FACHHOCHSCHULE BINGEN
University of Applied Sciences

Department 1 - Life Sciences and Engineering

Bachelor Programme Environmental Protection

Analysis of activity patterns of the Eurasian lynx (*Lynx lynx*) and its prey

Bachelor Thesis

submitted 25.08.2014

of

Reusch, Christopher

195497

carried out at Bavarian Forest National Park Administration

Analysis of activity patterns of the Eurasian lynx (*Lynx lynx*) and its prey

Author:	Christopher Reusch Fachhochschule Bingen Berlinstraße 109 55411 Bingen am Rhein Germany
Supervisors:	Frau Prof. Dr. Hietel (Fachhochschule Bingen), Dr. Marco Heurich (Bavarian Forest National Park Administration)
Commissioned by:	Bavarian Forest National Park Administration

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Abschlussarbeit "Analysis of activity patterns of the eurasian lynx (*Lynx lynx*) and its prey" selbstständig und ohne fremde Hilfe angefertigt habe. Ich habe dabei nur die in der Arbeit angegebenen Quellen und Hilfsmittel benutzt. Die Arbeit wurde in gleicher oder ähnlicher Form noch keiner anderen Prüfung vorgelegt und auch noch nicht veröffentlicht.

Spiegelau, den Christopher Reusch

Arbeit eingereicht am:
Arbeit angenommen am:
durch:

Bingen, den: .....
(Prof. Dr. Elke Hietel)

Betreuer: Frau Prof. Dr. Hietel (Fachhochschule Bingen) ,
Dr. Marco Heurich (Bavarian Forest National Park Administration)

Abstract

Activity patterns of animals are developed and stabilized as a part of evolution, but in addition they need to be adjusted, to respond to current environmental challenges. It has been suggested that the activity pattern of feline predators synchronised with their prey. In Europe the most important prey for the Eurasian lynx (*Lynx lynx*) is roe deer (*Capreolus capreolus*), closely followed by red deer (*Cervus elaphus*). In this study the activity patterns of Eurasian lynx, roe deer and red deer were observed and tested for a possible relationship towards each other in the Bavarian Forest National Park, Germany. Furthermore, the effect of moonlight on the activity of the Eurasian lynx and its prey was tested. Data was collected using GPS-GSM collars from VECTRONIC. The following hypothesis about lynx activity are tested:(1) The activity pattern of the Eurasian lynx follows the activity pattern of roe deer more strongly than the activity pattern of red deer. (2) The activity pattern of the Eurasian lynx increases with increasing brightness during the night. Lynx, roe deer and red deer showed a mainly crepuscular activity pattern with peaks at dawn and dusk, coinciding with seasonal variation in twilight times. Lynx activity was higher at dusk than at dawn throughout the year. Prey activity was highest in summer, while lowest activities were found during winter and autumn. Lynx, roe deer and red deer were more active during bright nights than during dark nights, perhaps indicating that lynx are more active because prey is more easily detected when active. The results of this study indicate that the main prey and brightness during the night affect lynx activity. The results in this study support the hypothesis, that lynx follow roe deer activity more strongly than red deer activity.

Contents

1 Introduction **1**

2 Material and methods **4**

2.1 Study area 4

2.2 Animal trapping 4

2.3 Data recording 5

2.4 Data preparation 6

2.5 Data analysis 7

2.5.1 Descriptive analysis 7

2.5.2 Modelling approach 7

3 Results **9**

3.1 Activity patterns 9

3.2 Modelling approach 10

4 Discussion **14**

5 Acknowledgements **19**

References **20**

Appendix A Overlap **26**

Appendix B Output of models M9, M10 and M11 **27**

List of Figures

1 Average circadian activity pattern per season and in total for lynx, roe deer and red deer, neglecting the individual. Mean activity was calculated per hour after the z-transformation and therefore does not represent absolute values. Mean twilight times (beginning of dawn/dusk until end of dawn/dusk) are indicated by grey bars and show a shift throughout the year. 9

2 Lynx activity in relation to snow height in cm. The solid line shows the predicted values for lynx activity at a certain snow height. Dashed lines indicate standard errors. Small lines along the x-axis show observed snow heights. 11

3 Lynx activity in relation to temperature in °C. The solid line shows the predicted values for lynx activity at a certain temperature. Dashed lines indicate standard errors. The small lines along the x-axis show observed temperatures. 11

4 Roe deer activity in relation to snow height in cm. The solid line shows the predicted values for roe deer activity at a certain snow height. Dashed lines indicate standard errors. Small lines along the x-axis show observed snow heights. 12

5 Roe deer activity in relation to temperature in °C. The solid line shows the predicted values for roe deer activity at a certain temperature. Dashed lines indicate standard errors. The small lines along the x-axis show observed temperatures. 12

6 Red deer activity in relation to snow height. The solid line shows the predicted values for red deer activity at a certain snow height. Dashed lines indicate standard errors. Small lines along the x-axis show observed snow heights. . . 12

7 Red deer activity in relation to temperature in °C. The solid line shows the predicted values for red deer activity at a certain temperature. Dashed lines indicate standard errors. The small lines along the x-axis show observed temperatures. 12

8 Overlap of circadian activity pattern per season and in total for lynx (black lines), roe deer (blue lines) and red deer (red lines). 26

List of Tables

1 Details and study periods of all nine collared lynx individuals 5

2 Variables that were used in models with respective scale, value range and description 6

3 Summary of GAMs calculated. Dependent variables varied between lynx, red and roe deer. Independent variables: roe; red; daytime; bright; season; s(snow) and s(temp) were added as smoothing splines; moon; cloud; s(id,bs=re) was added as random effect for the individuals of the dependent variable. N represents the number of observations per model. 8

4 Output of models M1- M6, with lynx as dependent variable. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 13

5 Output of model M7, with roe deer as dependent variable. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 13

6 Output of model M8, with red deer as dependent variable. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 13

7 Output of model M9 to M11. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. daytime:moon is not listed in this table (P > 0.05) 27

1 Introduction

Activity patterns of animals are developed and stabilized as a part of evolution (Lima and Dill, 1990), but in addition they need to be adjusted, to respond to current environmental challenges (e.g. increase in predator presence) (Monterroso et al., 2013). The activity of an animal can be affected by several abiotic factors, such as light and temperature, as well as biotic factors like prey acquisition and predator avoidance (Lucherini et al., 2009; Manfredi et al., 2011).

Although predators have a strong impact on the behaviour of their prey, predator-prey dynamics are not only regulated by the preys' strategies to avoid predators, but also by the predators' hunting abilities (Harmsen et al., 2010). The hypothesis that predators adjust their activity pattern according to their main prey is universally accepted (Schmidt et al., 2008; Pereira, 2010; Kolbe and Squires, 2007). For example Harmsen et. al (2010) state that predators and preys activity patterns match in times when the preys' vulnerability is at its highest (Manfredi et al., 2011; Theuerkauf et al., 2003). Predators that travel long distances and have an opportunistic feeding behaviour, adapt their activity patterns to the local prey available (Harmsen et al., 2010). According to Palomares and Delibes (1992) the circadian activity of carnivores is controlled by instinct, as well as by abiotic (e.g. daytime, season) and biotic (e.g. activity of its prey) factors. Eriksen et al. (2011) hypothesized that matching activities of wolf (*Canis lupus*) and moose (*Alces alces*) during summer can occur as an adjustment of predator to prey. They further suggested, that this synchronisation can also be a response to high temperatures during summer.

Hunting techniques of animals can be divided into ambush and cursorial predators. Cats are mainly ambush predators which attack from short distances and do not distinguish between age classes. Cursorial predators like wolves pursue their prey over long distances, which is why they choose mainly weak individuals, such as juveniles and senescent adults (Wilmers et al., 2007). While hunting, the Eurasian lynx (*Lynx lynx*) for example is mainly depending on his sense of hearing and his visual perception (Breitenmoser and Breitenmoser-Würsten, 2008), wherefore his hunting success is dependent on the activity of his prey (Harmsen et al., 2010). The activity of some cat species (e.g. Geoffroy's cat (*Leopardus geoffroyi*) and Irimore cat (*Prionailurus iriomotensis*)) is mostly concentrated during twilight and night times (Schmidt et al., 2008; Pereira, 2010). Emmons (1987) says that circadian activity of felid predators is synchronised with their prey. The activity of the Iberian lynx (*Lynx pardinus*) is mainly crepuscular and nocturnal (Penteriani et al., 2013), although their pattern varies considerably between individuals (e.g. age, season, habitat) (Beltrán and Delibes, 1994). The Canadian lynx (*Lynx canadensis*) has a higher activity in the afternoon and early evening during winter months (Kolbe and Squires, 2007). According to Schmidt (1999) the Eurasian lynx is active mostly during the night. The highest

activity of the Eurasian lynx can be observed during the first half of the night, which is mainly for hunting and eating purposes. Another activity peak appears during early morning (Breitenmoser and Breitenmoser-Würsten, 2008).

Prey is affected directly and indirectly by predators. Indirect effects on prey are for example increased vigilance and the avoidance of areas. The risk allocation hypothesis says that prey needs to consider how much time is spend on predator avoidance and activities like foraging. This might cause prey to respond less to a continuously high risk, than a risk that is more intense but less often (Lima and Bednekoff, 1999). In addition, the risky places hypothesis presumes that in an environment where risk is predictable prey might respond by avoiding times or areas with a higher risk (Lima and Dill, 1990). In order to reduce the chance of being killed behavioural changes of prey can occur, such as activity shifts to times with a lower risk of predation (Cromsigt et al., 2013), as well as omitting foraging and reproduction (Bednekoff, 2006; Lima and Dill, 1990; Harmsen et al., 2010). Another response to a high predation risk is that animals tend to increase refuging or reduce activity when away from shelter (Lima, 1998). Activity shifts to times with a lower risk can also happen after an increase in predator presence (e.g. voles changed their activity pattern to avoid weasels) (Eccard et al., 2008). It is also possible, that the animals decision to forage at a certain time is based on the ability to better recognise potential attacks of predators in connection with the light level (Lima and Dill, 1990). However, the possibility to respond to predation risk with a reduced activity may not be given in times of food shortage (Cromsigt et al., 2013).

Krop-Benesch et al. (2013) state that European roe deer (*Capreolus capreolus*) is crepuscular, while peaks at dawn and dusk vary with season (Stache et al., 2013; Cederlund, 1989; Georgii, 1981).The development of a third, smaller peak before midnight was discovered by Stache et al. (2013) between December and February. Red deer (*Cervus elaphus*) show a bimodal activity pattern with peaks at dawn and dusk, whereas these peaks are less pronounced during summer, due to more evenly distributed activity as days are longer and therefore light availability higher (Georgii, 1981). Because of their digestive system, ruminants (e.g. roe deer, red deer) have an ultradian rhythm to provide a continuous supply of nutrients through regular feeding bouts (Stache et al., 2013; Krop-Benesch et al., 2013; Cederlund, 1989).

Beside the effects predator and prey have on each other, environmental conditions like light availability affect activity patterns of animals (Lucherini et al., 2009). Moonlight for example affects predator and prey alike (Penteriani et al., 2013), by increasing detectability for both (Lucherini et al., 2009) and can have a strong impact on hunting success of predators (Rockhill et al., 2013). Rockhill et al. (2013) concluded that prey lower their activity during bright nights to avoid predation (e.g. rabbits (Penteriani et al., 2013)) , while predators may be more active due to higher hunting efforts (Manfredi et al., 2011). Harmsen et al. (2010) state that cats benefit from increased brightness during night hours with improved visibility,

while their prey is more exposed and thus more vulnerable. However, African ungulates (e.g. greater kudu (*Tragela- phus strepsiceros*), oryx (*Oryxgazella gazella*)) displayed increased activity during a full moon (Wronski et al., 2006). A study in Central America discovered that armadillos (*Dasypus novemcinctus*) and pacas (*Agouti paca*) lowered their activity in order to reduce predation risk. Jaguar (*Panthera onca*) responded to the decrease of prey activity likewise with a lower activity, while puma (*Puma concolor*) did not respond to brighter moonlight (Harmsen et al., 2010). In Spain rabbit (*Oryctolagus cuniculus*) and Iberian lynx were observed to react to bright nights with an increased activity (Penteriani et al., 2013).

Further environmental conditions such as temperature and snow are thought to influence the activity of animals (Stache et al., 2013). Lynx are well adapted to high snow conditions (O'Donoghue et al., 1998), due to the long legs, as well as the big furry paws (Breitenmoser and Breitenmoser-Würsten, 2008). Canada lynx were less active during high temperatures in summer, while in winter activity increased in the evening, when ambient temperatures were high compared to the morning (Kolbe and Squires, 2007). Cervids, such as roe deer are considered to be at a disadvantage at snow depths greater than 50 cm (Mysterud et al., 1997; Cederlund, 1989), due to decreased food availability and mobility (Cagnacci et al., 2011) and often respond with reduced activity (Cederlund et al., 1989; Beier and McCullough, 1990). Deer migration was connected to freezing temperatures and (particularly in mountainous areas) increasing snow depths (Beier and McCullough, 1990).

In Europe the most important prey for the Eurasian lynx is roe deer (Heurich et al., 2012; Herfindal et al., 2005;Jedrzejewski et al., 1993), closely followed by red deer (Breitenmoser and Breitenmoser-Würsten, 2008; Okarma et al., 1997). In the Bohemian Forest the Eurasian lynx was reintroduced in the 1980's (Wölfl et al., 2001). The lynx faces a lack of acceptance from supporters of ungulate hunting and animal husbandry. To gain approval from the local population towards the lynx and thus improve its protection, a better understanding of the relationship between lynx, roe deer and red deer is needed (Heurich et al., 2011).
Within the compass of this thesis the dependencies of the activity pattern of the Eurasian lynx were tested. Due to the preference of the Eurasian lynx for roe deer the first hypothesis investigates the relationship between lynx, roe deer and red deer:
(1) The activity pattern of the Eurasian lynx follows the activity pattern of roe deer more strongly than the activity pattern of red deer.
Due to the increased hunting effort for predators in bright nights the second hypothesis is:
(2) The activity pattern of the Eurasian lynx increases with increasing brightness during the night.
This is the first study to examine the relationship between activity patterns of Eurasian lynx, roe deer and red deer as well as the dependencies.

2 Material and methods

2.1 Study area

The study took place in the Bavarian Forest National Park in the south-east of Germany. The national park is located in the inner Bavarian Forest, about 150 km east of Munich (49°3'19"N, 16°12'9"E), at the border of the Czech Republic. The park covers an area of 244 km^2 and is connected to the adjacent Šumava National Park which covers 685 km^2. Together they form the Bohemian Forest, the largest strictly protected forested area in Central Europe (Stache et al., 2013). The region is sub-mountainous and altitude ranges between 650 m above sea level (a.s.l.) in the West and 1420 m a.s.l. in the East. The mean annual temperature varies between 3.8 and 5.1°C; the precipitation is between 1200 mm and 1800 mm (Bässler et al., 2009). A pronounced amount of the precipitation occurs as snow. Snow cover lasts from seven to eight month at higher elevation and from five to six months in valleys. 98% of the Bavarian Forest National Park is covered by forest, which can be divided in three major types:
1) Sub alpine spruce forest occurs above 1100 m with mainly Norway spruce (*Picea abies*) and occasionally mountain ash (*Sorbus aucuparia*) (16% of the area); 2) Mixed montane forest between 600 and 1100 m can be found on 68% of the area. Vegetation is formed by Norway spruce, white fir (*Abies alba*), European beech (*Fagus sylvatica*) and sycamore maple (*Acer pseudoplatanus*); 3) 16% of the area are covered by spruce forests, which are found in the valley bottoms where wet depressions often occur due to cold air pockets. Abundant tree species are Norway spruce, mountain ash and birches (*Betula pendula, Betula pubescens*) (Heurich and Neufanger, 2005).

2.2 Animal trapping

Study animals needed to be trapped prior to being collared. Lynx can be either trapped at game passes or at fresh kills, which they visit repeatedly for several days. This was accomplished by using foot snares or anaesthetized darts at fresh kills or box traps at game passes. After securely trapping the animal it was immobilized using the "Hellabrunner Mixture" with a blowgun (Heurich, 2011). Roe deer were exclusively trapped with box traps between October and March (month with snow cover). They were lured into the traps with bait, such as maize and marc. Once the animal was trapped it was immobilized by binding its legs and blindfolding it, to reduce stress (Weilnböck et al., 2012). To capture red deer, two methods were used: corrals and shooting darts with anaesthetics. To get the animals into the corrals, they were lured via food as bait. Once they were in the corral they were separated in smaller sections in which the collars could be put on. For the second method animals were attracted with food to a certain area for several days. After that they were immobilized with "Hellabrunner Mixture" by shooting darts (Heurich, 2011). The handling

protocol has been approved by the Ethics Committee of the Government of Upper Bavaria and fulfils their ethical requirements for research on wild animals. In addition, permits for wild animal capture were obtained from the Government of Lower Bavaria.

2.3 Data recording

The data were recorded with GPS-GSM collars from VECTRONIC Aerospace (GPS plus mini, Berlin, Germany) by the Bavarian Forest National Park. The collars used are especially made for each species to ensure that they fit exactly. The weight of the collar varies between species: lynx 300 g (1.5% of total weight); roe deer 450 g (1.8% of total weight); red deer 750 g (1.2% (female)/ 0.8% (male) of total weight) (Heurich, 2011). The activity is measured via a dual-axis acceleration sensor. The x-sensor records movement which is directed back and forth, whereas the y-sensor records left and right movements. Activity is measured every eight seconds simultaneously on both sensors and is stored as an average of five minute intervals. The values range from 0 (no activity) to 255 (high activity) (Löttker et al., 2009).

In total nine collared lynx were monitored from 2005-03-07 to 2013-02-28. A total of 1,017,147 observations (five minute intervals) were acquired, which equals 3,525 days. Six of the lynx were male and three were female, whereas the sex was not taken into account in this study. The lynx Matilda and Milan were recaptured and collared a second time (Table 1). In addition, data from 127 roe deer (72 male/ 55 female) was obtained, with 11,521,761 observations, between 2004-11-08 and 2012-09-18, covering a total amount of 40,545 days of observation. Red deer data were collected from 2002-03-13 to 2012-05-01, with a total of 4,418,338 observations (15,652 days) for 42 individuals (20 male/ 22 female).

Table 1: Details and study periods of all nine collared lynx individuals

Lynx	Sex	Period collared	Number of observations	Number of days
Ctirad	male	2011-01-15 - 2012-05-19	137,191	491
Emanuel	male	2010-03-29 - 2010-05-18	15,062	51
Kika	male	2011-03-22 - 2012-10-23	165,136	582
Kubicka	female	2010-03-17 - 2011-02-06	97,260	327
Matilda	female	2010-03-17 - 2011-03-02	220,573	762
		2011-03-02 - 2012-04-16		
Milan	male	2005-03-07 - 2005-07-25	67,901	243
		2005-11-10 - 2006-02-19		
Nimo	male	2012-03-13 - 2013-02-28	105,839	353
Patrik	male	2010-03-16 - 2011-02-16	101,193	338
Tessa	female	2011-02-27 - 2012-03-10	106,992	378
Total		2005-03-07 - 2013-02-28	1,017,147	3,525

Mean daily temperature in °C and snow height in cm were recorded at a meteorological station in Germany (Waldhäuser). Cloud cover, on a scale from 0 to eight was obtained from the nearest weather station "Großer Arber" (Deutscher Wetterdienst (www.dwd.de), 49°06'36.0"N 13°08'24.0"E) from 2002 to 2013 (0=sky completely clear, 8=sky completely cloudy). The percentage of the moon illumination was received from the Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil), from 2002 to 2013 (0=new moon, 1=full moon). Seasons were defined as spring (Mar- May), summer (Jun- Aug), autumn (Sep- Nov) and winter (Dec- Feb). Times of sunrise sunset and nautical twilight (NT), defined as -12° below horizon, were calculated with the statistic software "R".

2.4 Data preparation

Acceleration measurements can differ between individuals due to variation in collar circumference which is influenced by the animals neck, thickness of fur and the fluctuation of sensitivity of the activity sensor. To ensure that data collected by each individual are comparable with each other, a z-transformation was performed (Krop-Benesch et al., 2013). Since the goal of this study was to obtain knowledge on changes in activity, absolute values were not essential. Prior to the transformation, the activity values from both sensors were combined to one variable (act_x + act_y = act_xy), on which all activity calculations were based. Then act_xy was z-transformed separately for each individual, using the following equation:

$$(1)\ Z_i = \frac{X_i - \bar{X}}{S}$$

whereas X_i is the original value, $\bar{X}$ the mean of an individuals activity and S the standard deviation of an individuals activity (Krop-Benesch et al., 2013).

For the dependent variable hourly means of the transformed values were calculated separately for each individual . With this procedure, the effect of each individual can be taken into account. For the independent variable, hourly means of the transformed values were calculated neglecting the individual. For the variable "daytime" 4 categories were defined: dawn (nautical twilight (NT) morning- sunrise), day (sunrise- sunset), dusk (sunset- NT) and night (NT- NT). The study area is often affected by cloud cover, which can alter the effect of a full moon during maximum cloud cover. A variable "bright" was created taking cloud cover and percentage of moon illumination into account:

$$(2)\ bright = moon * \left(1 - \frac{cloud}{8}\right)$$

For better interpretation cloud was reversed by dividing it by eight so that 0 equals no brightness and one full brightness (Table 2).

Table 2: Variables that were used in models with respective scale, value range and description

Variable	Scale	Value range (from; to)	Description
Lynx	Continuous		Hourly means of z-transformed activity
roe	Continuous		Hourly means of z-transformed activity
red	Continuous		Hourly means of z-transformed activity
daytime	Categorical	dawn; day; dusk; night	dawn (NT morning- sunrise); day (sunrise- sunset); dusk (sunset- NT); night (NT- NT)
season	Categorical	spring; summer; autumn; winter	spring (Mar- May; summer (Jun- Aug); autumn (Sep- Nov); winter (Dec- Feb)
temp	Continuous	(-16.2; 25.9)	Mean air temperature per day (°C)
snow	Continuous	(0; 191)	Mean snowheight per day (cm)
moon	Continuous	(0; 1)	Percentage of the moon illuminated (%); 0= new moon, 1= full moon
cloud	Continuous	(0; 8)	0= sky completely clear; 8= sky completely cloudy
bright	Continuous	(0; 1)	0= dark; 1= full brightness $bright = moon * \left(1 - \frac{cloud}{8}\right)$
id	Categorical	(1; 9)	Name of the lynx individual

2.5 Data analysis

2.5.1 Descriptive analysis

Hourly means of the z transformed values from lynx, red and roe deer were calculated and plotted to distinguish patterns in daily activity (Podolski et al., 2013). Additional plots, both to identify seasonal and monthly patterns were produced.

Overlap

To quantify the relationship between activity patterns of lynx and roe deer/ red deer an overlap was performed. The "coefficient of overlapping" was used, which gives a value between 0 (no overlap) and one (complete overlap) and represents the area under the curve (Linkie and Ridout, 2011). Since data from acceleration sensors were used rather than data from camera traps, the measurements were standardised prior to the overlap. The following steps were performed for each species separately (lynx, roe deer, red deer): first a generalized additive model (GAM) was calculated with the activity as dependent variable. The independent variables were minute of the day as cyclic spline and the individual as random effect. After that the function "predict" was used to predict the activity per minute of the day, based on the previously calculated model. The predicted activities were then standardised:

$$(3) \quad \left(\frac{activity_i}{\sum_{i=1}^{z} activity} \right) \quad z = 1440 \ (minutes \ per \ day)$$

2.5.2 Modelling approach

In order to determine the dependencies of the lynx activity pattern a generalized additive model (GAM) was applied. The analysis contained lynx as dependent variable, roe and red deer as independent continuous measurement, temperature and snow as smooths, season and daytime as categorical variables, bright as explanatory variable, as well as in interaction with daytime and lynx identity as random effect.

Multicollinearity

To test whether multicollinearity (MCL) occurred between daytime and both, roe deer and red deer activity, models with lynx as dependent variable were fitted. MCL was tested individually for roe and red deer, by comparison of a full fit model containing all variables with models where daytime and red deer/ roe deer were omitted respectively (M2- M6: Table 3). All analyses and calculations were performed using the statistic software R (Version 3.1.0, www.r-project.org). Model calculations were carried out with GAMs with the package MGCV (Version 1.8-0) (Wood, 2006). Due to the large data set models were fit with the 'bam' function (Ratcliffe et al., 2014). Because of the small number of lynx and thus a weak effect of gender specific activity patterns, sex was not taken into account (Krop-Benesch et al., 2013).

Table 3: Summary of GAMs calculated. Dependent variables varied between lynx, red and roe deer. Independent variables: roe; red; daytime; bright; season; s(snow) and s(temp) were added as smoothing splines; moon; cloud; s(id,bs=re) was added as random effect for the individuals of the dependent variable. N represents the number of observations per model.

Model	Dependent	roe	red	daytime	bright	bright: daytime	season	s(snow)	s(temp)	moon	cloud	moon: cloud	moon: daytime	cloud: daytime	s(id,bs=re)	N
M1	lynx	⊠	⊠	⊠	⊠	⊠	⊠	⊠	⊠	□	□	□	□	□	⊠	72,124
M2	lynx	⊠	□	⊠	⊠	⊠	⊠	⊠	⊠	□	□	□	□	□	⊠	79,276
M3	lynx	⊠	□	□	⊠	□	⊠	⊠	⊠	□	□	□	□	□	⊠	79,276
M4	lynx	□	⊠	⊠	⊠	⊠	⊠	⊠	⊠	□	□	□	□	□	⊠	72,195
M5	lynx	□	⊠	□	⊠	□	⊠	⊠	⊠	□	□	□	□	□	⊠	72,195
M6	lynx	□	□	⊠	⊠	⊠	⊠	⊠	⊠	□	□	□	□	□	⊠	84,100
M7	roe	□	□	⊠	⊠	⊠	⊠	⊠	⊠	□	□	□	□	□	⊠	960,909
M8	red	□	□	⊠	⊠	⊠	⊠	⊠	⊠	□	□	□	□	□	⊠	372,425
M9	lynx	⊠	⊠	⊠	□	□	⊠	⊠	⊠	⊠	⊠	⊠	⊠	⊠	⊠	72,124
M10	lynx	⊠	⊠	⊠	□	□	⊠	⊠	⊠	⊠	□	□	⊠	□	⊠	72,124
M11	lynx	⊠	⊠	⊠	□	□	⊠	⊠	⊠	□	⊠	□	□	⊠	⊠	72,124

* reference categories: daytime= ”day”; season= ”summer”

3 Results

3.1 Activity patterns

Since the activity patterns of all nine lynx individuals were similar, the individual was not taken into account in the descriptive analysis. The general pattern was crepuscular. Activity values dropped to intermediate levels during the night and were lowest at midday. Highest activity levels were observed (in the evening) at or shortly after dusk, between 5 and 7 pm. In the morning, activity values peaked just before or at dawn around 4 am. Activity peaks varied between seasons, showing a co-occurrence with twilight throughout the year (Figure 1). In each season as well as in the total activity the morning peak was less distinct than the evening peak. However, the difference between the two peaks was most obvious in winter. The overall activity pattern of roe deer was crepuscular. Activity peaks were found during dusk and dawn and changed with season. From spring to autumn most activity was concentrated during twilight times, whereas in winter a third peak during midday and a fourth more distinctive peak during the night was found. Red deer had a crepuscular activity pattern, although it showed signs of nocturnality. The highest activity was located at dusk, while a second (lower) peak was found at dawn. During the night medium activity levels were observed, while just after dawn and at midday activity reached its minimum. Activity peaks varied in accordance with seasonal changes of dusk and dawn. In winter the morning peak was almost absent.

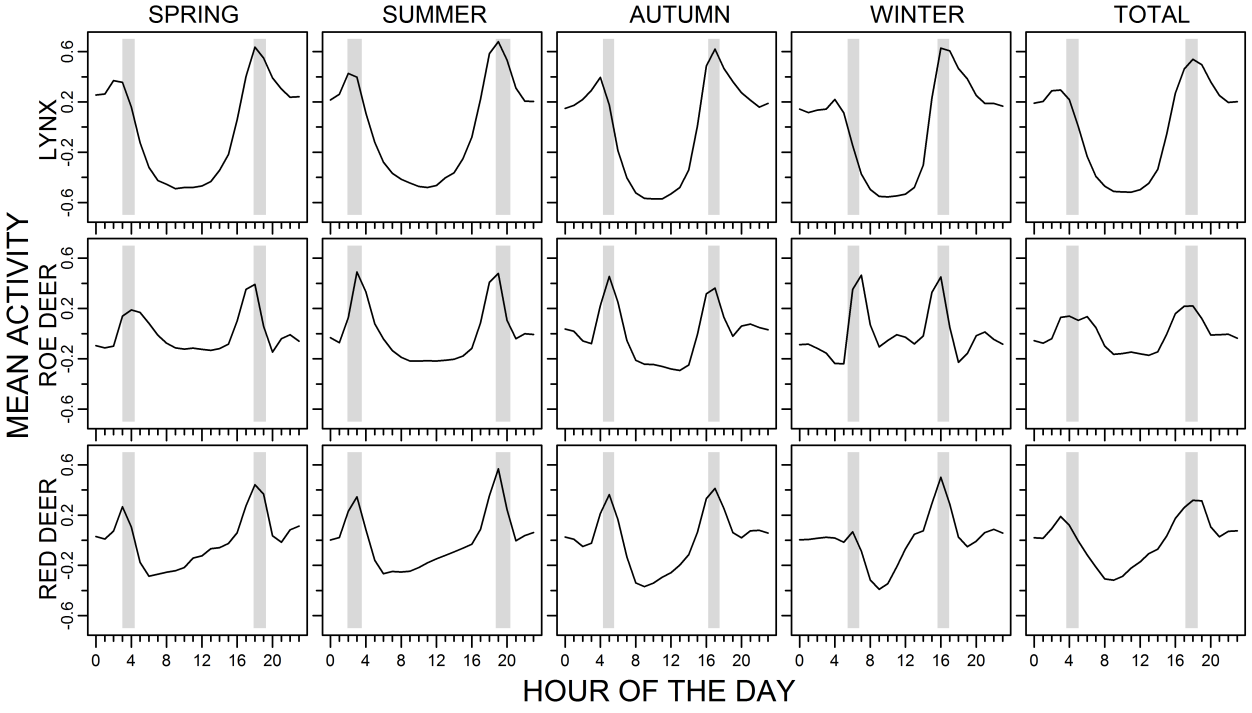

Figure 1: Average circadian activity pattern per season and in total for lynx, roe deer and red deer, neglecting the individual. Mean activity was calculated per hour after the z-transformation and therefore does not represent absolute values. Mean twilight times (beginning of dawn/dusk until end of dawn/dusk) are indicated by grey bars and show a shift throughout the year.

Overlap between lynx and roe deer varied with season. In winter the lowest overlap was observed (0.73). Towards spring (0.77) and summer (0.83) overlap of activity patterns increased more strongly, while a minor change between summer and autumn (0.84) was observed. The total overlap was 0.81. There was almost no variation of overlaps between activity patterns of lynx and red deer. The lowest overlap was observed in winter and spring (0.83), whereas a slight increase to 0.84 was found in summer and autumn, as well as for the total overlap (Appendix A).

3.2 Modelling approach

Prey activity

The activity of roe deer and red deer had a significant effect on the activity of the lynx ($P < 2e\text{-}16$, Table 4). The estimated effect of roe deer on lynx activity was approximately three times higher then the effect of red deer (M1: Table 4). Because of the strong effect of daytime on roe deer and red deer activity (Figure 1) some degree of multicollinearity was expected. To test the effect of daytime on prey activity one model for roe deer and red deer each was fitted (M7: Table 5/ M8: Table 6). The effect of daytime on activity was significant for roe deer, as well as for red deer. The stability of the parameter estimates was tested by fitting models M2 until M6 (Table 4), with lynx as dependent variable. Models were calculated for roe deer and red deer individually and tested by stepwise omitting the critical variables (roe deer/ red deer, daytime). The effect of prey on lynx activity was significant for the models that regarded daytime (M2; M4), as well as for the ones were it was not included (M3; M5). Estimates of roe deer, red deer and daytime had no change of sign. Although daytime had a significant effect on prey activity, the major parameter estimates did not change much and therefore multicollinearity considered a minor problem and was therefore neglected.

Daytime and season

The effect of daytime on lynx activity was significant for all categories, whith dusk showing the strongest effect (M1: Table 4). In all models including daytime, it had a significant effect on lynx activity (M2, M4, M6: Table 4). Activity of roe deer decreased during the night and increased during dawn and dusk, whith the effect of dusk being more than twice as strong as the effect of dawn (M7: Table 5). Red deer activity was affected significantly by daytime (M8: Table 6), with activities during dawn, dusk and night being higher than during the day. During dusk red deer was most active, while intermediate activities were observed during dawn and low activities in the night.

Lynx were less active during spring than in summer, while activity increased in autumn. Winter did not have a significant effect on lynx activity (M1: Table 4). Season had a significant effect on roe deer activity throughout the whole year. Roe deer activity was lower in spring than in summer, while activities during summer were highest. In autumn activity

decreased and reached its minimum, but increased again in winter (M7: Table 5). The activity of red deer was influenced significantly by all seasons. In winter activity was at its minimum but was found to increase in spring, while it reached its maximum in summer. In autumn a decrease of activity occurred (M8: Table 6).

Light regime in the night

In the main model lynx activity in general decreased with increasing brightness (M1: Table 4). Activity during the night however was significantly higher on bright nights, than in dark nights. The effect was not statistically significant during dusk and dawn. Overall roe deer activity decreased significantly during times of higher light availability during the night. Compared to activity during the day, activity increased at dusk and during the night with increasing illumination (M7: Table 5). Red deer activity was lower during periods of high nightly light availability. In interaction with daytime the effect was significant during dawn, dusk and night (Table 6).

Models M9, M10 and M11 (Table 3) were fitted for better interpretation of the variable "bright" by analysing the original components (cloud/ moon). Moon and cloud were not significant as long as they were in separate models (M10; M11). In interaction with each other cloud and moon had a significant effect on lynx activity (M9). Cloud itself was not statistically significant, while moon did have a significant effect (M9). Cloud in interaction with daytime affected lynx activity significantly during dawn and night (M9; M11). When significance was given, the effect of moon and cloud:daytime was negative (Appendix B).

Weather conditions

Temperature and snow were significant in all models (Table 3). The effect of snow on lynx activity was weak over a large range of given snow heights (Figure 2). Although activity decreased at snow heights above 150 cm, this effect could be influenced by the small amount of observations. Activity increased below five °C and decreased above five °C (Figure 3).

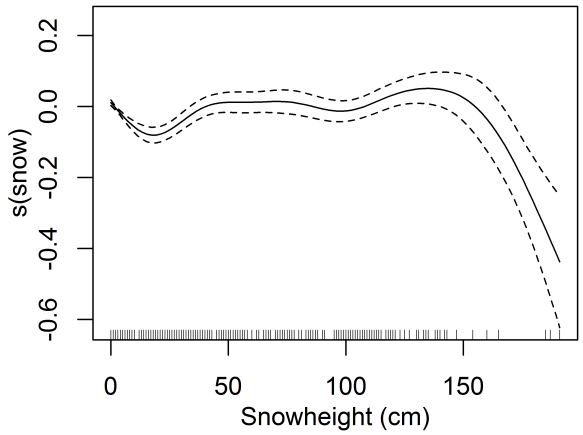

Figure 2: Lynx activity in relation to snow height in cm. The solid line shows the predicted values for lynx activity at a certain snow height. Dashed lines indicate standard errors. Small lines along the x-axis show observed snow heights.

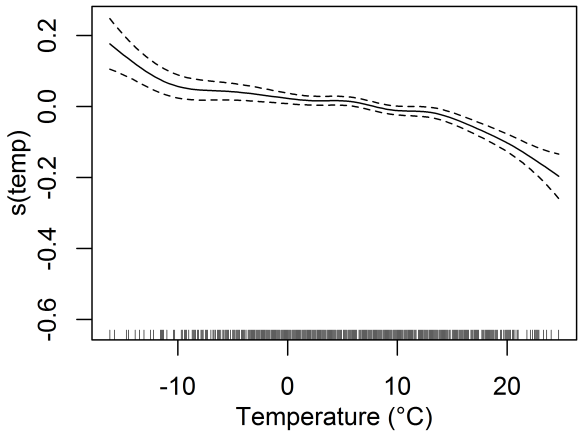

Figure 3: Lynx activity in relation to temperature in °C. The solid line shows the predicted values for lynx activity at a certain temperature. Dashed lines indicate standard errors. The small lines along the x-axis show observed temperatures.

Roe deer activity decreased with increasing snow height, while the steepest slope was between 0 and 50 cm (Figure 4). Activity was highest below minus 10°C, whereas the number of observation declined towards temperatures under minus 10°C (Figure 5). Activity tended to decrease with rising temperatures, reaching its minimum above 20°C.

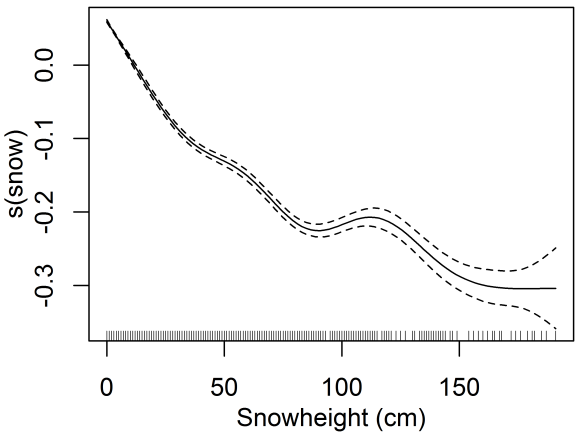

Figure 4: Roe deer activity in relation to snow height in cm. The solid line shows the predicted values for roe deer activity at a certain snow height. Dashed lines indicate standard errors. Small lines along the x-axis show observed snow heights.

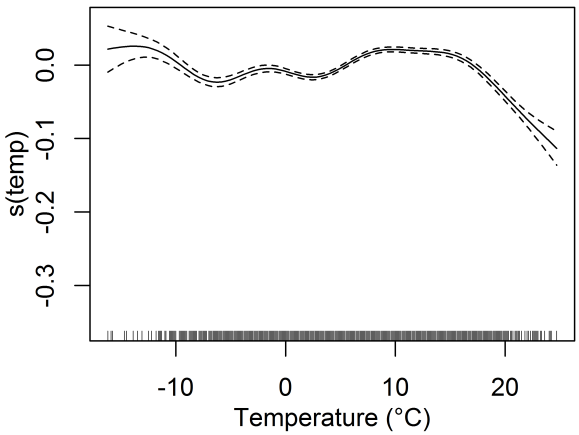

Figure 5: Roe deer activity in relation to temperature in °C. The solid line shows the predicted values for roe deer activity at a certain temperature. Dashed lines indicate standard errors. The small lines along the x-axis show observed temperatures.

Red deer activity was highest without snow cover, although it was affected strongly by snow heights up to 50 cm, where activity reached its minimum (Figure 6). Activity levels at snow heights above 50 cm were intermediate, while observations of snow height above 150 cm were scarcer. Activity was lowest at temperatures below 0°C, wheras activity increased more strongly under -10°C, which is probably owed to the small number of observations (Figure 7). Between 0 and 20°C an increase in red deer activity was observed, whereas it decreased again above 20°C.

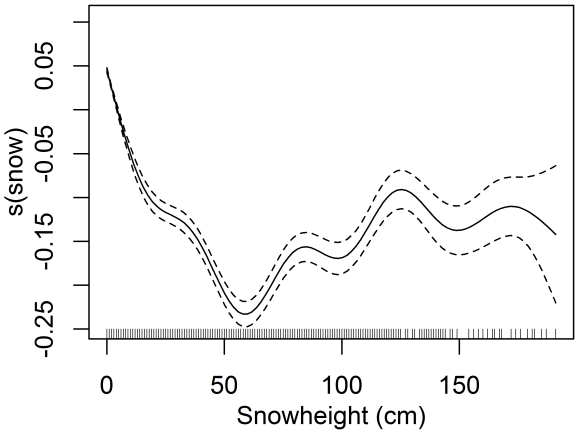

Figure 6: Red deer activity in relation to snow height. The solid line shows the predicted values for red deer activity at a certain snow height. Dashed lines indicate standard errors. Small lines along the x-axis show observed snow heights.

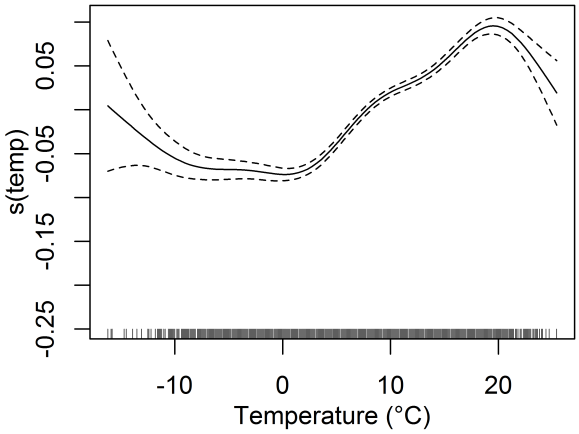

Figure 7: Red deer activity in relation to temperature in °C. The solid line shows the predicted values for red deer activity at a certain temperature. Dashed lines indicate standard errors. The small lines along the x-axis show observed temperatures.

Table 4: Output of models M1- M6, with lynx as dependent variable. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	M1			M2			M3			M4			M5			M6		
Variable	Est.	SE	P	Est.	SE	P	Est.	SE	P	Est.	SE	P	Est.	SE	P	Est.	SE	P
(Intercept)	-0.2778	0.0104	***	-0.3004	0.0082	***	-0.0726	0.0093	***	-0.2388	0.0097	***	0.0246	0.0095	**	-0.2656	0.0077	***
roe	0.2423	0.0093	***	0.2451	0.0078	***	0.3617	0.0078	***	–	–	–	–	–	–	–	–	–
red	0.0899	0.0058	***	–	–	–	–	–	–	0.1265	0.0056	***	0.2934	0.0057	***	–	–	–
bright	-0.0441	0.0183	*	-0.0449	0.0174	*	0.0616	0.0133	***	-0.0471	0.0184	*	0.0510	0.0138	***	-0.0454	0.0173	**
daytimedawn	0.4851	0.0149	***	0.5114	0.0141	***	–	–	–	0.5301	0.0149	***	–	–	–	0.5592	0.0137	***
daytimedusk	0.7320	0.0154	***	0.7795	0.0143	***	–	–	–	0.8256	0.0151	***	–	–	–	0.9098	0.0135	***
daytimenight	0.6014	0.0075	***	0.6043	0.0071	***	–	–	–	0.5870	0.0075	***	–	–	–	0.6080	0.0069	***
seasonautumn	0.0230	0.0102	*	0.0249	0.0094	**	0.1462	0.0101	***	-0.0421	0.0010	***	0.0392	0.0106	***	-0.0543	0.0090	***
seasonspring	-0.0763	0.0098	***	-0.0577	0.0088	***	-0.0395	0.0094	***	-0.1036	0.0098	***	-0.1167	0.0104	***	-0.0841	0.0088	***
seasonwinter	0.0233	0.0155		0.0347	0.0149	*	0.1458	0.0160	***	-0.0355	0.0154	*	0.0394	0.0164	*	-0.0404	0.0147	**
bright:daytimedawn	0.0581	0.0521		0.0810	0.0499		–	–	–	0.0537	0.0524		–	–	–	0.0956	0.0492	.
bright:daytimedusk	-0.0373	0.0544		-0.0198	0.0519		–	–	–	-0.0160	0.0546		–	–	–	0.0016	0.051	
bright:daytimenight	0.0546	0.0261	*	0.0712	0.0252	**	–	–	–	0.0620	0.0262	*	–	–	–	0.0695	0.0249	**

* reference categories: daytime= "day";
season= "summer"

Table 5: Output of model M7, with roe deer as dependent variable. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	M7		
Variable	Est.	SE	P
(Intercept)	0.1256	0.0084	***
bright	-0.0101	0.0046	*
daytimedawn	0.2013	0.0036	***
daytimedusk	0.4748	0.0036	***
daytimenight	-0.0506	0.0018	***
seasonautumn	-0.2401	0.0025	***
seasonspring	-0.0907	0.0024	***
seasonwinter	-0.1873	0.0034	***
bright:daytimedawn	0.0069	0.0130	
bright:daytimedusk	0.0982	0.0138	***
bright:daytimenight	0.0417	0.0066	***

* reference categories: daytime= "day";
season= "summer"

Table 6: Output of model M8, with red deer as dependent variable. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	M8		
Variable	Est.	SE	P
(Intercept)	-0.0733	0.0085	***
bright	-0.0489	0.0071	***
daytimedawn	0.3708	0.0062	***
daytimedusk	0.6538	0.0060	***
daytimenight	0.1526	0.0031	***
seasonautumn	-0.0875	0.0037	***
seasonspring	-0.0226	0.0038	***
seasonwinter	-0.1324	0.0058	***
bright:daytimedawn	0.0549	0.0209	**
bright:daytimedusk	0.0596	0.0213	**
bright:daytimenight	0.0667	0.0106	***

* reference categories: daytime= "day";
season= "summer"

4 Discussion

Lynx activity was crepuscular and nocturnal, while dusk had the strongest effect throughout the year, followed by night and dawn. Breitenmoser and Breitenmoser-Würsten (2008) also observed higher activities during dusk and night, where lynx mainly hunt and eat. Previous studies in the Bavarian Forest (Podolski et al., 2013), as well as in Switzerland (Bernhart, 1990) support the hypothesis that lynx have a mainly crepuscular activity pattern. Roe deer was most active during twilight, while activities during the day dominated night-time activities. Red deer showed also a crepuscular activity pattern, with intermediate activity during the night and low activity during the day. In other studies a mainly crepuscular activity pattern for cervids, such as roe deer (Cederlund, 1989; Krop-Benesch et al., 2013) and red deer (Georgii, 1981) was observed too.

The effect of roe deer and red deer on lynx activity was statistically significant, whereas the effect of roe deer was higher than the effect of red deer. This is supported by Okarma et al. (1997), who found that in the Bialowieza Primeval Forest lynx also preferred ungulates as prey (85% of total kills), while 62% were roe deer and 22% red deer (Podolski et al., 2013). One explanation could be that because of red deers' large size it is mainly preyed upon by adult male lynx (Okarma et al., 1997). Other studies also confirm, that where lynx, roe deer and red deer are abundant roe deer is their main prey, followed by red deer (Jedrzejewski et al., 1993; Breitenmoser and Breitenmoser-Würsten, 2008;Podolski et al., 2013). This could have an effect on lynx activity pattern, since predators are known to synchronize their activity patterns with their main prey (Harmsen et al., 2010). Similar patterns were found in other studies. Harmsen et al. (2010) found that jaguar and puma were active at times when their main prey was foraging above ground. In Sumatra tiger (*Panthera tigris sumatrae*) activity peaked contemporary with muntjac (*Muntiacus muntjac*), one of its main prey species (Linkie and Ridout, 2011). The observations of this study support the hypothesis that the activity pattern of lynx is a result of its preference for roe deer over red deer.

Lynx hunting strategy is mainly based on their sense of hearing and their eyesight (Breitenmoser and Breitenmoser-Würsten, 2008). This makes them well adapted to light conditions during twilight where the chance of being detected by its prey is low, but hunting still possible. According to Breitenmoser and Breitenmoser-Würsten (2008) stalking predators need to be aware of their preys' habits as well as their distribution in their territory, to be able to catch their prey off guard. This would indicate that consciousness of preys feeding habits is compulsory for successful hunting of lynx. This could explain why activity peaks of lynx coincide with activity peaks of their main prey, also considering that actively foraging animals are more easily detected.

Timing of twilight peaks of lynx coincided with seasonal changes of dusk and dawn and

concurred with peaks of roe deer and red deer. The coefficient of overlap was high between lynx and roe deer/ red deer throughout the year. Theuerkauf et al. (2003) observed that wolves activity patterns followed seasonal changes in sunrise and sunset, which agreed with activity peaks of their prey (red deer). In winter lynx activity was concentrated at dusk, which is supported by Kolbe and Squires (2007) who found that Canada lynx were most active in the afternoon and early evening during winter. This shift could be related to the higher ambient temperatures at dusk than at dawn. Activity of roe deer in winter was generally lower than in spring and summer, but evenly high at dusk and dawn, with two smaller peaks during midday and before midnight. Activity was generally concentrated during the day, compared to the other seasons (Jeppesen, 1989). A smaller, less distinctive peak before midnight was also discovered by Stache et al. (2013). A possible explanation for this is the ultradian rhythm of ruminants, which ensures a constant supply of nutrients (Stache et al., 2013). During winter however, food is scarce and mobility decreases with increasing snow depth (Cagnacci et al., 2011), which could explain the need to increase foraging frequency. The observations in this study support the theory, that roe deer decrease their activity with increasing snow height. These findings are strengthened by Cederlund and Lindstrom (1983), who found that snow depth above 50 cm may cause greatly limited mobility and therefore a decrease in activity. Heurich et al. (2012) observed that mortality of roe deer, caused by starvation greatly increased with high snow cover, rather than low temperatures. Arnold et al. (2004) discovered, that ruminants are able to decrease their body temperature during times of food shortage and extreme climatic conditions as an energy saving measure. Roe deer activity in this study decreased rapidly above 17°C, while the effect of temperatures below 0°C was less distinct. This may indicate that roe deer respond to colder temperatures with increased activity at warmer ambient temperatures during the day (Beier and McCullough, 1990) to lower the need for metabolic heat production. For red deer the observed activity pattern during winter was similar to the lynx, with activity concentrated during dusk. A different daily activity pattern was found in Bialowieza Forest, where winter daytime activity of red deer was higher than night-time activity (Kamler et al., 2007). Georgii and Schröder (1983) observed a crepuscular activity throughout the year, whereas peaks were more pronounced in winter. A potential explanation for the low activity at dawn is the trapping of red deer in enclosures during winter months as a population control measure (Heurich et al., 2011). In these enclosures food is provided externally at noon, which might alter the effect of dawn on their circadian activity, by adapting to imposed feeding times. Winter enclosures may also explain the increase in red deer activity above snow heights of 50 cm. Due to the entrapment of animals, movement is concentrated in one area, which prevents snow accumulation by trampling of the and therefore distorts the effect of snow height on activity. Since roe deer activity was evenly distributed at dusk and dawn and most red deer spend the winter months in enclosures, the increase in lynx activity

during dusk is more likely a response to higher temperatures, than to prey activity. The total overlap between lynx and red deer was only slightly higher than with roe deer. This can be explained by the low overlap during winter, which can be a result of the increased activity of roe deer during the day. This however does not alter the conclusion, that roe deer is the preferred prey of lynx, since red deer availability during winter is reduced according to its entrapment. The higher overlap can be a result of red deers' tendency for nocturnality.

Lynx activity was generally lower during spring than during other seasons. Morning peaks however became more distinct again, which could be related to increasing ambient temperatures during dawn. Prey activity during spring was higher than in winter, but lower than in summer. Similar patterns for cervids were found for red deer in the Alps (Georgii, 1981) and roe deer in Bavaria (Krop-Benesch et al., 2013), where an increase of activity was observed from winter to spring. This increase could be related to increasing temperatures, as well as to the beginning of the vegetation period and therefore increasing food availability (especially due to declining snow heights). Beier and McCullough (1990) observed that the absence of snow between one and 13 days was an indicator for spring migrations. According to Pagon (2011) male roe deer show an increase in activity during spring because of territory establishment and defence during the territorial season. In this study more than half of the collared roe deer were male, which could mean that increased activity of male roe deer during territorial season represents the high general activity during spring. Red deer was crepuscular, with low activity during the day. The release of red deer from the winter enclosures may explain the restored morning peak.Red deer might also react with an increase in activity when set free after being entrapped during winter. That lynx activity was lowest during spring was unexpected. Actively foraging animals are more easily detected (Harmsen et al., 2010) and therefore it would seem consistent that lynx would respond to an increase of prey with increased activity.

Lynx activity at dawn and resting time during the day were highest in summer. Theuerkauf et al. (2003) hypothesized that wolves increased activity during cooler morning hours, when local mean temperatures were high (Theuerkauf et al., 2003). Podolski et al. (2013) and Kolbe and Squires (2007) found that lynx respond to high temperatures with reduced activity. In Piñero, jaguar and puma were observed to show higher activity during the wet season, which was connected to lower ambient temperatures (Scognamillo et al., 2003). This hypothesis is consistent with the results of this study, showing a negative correlation of lynx activity with increasing temperatures. Roe deer activity was highest during summer, with slightly higher activity levels at dawn than at dusk. Red deer activity also peaked during summer, but activity was highest during dusk and second highest during dawn. Beier and McCullough (1990) state that white- tailed deer were less active during high and low, than during intermediate temperatures in summer, which could explain why activity is concentrated during twilight times. The high activities of roe deer can be explained with the rutting

season, which reaches its peak at the beginning of august (Pagon, 2011; Krop-Benesch et al., 2013). Coefficients of overlap were higher in summer than the total overlap between lynx, roe deer/ red deer, which can be explained with concentrated activity during twilight for all three species. An increase during warmer month may also be owed to increasing cover during the vegetation period, which might cause prey species to feel more save while foraging. The increase of lynx activity from spring to summer could also be a result of increased prey movements and scattering due to territorial establishment, which induces the need to compensate with increased activity for increased hunting effort.

In autumn lynx activity was highest compared to other seasons, while roe deer and red deer activity decreased. The general pattern was crepuscular, while nocturnal activity of prey increased A decreased activity of roe deer during autumn was also observed by Krop-Benesch et al. (2013) and Pagon (2011). This decrease is probably caused by the end of the rutting season and therefore decreased energy requirements and activity. Beier and McCullough (1990) found that activity of white- tailed deer decreased after the rutting season, which supports the findings in this study. Red deer in the Alps increased their nocturnal activity from summer to autumn. A possible reason for this is that as days grow shorter and colder, cervids may need to be more active during the night to meet their energy demands. In autumn roe deer start to form small social groups after the rutting season (Pagon, 2011; Krop-Benesch et al., 2013). Big congregations of animals may increase vigilance and the chance of detection for predators. Lima and Bednekoff (1999) however suggest that an increase in group size may increase risk since they are more easily detected.

In comparison to dark nights, activity was higher during bright nights for all three species. Activity of bobcats (*Lynx rufus*) increased with increasing lunar illumination to compensate for reduced activity of its prey (Rockhill et al., 2013). On the contrary, white maned wolfes (*Chrysocyon brachyurus*) were observed to reduce their activity during the full moon which was explained as a measure to preserve energy or as a response to decreased hunting efficiency (Sábato et al., 2006). Wolves in the Bialowieza Forest were more active during bright nights, than during dark nights (Theuerkauf et al., 2003). A reaction to bright nights was also found in armadillos and pacas, which lowered their activity to reduce predation risk. In response to the decreased activity of their favourite prey (armadillo) jaguars also lowered their activity during bright nights (Harmsen et al., 2010). Because prey species often responded to bright nights with decreased activity (Penteriani et al., 2013; Manfredi et al., 2011), a decline in roe deer and red deer activity was expected. The results however do not support this hypothesis as prey activity increased along with predator activity. A possible explanation for this observation might be that prey increases foraging activity because of increased visibility. Due to the relationship between hunting success and prey activity (Harmsen et al., 2010) lynx might respond with increased activity. Furthermore, increased prey activity may compensate for increased detectability of predators during bright nights (Lucherini et al., 2009).

Cromsigt et al. (2013) states that prey may be able to reduce predation risk by altering their activity pattern. The observed activity patterns in this study however do not suggest that roe deer or red deer responded to predation risk with an activity shift. The predation risk allocation hypothesis say that prey may respond less to a continuously high risk, than a risk that is strong but rare (Lima and Bednekoff, 1999). In conformity with Breitenmoser and Breitenmoser-Würsten (2008) lynx need to have knowledge on prey habits and feeding sites. This ensures the surprise effect of the predator while hunting and therefore delayed vigilance of its prey. After making a kill, lynx usually move to a different part of their territory where vigilance is still low. After the lynx left his current hunting area, vigilance of the prey decreases due to the increasing importance of other needs, such as foraging (Lima and Bednekoff, 1999). This may ensure that predation risk remains unpredictable and prevents prey to respond with behavioural changes (Lima and Dill, 1990).

In conclusion, this study indicates that activity patterns of lynx and its main prey are related to each other. Anti-predator behaviours, such as activity shifts to times with lower predator presence were not observed. This strengthens the hypothesis, that lynx adjust their activity pattern to the activity of their main prey. The hypothesis that roe deer activity affects lynx activity stronger that red deer activity is supported by the results of this study. Furthermore, a strong connection between activity patterns and abiotic factors, such as daytime, season, temperature and snow height was detected. Daytime and season highly affected activity patterns of all three species, by showing a co-occurrence of activity peaks with twilight times throughout the year. Lynx reacted to increasing temperatures with decreasing activity, whereas a response to snow height was only found above 150 cm. Roe deer lowered its activity at temperatures above 20°C, while no strong effect was found below 10°C. Red deer activity peaked at 20°C and declined below and above. Both prey species were more sensitive to snow, as activity decreased with increasing snow height. In bright nights activity of all three species was higher than in dark nights. The hypothesis that the activity patterns of Eurasian lynx increase with increasing brightness during the night, is supported by the results of this study.

Although activity data from acceleration sensors can provide insight in animals activity patterns, GPS measurements and camera-trap data are needed for a more detailed insight into the relationship between the Eurasian lynx and its main prey.

5 Acknowledgements

I thank Dr. Marco Heurich for giving me the opportunity to carry out my final thesis in collaboration with the Bavarian Forest National Park and for allowing me to use the projects' previously collected data. I also thank him for his patient guidance, encouragement and useful critiques of this study.

Furthermore I would like to express my great appreciation to Benno Wölfing. . His statistical advice was of great help.

Last but not least I thank my supervisor Prof. Dr. Elke Hietel for guiding me through my thesis.

Katharina Reusch made helpful edits and comments on several previous versions of this report.

Finally, I want to thank my family and friends who always have supported me during my work.

Spiegelau, August 2014
Christopher Reusch

References

Arnold W. , Ruf T. , Reimoser S. , Tataruch F. , Onderscheka K. , and Schober F. , (January 2004). Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *American journal of physiology. Regulatory, integrative and comparative physiology*, 286(1):R174–181.

Bässler C. , Förster B. , Moning C. , and Müller J. , (2009). The BIOKLIM project: biodiversity research between climate change and wilding in a temperate montane forest : the conceptual framework. *Waldökologie, Landschaftsforschung und Naturschutz*, 7:21–34.

Bednekoff P. A. , (2006). Antipredator Defenses in Birds and Mammals. *The Condor*, 108 (2):484.

Beier P. and McCullough D. R. , (1990). *Factors influencing white-tailed deer activity patterns and habitat use*. Number 109. Wildlife Society.

Beltrán J. and Delibes M. , (1994). Environmental Determinants of Circadian Activity of Free-Ranging Iberian Lynxes. *Journal of Mammalogy*.

Bernhart F. , (1990). Untersuchungen des Aktivitätsmusters des Luchses *Lynx lynx* in der Schweiz: Experimente und Felduntersuchungen. *Licentiate thesis. University of Bern*, page 78.

Breitenmoser U. and Breitenmoser-Würsten C. , (2008). *Der Luchs: Ein Grossraubtier in der Kulturlandschaft*. SALM VERLAG.

Cagnacci F. , Focardi S. , Heurich M. , Stache A. , Hewison a. J. M. , Morellet N. , Kjellander P. , Linnell J. D. C. , Mysterud A. , Neteler M. , Delucchi L. , Ossi F. , and Urbano F. , (December 2011). Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, 120(12):1790–1802.

Cederlund G. and Lindstrom E. , (1983). Effects of severe winters and fox predation on roe deer mortality. *Acta theriologica*, 28(7):129–145.

Cederlund G. , (March 1989). Activity patterns in moose and roe deer in a north boreal forest. *Ecography*, 12(1):39–45.

Cederlund G. , Bergström R. , and Sandegren F. , (June 1989). Winter activity patterns of females in two moose populations. *Canadian Journal of Zoology*, 67(6):1516–1522.

Cromsigt J. P. , Kuijper D. P. , Adam M. , Beschta R. L. , Chruski M. , Eycott A. , Kerley G. I. , Mysterud A. , Schmidt K. , and West K. , (2013). Hunting for fear: innovating management of human-wildlife conflicts. *Journal of Applied Ecology*, 50:544–549.

Eccard J. A. , Pusenius J. , Sundell J. , Halle S. , and Ylönen H. , (October 2008). Foraging patterns of voles at heterogeneous avian and uniform mustelid predation risk. *Oecologia*, 157(4):725–734.

Emmons L. H. , (April 1987). Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology*, 20(4):271–283.

Eriksen A. , Wabakken P. , Zimmermann B. , Andreassen H. P. , Arnemo J. M. , Gundersen H. , Liberg O. , Linnell J. D. C. , Milner J. M. , Pedersen H. C. , Sand H. k. , Solberg E. J. , and Storaas T. , (February 2011). Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. *Animal Behaviour*, 81(2):423–431.

Georgii B. , (1981). Activity patterns of female red deer (*Cervus elaphus* L.) in the Alps. *Oecologia*, 47(2):127–136.

Georgii B. and Schröder W. , (May 1983). Home range and activity patterns of male red deer (*Cervus elaphus* L.) in the alps. *Oecologia*, 58(2):238–248.

Harmsen B. J. , Foster R. J. , Silver S. C. , Ostro L. E. , and Doncaster C. , (May 2010). Jaguar and puma activity patterns in relation to their main prey. *Mammalian Biology*, 76(3):320–324.

Herfindal I. , Linnell J. D. C. , Odden J. , Nilsen E. B. , and Andersen R. , (January 2005). Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoology*, 265(1):63–71.

Heurich M. , (2011). Berücksichtigung von Tierschutzaspekten beim Fang und der Markierung von Wildtieren. In *12. Internationale Fachtagung zu Fragen von Verhaltenskunde, Tierhaltung und Tierschutz, Deutsche Veterinär- medizinische Gesellschaft,Gießen,Germany*, pages 142–158.

Heurich M. and Neufanger M. , (2005). *Die Wälder des Nationalparks Bayerischer Wald. Ergebnisse der Waldinventur 2002/2003 im geschichtlichen und waldökologischen Kontext.* Nationalparkverwaltung Bayerischer Wald, Grafenau.

Heurich M. , Baierl F. , Günther S. , and Sinner K. F. , (2011). Management and conservation of large mammals in the Bavarian Forest National Park. *17*, pages 1–18.

Heurich M. , Möst L. , Schauberger G. , Reulen H. , Sustr P. , and Hothorn T. , (January 2012). Survival and causes of death of European Roe Deer before and after Eurasian Lynx reintroduction in the Bavarian Forest National Park. *European Journal of Wildlife Research*, 58(3):567–578.

Jedrzejewski W. , Schmidt K. , Milkowski L. , Jedrzejewska B. , and Okarma H. , (October 1993). Foraging by lynx and its role in ungulate mortality: the local (Bialowieza Forest) and the Palaearctic viewpoints. *Acta Theriologica*, 38(4):385–403.

Jeppesen J. , (1989). Activity patterns of free-ranging roe deer (*Capreolus capreolus*) at Kaloe. *Danish Review of Game Biology (Denmark)*.

Kamler J. F. , Jedrzejewska B. , and Jedrzejewski W. , (2007). Activity patterns of red deer in Bialowieza National Park, Poland. *Journal of Mammalogy*, 88(2):508–514.

Kolbe J. A. and Squires J. R. , (July 2007). Circadian Activity Patterns of Canada Lynx in Western Montana. *Journal of Wildlife Management*, 71(5):1607–1611.

Krop-Benesch A. , Berger A. , Hofer H. , and Heurich M. , (March 2013). Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-collars. *Italian Journal of Zoology*, 80(1):69–81.

Lima S. L. , (January 1998). Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, 48(1):25–34.

Lima S. L. and Bednekoff P. A. , (June 1999). Temporal Variation in Danger Drives Anti-predator Behavior: The Predation Risk Allocation Hypothesis. *The American Naturalist*, 153(6):649–659.

Lima S. L. and Dill L. M. , (April 1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68(4):619–640.

Linkie M. and Ridout M. S. , (July 2011). Assessing tiger-prey interactions in Sumatran rainforests. *Journal of Zoology*, 284(3):224–229.

Löttker P. , Rummel A. , Traube M. , Stache A. , Šustr P. , Müller J. , and Heurich M. , (December 2009). New Possibilities of Observing Animal Behaviour from a Distance Using Activity Sensors in Gps-Collars: An Attempt to Calibrate Remotely Collected Activity Data with Direct Behavioural Observations in Red Deer *Cervus elaphus*. *Wildlife Biology*, 15(4):425–434.

Lucherini M. , Reppucci J. I. , Walker R. S. , Villalba M. L. , Wurstten A. , Gallardo G. , Iriarte A. , Villalobos R. , Perovic P. , Garin I. , Aihartza J. , Zuberogoitia I. , and Zabala J. , (December 2009). Activity Pattern Segregation of Carnivores in the High Andes. *Journal of Mammalogy*, 90(6):1404–1409.

Manfredi C. , Lucherini M. , Soler L. , Baglioni J. , Vidal E. L. , and Casanave E. B. , (May 2011). Activity and movement patterns of Geoffroy's cat in the grasslands of Argentina. *Mammalian Biology*, 76(3):313–319.

Monterroso P. , Alves P. C. , and Ferreras P. , (December 2013). Catch Me If You Can: Diel Activity Patterns of Mammalian Prey and Predators. *Ethology*, 119(12):1044–1056.

Mysterud A. , Bjø rnsen B. r. H. , and Ø stbye E. , (March 1997). Effects of Snow Depth on Food and Habitat Selection by Roe Deer *Capreolus capreolus* along an Altitudinal Gradient in south-central Norway. *Wildlife Biology*, 3(1):27–33.

O'Donoghue M. , Boutin S. , Krebs C. J. , Zuleta G. , Murray D. L. , Hofer E. J. , and Ofer E. L. J. H. , (June 1998). Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, 79(4):1193–1208.

Okarma H. , Jedrzejewski W. , Schmidt K. , Kowalczyk R. , and Jedrzejewska B. , (1997). Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. *Acta Theriologica*, 42:203 – 224.

Pagon N. , (January 2011). Aspect of some ecological characteristics of roe deer (*Capreolus capreolus* L., 1758) population in North-Eastern Apennines, Arezzo Province, Italy. *PhD thesis, University of Sassari, Italy.*

Palomares F. and Delibes M. , (1992). Circadian activity patterns of free-ranging large gray mongooses, *Herpestes ichneumon* in southwestern Spain. *Journal of Mammalogy*, 73: 173–177.

Penteriani V. , Kuparinen A. , del Mar Delgado M. , Palomares F. , López-Bao J. V. , Fedriani J. M. , Calzada J. , Moreno S. , Villafuerte R. , Campioni L. , and Lourenço R. , (November 2013). Responses of a top and a meso predator and their prey to moon phases. *Oecologia*, 173(3):753–66.

Pereira J. , (September 2010). Activity pattern of Geoffroy's cats (*Leopardus geoffroyi*) during a period of food shortage. *Journal of Arid Environments*, 74(9):1106–1109.

Podolski I. , Belotti E. , Bufka L. , Reulen H. , and Heurich M. , (March 2013). Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx ynx* in relation to availability of kills. *Wildlife Biology*, 19(1):69–77.

Ratcliffe N. , Crofts S. , Brown R. , Baylis A. M. M. , Adlard S. , Horswill C. , Venables H. , Taylor P. , Trathan P. N. , and Staniland I. J. , (June 2014). Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. *Journal of Biogeography*, 41(6):1183–1192.

Rockhill A. P. , DePerno C. S. , and Powell R. A. , (January 2013). The effect of illumination and time of day on movements of bobcats (*Lynx rufus*). *PloS one*, 8(7):e69213.

Sábato M. A. L. , Melo L. F. B. de, Magni E. M. V. , Young R. J. , and Coelho C. M. , (September 2006). A note on the effect of the full moon on the activity of wild maned wolves, *Chrysocyon brachyurus*. *Behavioural processes*, 73(2):228–30.

Schmidt K. , (December 1999). Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in Bialowieza Primeval Forest, Poland. *Journal of Zoology*, 249(4):417–425.

Schmidt K. , Nakanishi N. , Izawa M. , Okamura M. , Watanabe S. , Tanaka S. , and Doi T. , (June 2008). The reproductive tactics and activity patterns of solitary carnivores: the Iriomote cat. *Journal of Ethology*, 27(1):165–174.

Scognamillo D. , Maxit I. E. , Sunquist M. , and Polisar J. , (March 2003). Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *Journal of Zoology*, 259(3):269–279.

Stache A. , Heller E. , Hothorn T. , and Heurich M. , (2013). Activity patterns of European roe deer (*Capreolus capreolus*) are strongly influenced by individual behaviour. *Folia Zoologica (Czech ...*, 62(1):67–75.

Theuerkauf J. , Jedrzejewski W. , Schmidt K. , Okarma H. , Ruczynski I. , Śniezko S. , and Gula R. , (February 2003). Daily patterns and duration of wolf activity in Bialowieza Forest, Poland. *Journal of Mammalogy*, 84(1):243–253.

Weilnböck G. , Wöhr C. , Erhard M. , Menges V. , Scheipl , Möst L. , Palme R. , and Heurich M. , (2012). Zur Stressbelastung des Rehwilds (*Capreolus capreolus*) beim Fang mit der Kastenfalle. *KTBL-Schrift 496: Aktuelle Arbeiten zur artgemäßen Tierhaltung 2012. 44. Internationale Arbeitstagung Angewandte Ethologie bei Nutztieren der DVG*, pages 22–31.

Wilmers C. C. , Post E. , and Hastings A. , (November 2007). The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology*, 76(6):1037–1044.

Wölfl M. , Bufka L. , Červený J. , and Koubek P. , (2001). Distribution and status of lynx in the border region between Czech Republic, Germany and Austria. *Acta theriologica*, 46 (2):181–194.

Wood S. N. , (2006). *Generalized additive models: an introduction with R.* Chapman Hall/CRC.

Wronski T. , Apio A. , and Plath M. , (November 2006). Activity patterns of bushbuck (*Tragelaphus scriptus*) in Queen Elizabeth National Park. *Behavioural processes*, 73(3): 333–41.

A Overlap

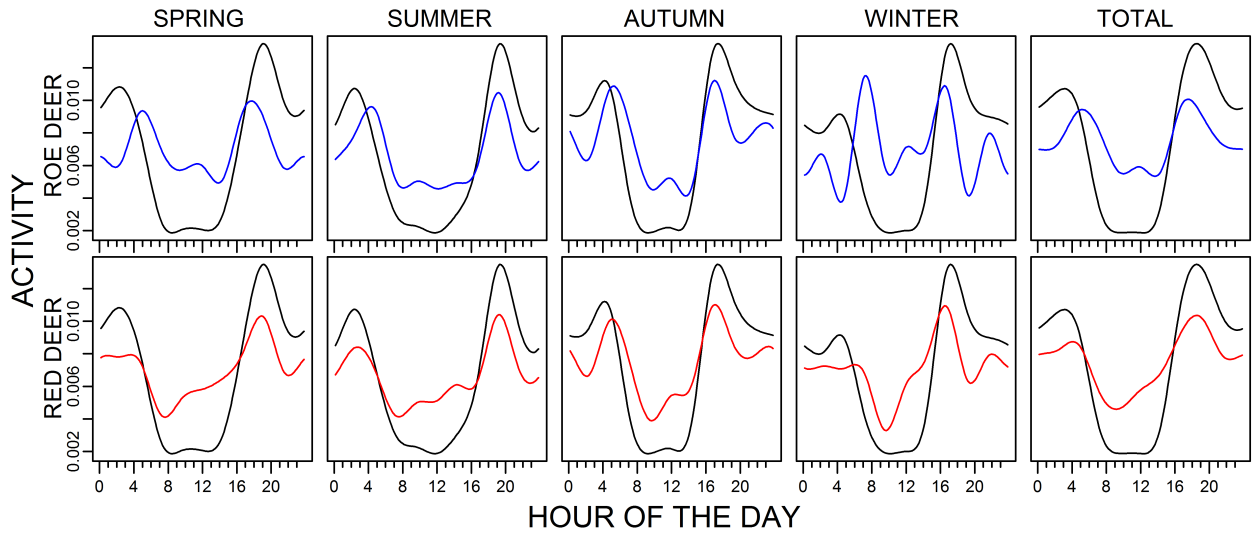

Figure 8: Overlap of circadian activity pattern per season and in total for lynx (black lines), roe deer (blue lines) and red deer (red lines).

B Output of models M9, M10 and M11

Table 7: Output of model M9 to M11. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. daytime:moon is not listed in this table (P > 0.05)

	M9			**M10**			**M11**		
Variable	Est.	SE	P	Est.	SE	P	Est.	SE	P
(Intercept)	-0.2593	0.0167	***	0.2781	0.0117	***	-0.2902	0.0142	***
roe	0.2424	0.0093	***	0.2422	0.0093	***	0.2422	0.0093	***
red	0.0901	0.0058	***	0.0907	0.0058	***	0.0901	0.0058	***
daytimedawn	0.5403	0.0293	***	0.4974	0.0214	***	0.5440	0.0252	***
daytimedusk	0.7095	0.0319	***	0.7293	0.0218	***	0.7071	0.0280	***
daytimenight	0.6452	0.0150	***	0.6145	0.0106	***	0.6473	0.0130	***
seasonautumn	0.0175	0.0104	.	0.0205	0.0101	*	0.0179	0.0104	.
seasonspring	-0.0795	0.0010	***	-0.0791	0.0097	***	-0.0806	0.0098	***
seasonwinter	0.0263	0.0156	.	0.0213	0.0155		0.0233	0.0155	
moon	-0.0681	0.0196	***	-0.0079	0.0114		–	–	–
cloud	-0.0035	0.0021	.	–	–	–	0.0016	0.0015	
moon:cloud	0.0107	0.0029	***	–	–	–	–	–	–
cloud:daytimedawn	-0.0093	0.0041	*	–	–	–	-0.0010	0.0041	*
cloud:daytimedusk	0.0037	0.0045		–	–	–	0.0035	0.0045	
cloud:daytimenight	-0.0070	0.0021	***	–	–	–	-0.0073	0.0021	***

* reference categories: daytime= "day"; season= "summer"