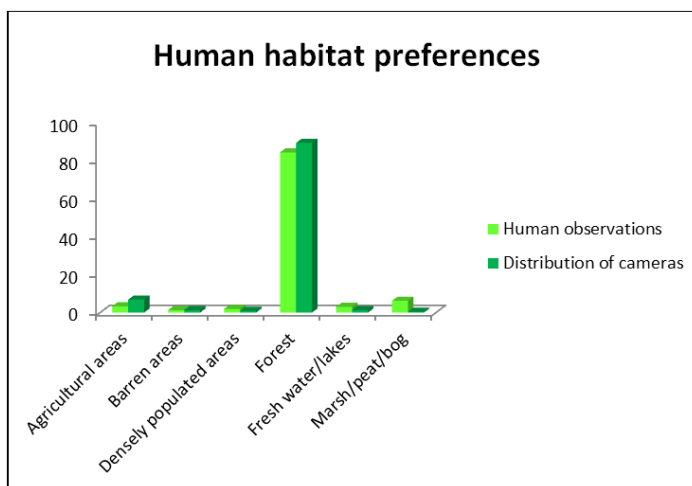


Figure 10. Habitat preferences of humans compared to the distribution of cameras.

4.0 Discussion

Perhaps the most striking result of my research is the fact that the roe deer through changes in activity patterns, showed a greater response to moonlight than the predators. This indicates that it benefits more from high moon illumination than the lynx and fox. My results indicate an avoidance in activity peaks of prey to that of predators, but also a synchronization of predator to prey activity. Human activity seems to play an important role in shaping the activity patterns of animals. My results imply that the fox has learned to benefit from human activity by travelling along roads. My study is one of the first to compare the activity patterns of a complete assemblage of predators and prey in a northern boreal ecosystem.

4.1 Circadian activity patterns

All the studied species of animals displayed crepuscular and nocturnal activity patterns throughout the year, while humans were mainly diurnal. Roe deer maintained a higher activity level during the day than I expected.

The crepuscular and nocturnal activity patterns observed in this study are in compliance with those of previous research for lynx (Kolbe and Squires 2007, Podolski, Belotti et al. 2013), fox (Ables 1969; Weber et al. 1994), and roe deer (Pagon et al. 2013). Basille et al. (2009) found evidence that lynx activity and movement patterns were determined by a trade-off between abundance of prey and the risk following human presence (Basille et al. 2009; Bunnefeld et al. 2006). The lynx and roe deer are both crepuscular, but with displacements in activity peaks. The lynx, being more shy of human activity than the roe deer, might avoid the later hours of the morning when humans are active, explaining the displacement in their activity peaks. My results might indicate a synchronization of lynx activity to that of roe deer. The same pattern was found by Ferguson et al. (1988) who discovered a synchronization in the activity of black-backed jackals (*Canis mesomelas*) to that of its prey. Kolbe and Squires (2007), however, suggested that lynx did not have to synchronize its activity patterns with that of the snowshoe hare (*Lepus americanus*) to hunt efficiently. The roe deer being more active during the day than I expected, might indicate a higher tolerance of human activity and also help them to avoid lynx predation. Another explanation for the crepuscular activity pattern of the lynx is that it might have a higher hunting success during dusk and dawn, with sight being

an important part of its hunting strategy. However, increased visibility may also be a disadvantage for the lynx making it easier for the roe deer to spot it. Being a potential prey for lynx, the red fox is constantly in danger of intraguild predation. My results show that it is active in other parts of the night than the lynx. In this way it can reduce the predation risk. But this might also be due to the fact that the fox has a higher hunting success in dark nights as implied by Penteriani et al. (2013). The fox's nocturnal activity level might also be a strategy to avoid predation by diurnal raptors. The roe deer and lynx are in a classic arms race. To a certain degree the roe deer avoids predation by lynx by having a displacement in activity pattern and by being more tolerant of human activity. The lynx will never achieve a full synchronization with roe deer activity patterns unless it becomes more tolerant of human activity. The lack of synchronization might also be due to reduced hunting success in brighter morning hours. Although benefitting from human activity the roe deer is also hunted by humans and carefully has to balance its activity patterns to that of humans.

The roe deer being crepuscular might be explained by several factors. When feeding the roe deer has to make a trade-off between feeding and looking for predators, and is therefore more vulnerable. Standing up it is easier to see and has left a scent trace travelling to the feeding site which makes it easier for lynx to track it down. Molinari-Jobin et al. (2007) found roe deer to be predated mainly when ruminating, while chamois (*Rupicapra rupicapra*) were predated mostly when feeding. Avoiding the predator in time is one way for prey to reduce predation risk. Especially the lynx, but also the fox, poses a threat to the roe deer all year around. It is therefore likely to assume that they are more important in modifying the behavior of the roe deer all year around than human hunters. On the other hand, there is a much bigger density of human hunters than of lynx and they might therefore have a bigger influence during the hunting season (Herfindal et al. 2005; Theuerkauf & Rouys 2008) as found for African ungulates by Crosmarj et al. (2012). Eriksen et al. (2011) suggested that the synchronization of activity patterns of predator and prey might be ratio dependent, making prey adapt to the most abundant predator. Humans, being a potential predator on all studied species, are associated with danger and human activity in general might modify animal behavior. This might be the cause of the roe deer in my study being crepuscular and not diurnal which would be a good strategy to avoid predation by lynx and fox. During the night it is dark and hard for the roe deer to spot potential predators, hence it is safer to forage during the crepuscular periods with higher visibility. My results indicate that roe deer need a certain amount of light

and visibility to forage as safe as possible. Summing up the roe deer experiences predation pressure from both human and animal predators and is likely most vulnerable when moving and especially while feeding. This plays an important role in shaping its circadian activity pattern.

Although the camera traps are effective in catching animals around the clock they rely on the animals being on the move. Many of them are also placed on tracks and other passages used by the animals when moving from one location to the other. If an animal was to rest in the same place as it forages it might be to a certain degree active and exposed to predation, but not get caught on camera and therefore be considered inactive. It is difficult to conclude on the matter of avoidance vs synchronization of lynx and roe deer activity patterns. There is no way to know if there are real adjustments in activity peaks of one species to that of the other or if it is just a result of the same environmental factors and human disturbance affecting both species, shaping the activity patterns.

4.2 Seasonal variation in activity levels

The roe deer was more active during summer than during winter, for lynx however, the situation was opposite. Although not significant there was a strong tendency towards fox also being more active during winter than in summer.

A possible explanation for this is that the roe deer is more restricted by snow, having a higher locomotion cost when moving in snow than the lynx and fox (Mysterud et al. 1997; Ratikainen et al. 2007). Being a browser, depending on high quality food (Mysterud et al. 1997), it carefully needs to balance its costs and benefits in foraging. Thus it is common to find groups of roe deer frequenting feeding stations during winter (Andersen et al. 2005). These animals would not be caught on camera since they are not placed at feeding stations. Still they could be caught travelling to and from such stations if they were to rest in other areas. The general scarcity of food might be the cause lynx and fox being more active in winter than in summer, needing more time to find and handle prey. The decreased activity of the roe deer might also be the direct cause of the increase in lynx activity, it being a roe deer hunting specialist. These results might also be affected by the rough divide of seasons in my study, encompassing different life history events. All the studied species give birth and rear offspring during spring and summer. This is a period with high activity due to food search and

caring for the young (Kolbe & Squires 2007; Schmidt 1999). The rutting period for roe deer starts in July/August (Østbye 2014) and is a period with increased activity, especially in males. The mating period being in the summer season in my analysis might be the cause of the roe deer having a higher activity level in summer than in winter contrasting the patterns of the other two species, mating during winter. I think that snow conditions are one of the main reasons explaining the differences in seasonal patterns and the mating periods of the animals being another.

4.3 Activity on moonlit nights - shifting to nocturnal activity in nights with moonlight

Contradictory to my predictions the roe deer was more active on nights with moonlight than on dark nights. The predators were also more active in moonlit nights in compliance with my predictions. During both summer and winter with no moon the roe deer showed similar activity patterns as the average for the entire year, being more active during the crepuscular periods than during the night. During both seasons with moon it shifted to a nocturnal activity level.

Both predators were more active in moonlit than in dark nights in compliance with my predictions and results of previous research (Beltrán & Delibes 1994; Penteriani et al. 2011; Penteriani et al. 2013). Moonlit nights offering high illumination should yield favorable hunting conditions for predators such as the lynx using sight as a large part of their hunting strategy (Sundquist & Sundquist 2002). This in turn should make moonlit nights a risky period for prey such as roe deer and fox (Sunde et al. 2000), hereby inducing a shift in activity patterns (Clarke 1983; Penteriani et al. 2013). Moonlight avoidance has been documented in several animals such as rabbits (Kolb 1992; Penteriani et al. 2013), gerbils (Kotler et al. 2010), the banner-tail kangaroo rat (*Dipodomys spectabilis.*) (Lockard & Owings 1974), and the Indian crested porcupine (*Hystrix indica*) (Alkon & Saltz 1988). My results show that roe deer had the most marked changes in activity as a result of moon illumination of all the studied species hereby contradicting these findings. Penteriani et al. (2013) also stated that the moon had a stronger effect on prey than predator. Villafuerte et al. (1993), however, found the activity of rabbits to be positively related to moonlight, while Pagon et al. (2013) failed to find any alteration in activity patterns of roe deer between new and full moon. The nocturnal

activity pattern of the roe deer in both seasons with moonlight might be especially beneficial during the hunting season. Humans, being almost exclusively visual predators are restricted to hunting within the light hours of the day. Moonlight making it safer to forage during the night would mean a decrease in human hunting mortality. For my study it seems as if moonlight makes it easier for roe deer to detect the predator and therefore do not avoid but rather increase their activity in moonlit nights. This indicates that roe deer benefits more from high moon illumination than the lynx and fox.

The fox in my study displayed a crepuscular activity pattern in winter with moon. For the intra-guild predator the fox (Linnell et al. 1998a) activity in moonlight will be a trade-off between exploiting the improved hunting conditions and avoiding encounters with lynx as shown by Mukherjee et al. (2009) and Penteriani et al. (2013). Ferguson et al. (1988) who studied black-backed jackals suggested that it was easy for prey to detect the jackals during full moon, causing a decrease in hunting efficiency, making the jackals inactive at the brightest moon phases. They also suggested that a reduced activity level in medium-size predators could be a mechanism to avoid encounters with larger predators (Ferguson et al. 1988) as did Emmons et al. (1989). This might help to explain the activity pattern of the fox in my study. Also results by Penteriani et al. (2013) showed that fox avoided nights with bright moonlight, both because the conditions for rabbit hunting were better in dark nights and to avoid encounters with lynx. My results indicate that the fox avoids the lynx, but also that its own hunting success on prey is lower during bright moonlight, thus confirming a trade-off between foraging and predation risk.

Even at northern latitudes heat stress may influence the diurnal activity patterns of animals (van Beest & Milner 2013). The decrease in activity in roe deer at midday during summer in my study might be due to high temperatures, as shown for Iberian lynx by Beltrán and Delibes (1994). They suggested that especially adult lynx are less affected by low temperatures, but more sensitive to high summer temperatures (Beltrán & Delibes 1994). This would also help to explain the lack of decrease in crepuscular activity for roe deer during winter with moon in my study.

4.4. More fox in the vicinity of main roads

In my study more fox were caught on the camera traps that were close to roads. Fox are generalist predators and have adapted to life near humans. They have learned to take advantage of the benefits following human activity and settlements. It is likely to assume that the fox benefits from travelling along roads both due to reduced energetic costs, especially in winter, and the chance of finding easily accessible food. Travelling along roads might also help it avoid predation from lynx, which is thought to be shy of humans.

5.0 Conclusions

My results show that circadian activity patterns of animals can be investigated easily and cost-effective by using automatic camera traps. Results indicate both avoidance and synchronicity in activity peaks of the studied species of predators and prey. All the studied species also preferred to be active on moonlit nights, but prey showed the greatest response to the change in conditions following the moonlight. In addition to these factors I have also found seasonal variation in activity and I believe that human activity in this multi-use landscape plays an important part in shaping animal activity patterns. Being to my knowledge the first of its kind to document activity patterns and effects of moonlight in a northern boreal forest ecosystem using camera traps, this study is unique. Although I have investigated several interesting connections between circadian activity patterns and other factors, there are still many interesting questions to be addressed. Investigating the sequence and temporal delays between predator and prey species captured by the same camera traps would be particularly interesting. In the future the focus of the camera trap studies needs to be not only on rare exotic species, but also on the more “common” animals of our fauna. This kind of data can be used to shed light on ecological mechanisms acting in systems with several species.

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