Inland Norway
University of
Applied Sciences

Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

Elena Iannino

MSc Thesis

Assessing the potential of camera traps for estimating activity pattern compared to GPS activity sensors: a case study on Eurasian lynx *Lynx lynx* in southeastern Norway

Master in Applied Ecology
June 2022

Abstract

Animals tend to have predictable activity patterns, based on their ecological and physiological needs, alternating between periods of activity and resting. Investigating factors influencing activity patterns for different species or populations can convey an understanding of physiology, niche theory, community structure and animal behaviour. The study of activity patterns of wild species is often challenging in the field, recent developments in technology have led to different methods being applied that can vary in the degree of invasiveness towards animal's welfare and the financial and logistical efforts required to operate them. The gold-standard approach for quantifying the detailed movements and activity patterns of wildlife is through the use of Global Positioning System (GPS) collars and respective activity sensors. Most recently, the development of digital camera traps, that allow detection and monitoring of elusive wildlife while being non-intrusive and implementable over large areas, have become a new potential tool for estimating activity patterns. Nevertheless, there are still few studies that compare activity measurements obtained from camera traps data to those obtained from motion sensors/accelerometer data of GPS collars. The present study aims to examine the differences that might occur between data from animal mounted activity sensors and data from camera traps, assessing the accuracy of camera traps' activity pattern estimation compared to the pattern resulting from GPS collar activity sensors. I therefore compared activity pattern estimation and circular datasets obtained from GPS collar accelerometers from 18 Eurasian lynx (8 females and 10 males) monitored during an 8 year study period (from 2008 to 2015) in the southern part of Norway and data from Eurasian lynx detections recorded from more than 300 camera traps distributed in the same area during a period of 11 years (from 2010 to 2020). My study results suggest that: 1) Accelerometer and activity sensors in GPS collars are a robust method for studying general activity pattern of wildlife with the potential of investigating behaviours at a very fine temporal scale; 2) Camera traps can be used to estimate overall activity curves with comparable estimations to the ones obtained from accelerometers, however, it requires a large number of camera traps and proper camera trapping study design while keeping in mind the fundamental differences that occur between data collected from these two methodologies; 3) A lower number of camera traps, and consequently a lower number of detections, results in a less accurate activity estimation from camera traps. This is particularly evident when using less than 65 camera traps and/or working with less than 96 detections.

Contents

Introduction

Animals tend to have predictable activity patterns, based on their ecological and physiological needs, alternating between periods of activity and resting (Rawcliffe *et al*., 2014). Animal activity is affected by a variety of factors, some of them depending on individual characteristics, including age, sex, reproductive status, body condition and energy budgets (Podolski *et al*., 2013, Rawcliffe *et al*., 2014), and others that originate from external sources such as disturbance, predation risk, access to food / prey, temperature (Beltran & Delibes 1994), light (Heurich *et al*., 2014) and season (Manfredi *et al*., 2011; Heurich *et al*., 2014). Investigating factors influencing activity patterns for different species or populations can convey an understanding of physiology, niche theory, community structure and animal behaviour (Podolski *et al*., 2013; Frey *et al*., 2017; Edwards *et al*., 2020). Furthermore, conservation management can benefit from knowledge derived from activity studies, for example research has shown that many wildlife species change their activity patterns as a consequence of anthropogenic disturbance (Gaynor *et al*., 2018; Edwards *et al*., 2020), hunting pressure (Van Doormaal *et al*., 2015; Edwards *et al*., 2020) and the reintroduction of predators that affect prey species' diel patterns (Tambling *et al*., 2015; Edwards *et al*., 2020).

Although, the study of activity patterns of wild species is often challenging in the field, recent developments in technology have led to different methods being applied that can vary in the degree of invasiveness towards animal's welfare and the financial and logistical efforts required to operate them. The gold-standard approach for quantifying the detailed movements and activity patterns of wildlife is through the use of Global Positioning System (GPS) collars (Cagnacci *et al*., 2010; Kays *et al*., 2015). Many modern GPS collars are equipped with a motion sensor or accelerometer that constantly monitors animal activity at fine temporal scales independently from its spatial data (Lottker *et al*., 2009; Podolski *et al*., 2013; Edwards *et al*., 2020). These sensors record neck and upper body movement, providing the opportunity to remotely categorize animal behaviour in addition to overall activity (Lottker *et al*., 2009; Wang *et al*., 2015; Roberts *et al*., 2016). The most advanced sensors store three different values differentiated as vertical and horizontal motion and tilt angle, less complex models record only vertical and horizontal motion, or simply any forceful motion (Wang *et al*., 2015; Roberts *et al*., 2016). Motion sensors and accelerometers record behaviour at high temporal resolution, and some studies have already demonstrated that the estimations made from these tools is comparable to direct continuous observation (Gervasi *et al*., 2006; Gonzales *et al*., 2014; Roberts *et al*., 2016; Edwards *et al*., 2020). This method of studying wildlife behaviour is particularly relevant for elusive, mainly night active, forest living species that are difficult to observe directly, such as the Eurasian lynx *Lynx lynx* (Podolski *et al*., 2013). This species has indeed already been investigated through the lens of accelerometer data: a study conducted by Heurich *et al*. (2014), as well as one conducted by Podolski *et al*. (2013), demonstrated that collar activity sensors allow the identification of factors that modulate lynx activity.

Most recently, the development of digital camera traps, that allow detection and monitoring of elusive wildlife while being non-intrusive and implementable over large areas (Kelly & Holub, 2008; Sollmann *et al*., 2011), have become a new potential tool for estimating activity patterns (Edwards *et al*., 2020). Timestamps on camera trap images reflect wildlife occurrences captured in points in space and time, hence producing fine-scale temporal data (Sollmann 2018; Edwards *et al*., 2020). However, until recently there have been some challenges with the statistical analysis of camera derived activity data. Temporal data (i.e. date, hour, minute), that repeat cyclically, can be described as occurring around a circle and therefore transformed in radians format from 0 to $\pi 2$ in order to make them analysable, resulting in so-called circular data (Lee, 2010). Thereby, advances in analytical studies and, specifically, in analyses of circular data recorded by camera traps (Meredith & Ridout, 2021; Rowcliffe *et al*., 2014; Edwards *et al*., 2020) allows researchers to extract more details of activity of the animals detected (Edwards *et al*., 2020). Following on from these innovations in the analytical field of circular data, a variety of studies has been made trying to estimate wildlife activity patterns from camera trap detection data. A wide range of species have already been studied using these novel activity estimation methods, including 6 different species of Asian wild cat in Thailand (Lynam *et al*., 2013), 13 species of mammal in Barro Colorado Island (Rawcliffe *et al*., 2014), coyote *Canis latrans*, fox squirrel *Sciurus niger*, wild turkey *Melleagris gallopavo* and while-tailed deer *Odocoileus virginianus* in North Carolina (Lashley *et al*., 2018), grey wolf *Canis lupus* in Canada (Frey *et al*., 2017) and brown hyaena *Hyaena brunnea* in Namibia (Edwards *et al*., 2020).

These two methods for remotely estimating wildlife activity patterns are certainly both challenging and promising, nevertheless there are still few studies that compare activity measurements obtained from camera traps data to those obtained from motion sensors/accelerometer data (Frey *et al*., 2017; but see Lashley *et al*., 2018 and Edwards *et al*., 2020).

Camera traps have the clear advantage that they do not require live-capturing wild animals and equipping them with collars which requires considerable time, cost, technical capacity, the involvement of veterinarians and often complex research animal ethics permitting processes in addition to the associated animal welfare considerations. However, it is important to remember the difference in quantity and the nature of the data obtained from the two methods: accelerometers provide a continuous records of activity (with very short interval that can be set as low as a few seconds), recording a wide range of behaviours (running, walking, resting, grooming, etc) (Heurich *et al*., 2014). On the other hand, camera traps capture single points in space and time exclusively when the animal is moving, which is a subset of the overall activity of an animal (Edwards *et al*., 2020).

Keeping in mind these considerations, the present study aims to examine the differences that might occur between data from animal mounted activity sensors and data from camera traps, assessing the accuracy of camera traps' activity pattern estimation compared to the pattern resulting from GPS collar activity sensors. I therefore compared activity pattern estimation and circular datasets obtained from GPS collar accelerometers from 18 Eurasian lynx (8 females and 10 males) monitored during an 8 year study period (from 2008 to 2015) in the southern part of Norway and data from Eurasian lynx detections recorded from more than 300 camera traps distributed in the same area during a period of 11 years (from 2010 to 2020). With the aim of assessing activity estimation from the two sampling methods shown, I investigated the following questions:

- Looking at accelerometer data, which factors explain variation in Eurasian lynx activity pattern?
- Are camera traps reliable for estimating Eurasian lynx activity pattern and variation within it compared to accelerometer estimations?
- What is the effort, in terms of number of camera traps, required for obtaining reliable activity estimations?

Materials

Study area

This study was conducted in 5 south-eastern counties of Norway (61°N, 12°E): Innlandet, Viken, Oslo, Vestfold og Telemark, and Agder (~ 111.019 km2 area), in the boreal zone (Fig. 1). The north-western part of the study area is characterized by a wide range of gradient from valleys to hills/mountains that can reach 1000m a.s.l. and relatively low human population densities. This area is associated with boreal forests with Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. On the other hand, the south-eastern side of the area has shorter gradients of altitude and higher human population densities; here there are mainly patches of mixed coniferous deciduous forests alternated with cultivate lands. In the study area there are 4 large carnivores species present: brown bear *Ursus arctos*, grey wolf *Canis lupus*, Eurasian lynx and wolverine *Gulo gulo*. Moreover, there are several other species that function as prey or mesopredators present including moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, badger *Meles meles*, red fox *Vulpes vulpes*, pine marten *Martes martes* and mountain hare *Lepus timidus*. Eurasian lynx are widespread throughout the study site after having recolonized the area during the last 20 years of the 20th century. From the last Scandinavian inventory of lynx, in the study area it has been estimated the presence of 33 family groups and number of individuals between 165 and 198; with quota regulated hunting being used to stabilise the population at politically determined levels (Frank & Tomvo, 2021).

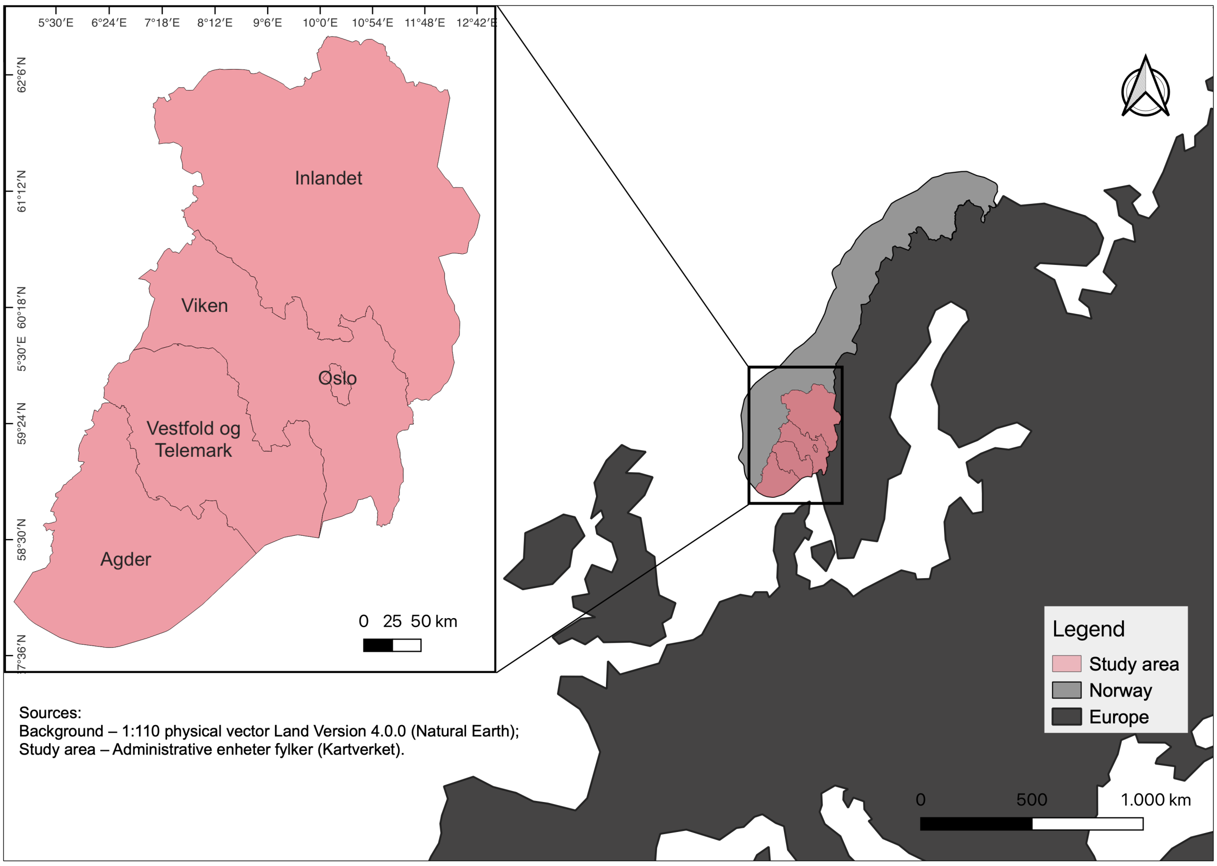


Fig.1 : Map with location of the study area.

Accelerometer data

Accelerometer data were obtained from 18 lynx (8 females and 10 males) live-captured between 2006 and 2011 under the auspices of the SCANDLYNX project and monitored using Global Positioning System (GPS) collars equipped with accelerometers (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). Lynx were captured using a combination of methods including walk-through box-traps and foot snares following the procedures described in greater detail by Gervasi *et al*. (2014) and Arnemo *et al*. (2011). All procedures were approved by the Norwegian Experimental Animal Authority and the Norwegian Environment Agency. Accelerometer sensors recorded an activity value every 8 seconds which were averaged over 5 minute intervals. Overall, data from the accelerometers covered an 8 year period, from 2008 to 2015, resulting in 1.5 million data recordings of activity.

Camera traps data

Camera trap detections of lynx were obtained from 327 camera traps (Reconyx HC500, PC900 & HP2X, Holmen, Wisconsint, USA) distributed in the study area within the frames of the SCANDCAM project. Camera traps were placed in order to maximize lynx encounters on locations where lynx were expected to travel. They were active year-round with SD cards and batteries changed every couple of months; more details on camera traps placement and period of activity can be found in Hofmeester *et al*. (2021) and in viltkamera.nina.no. Images were processed using an Artificial Intelligence system utilized within the SCANDCAM project; images of people were automatically deleted, and species were identifying firstly by the network and later checked by staff and students from the Norwegian Institute for Nature Research (NINA). Data used in this study resulted from 11 years of monitoring, from November 2010 to December 2020, for a total of 2292 independent detections of lynx.

Methods

The activity pattern of lynx has been shown to vary in amount and distribution during the day due to the impact of different factors (Heurich *et al*., 2014); I explored the major factors that affect activity by modelling accelerometer data only. In this way, only the most impactful variables on lynx activity pattern found in accelerometer models were used as parameters for making the comparison between accelerometer and camera trap datasets.
Firstly, some variables were added to both datasets: mean air temperature per hour, mean wind speed per hour, hours of daylight per day (hours of light from now on), moon phases per day and light phase per observation (with 4 levels: dawn, daylight, dusk and night).
The first two weather variables were obtained from 6 meteorological stations distributed across the study area (Trysil vegstasjon, Dombas – Nordigard, Gulsvik II, Oslo – Blindern, Hoydalsmo II and Nelaug), data are all from the Norwegian Climate Centre's website (https://seklima.met.no). These specific 6 meteorological stations have been selected after having done a screening of all the data collected by ~ 200 stations present in the study area. The aim of the selection was to find meteorological stations that have recorded weather data continuously, and with a time resolution of

hours, throughout a total period of 12 years (i.e. interval of time when accelerometer and camera traps data were collected). After the selection of meteorological stations has been done, the weather data have been adapted to both accelerometer and camera traps data, attributing to each observations the weather data from the spatially closest meteorological station.
The light variables were calculated using the Suncalc package version 0.5.0. (Thieurmel & Elmarhraoui, 2019) in R 1.4.1717. The Suncalc package uses date, time and coordinates of data for extrapolating respective times of daylight changes and moon phases. Therefore, each light variable is geo-referred and accounts for change in daylight over the year. In this study, getSunlightTimes function has been used for obtaining datetime of sunrise, sunset, dusk and dawn from which the variables hours of light per day and light phase per observation were calculated; getMoonIllumination has been used for obtaining the continuous variable of moon phase (as circular data ranging from 0 to 1, where 0 = new moon and 1 = full moon). For the accelerometer data the coordinates used refer to the location of each lynx's initial capture; for the camera trap data the coordinates refer to each camera's location. All the analyses used Central European Time (CET/UTM+1). Distribution and locations of camera traps, lynx captures, and meteorological stations selected can be found in Fig. 2.

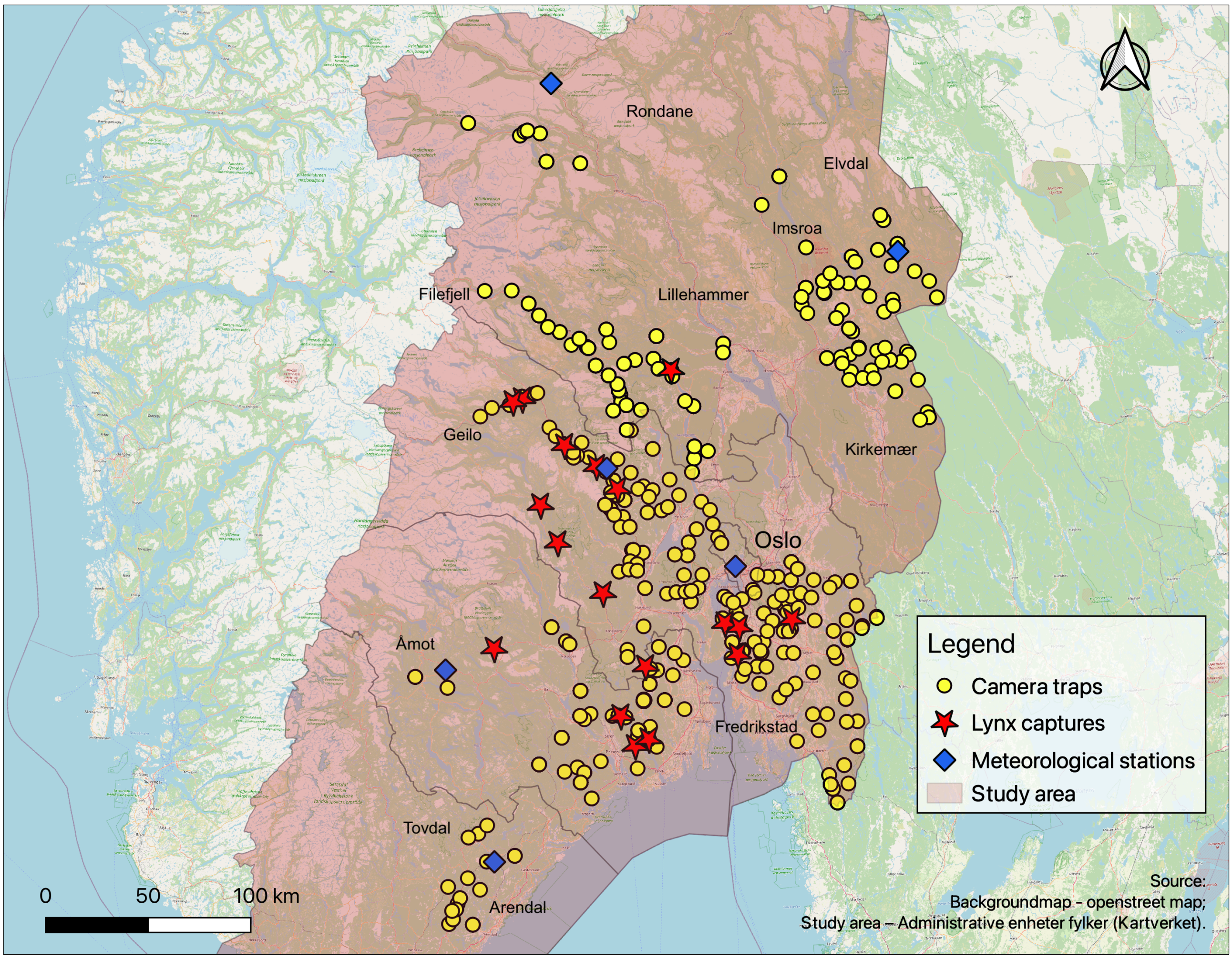


Fig.2 : Map with distribution of camera traps, lynx captures and meteorological stations selected over the study area.

Accelerometer models

The accelerometers on our collars measured acceleration in two axis: forward/backward motion (axis x) and sideward/rotary motion (axis y) (Heurich *et al*., 2014). The values recorded range from 0 (no activity) to 255 (± 2G) and they were determined based on the average values across 5 minutes. Only x-activity values were analysed in this study since the two axis are highly correlated (Heurich *et al*., 2014). Based on previous studies using identical equipment from the same manufacturer (Heurich *et al*., 2014; Podolski *et al*., 2013) all values from 0 to 27 were considered as "inactive" while all the values that range from 28 until 255 were considered as "active". Therefore, x-activity values were utilized to assess two different measurements of activity: amount of activity time per day (i.e. percentage of time the lynx spent active per day) and distribution of activity throughout the day as a binomial variable where 0 = recordings of inactivity (value <= 27) and 1 = recordings of activity (value > 27). The measurements were therefore used as response variables in two different General Mixed Effect Model TMBs (GLMMTMB) (Model 1 – Model 2). This type of model accounts for random effects as well as temporal correlation within the data. In both models, the individual ID of each lynx was set as a random effect for taking into account possible random variation in activity pattern between individuals. Moreover, ar1() covariance structure (autoregressive order-1, homogeneous variance) was applied to date random effects since activity pattern of lynx show a cyclical trend that is repeated every day and data that are recorded continuously (like accelerometer data) are expected to be temporally correlated.
The two models with the mentioned response variables and respective exploratory variables are shown in Table 1.

Models	Variable	Scale	Value range	Description
Model 1	Percentage of activity per day (**Response variable**)	Continuous	0 - 100 (%)	Percentage of time the lynx spent active during the day
Model 1	Hours of light	Continuous	0.00 - 19.05	Number of hours of light during the day
Model 1	Moon phases	Continuous	0.00 - 1.00	Different moon phases as circular data from 0 = new moon to 1 = full moon
Model 1	Season	Categorical	Winter, spring, summer, fall	Time of the year according to seasonality (21.3; 21.6; 23.9; 21.12)
Model 1	Mean air temperature per day	Continuous	-21.8 - 25.3 (C°)	Value of air temperature averaged per day
Model 1	Mean wind speed per day	Continuous	0.0 - 8.6 (m/s)	Value of wind speed averaged per day
Model 1 - Model 2	Date	Factor	From 24/03/2008 to 07/02/2015	Date of recordings
Model 1 - Model 2	Animal ID	Categorical	1 - 18	Lynx individual ID
Model 2	Activity/Inactivity (**Response variable**)	Binomial	0 - 1	0 = recordings of inactivity (value <= 27) and 1 = recordings of activity (value > 27)
Model 2	Phases of a day	Categorical	Daylight, night, dawn to sunrise, sunset to dusk	Phase of the day according to day, night and civil twilight (sunrise and sunset)
Model 2	Hour	Continuous	0 - 24	Hour of the day
Model 2	Mean air temperature per hour	Continuous	-21.8 - 25.3 (C°)	Value of air temperature averaged per hour
Model 2	Mean wind speed per hour	Continuous	0.0 - 8.6 (m/s)	Value of wind speed averaged per hour

Table 1: Model 1, Model 2 and respective variables.

Activity estimation overlap between accelerometer and camera traps

From the accelerometer models results, the variables that affected significantly amount and/or distribution of activity per day have been identified. Therefore, these variables have been considered as the main factors affecting variation in daily activity of lynx and hence used as parameters for the comparison between accelerometer and camera traps data.

In order to compare activity pattern estimations from accelerometers and camera traps, temporal overlap analysis was conducted. Overlap analyses were conducted in R 1.4.1717 using package Overlap version 0.3.4 (Meredith & Ridout 2021). This package calculates a non-parametric estimation of temporal overlap between the two datasets, using Kernel density estimation. The coefficient of overlap is a continuous variable that ranges from 0 to 1, where 0 equals no overlap and 1 implies total overlap. The coefficient is defined by different Δ estimators that account for different sample sizes respectively. In this case, a $\Delta 4$ estimator was chosen for each overlap analysis as advised by Meredith & Ridout (2021) for large sample (> 75). Moreover, this package plots a probability function of the distribution of the data, resulting in a visual representation of the two activity pattern estimations and the respective areas overlapped (Edward *et al*., 2020). Confidence intervals for each analysis were calculated using 1000 bootstrap, basic0 values were selected.

Determining how many camera traps are needed to produce reliable estimates of activity pattern

In order to define the number of camera traps needed to produce reliable estimates of activity pattern, I down-sampled the camera trap dataset and repeated the overlap analyses with the accelerometer dataset.
For down-sampling the dataset, I randomly selected one time 50%, 40%, 30%, 20%, 10% and 5% of the total number of camera trap from the main dataset. Hence, overlap analyses were repeated between each down-sampled camera trap dataset and the full accelerometer dataset following the same methodology as used in the previous. These overlap analyses have been made taking into consideration the same parameters used for the comparison in the previous overlap analysis.

Results

Models with accelerometer data

Amount of activity per day

The percentage of activity per day for all the individuals was 39.4% collectively, with a pronounced difference between the sexes (F = 36%; M = 41.5%). Taking into consideration seasonal changes, in fall lynx showed the highest percentage of daily activity (43.1%), followed by winter recordings (39.4%) and summer recordings (38.5%); lowest percentage of activity was recorded in spring (37.2%).

The candidate set of 15 GLMMTMB models with the response variable Percentage of activity per day were ranked using the Akaike Information Criterion (AIC), from the lowest to the highest AIC value (Tab. 2). The best model (Model 1 from now on) was selected as the one with the lowest AIC value. Model 1 shows that the variance of total amount of daily activity is affected by the predictors Hours of light per day ($p < 0.01$) and Season (fall: $p < 0.01$; winter: $p > 0.05$; spring: $p > 0.05$; summer: $p > 0.05$); it includes as random factors the Individual ID and the temporal correlation factor (ar1) on Date (*Corr* = 0.36). With regards to Model 1 predicted values, percentage of daily activity is predicted to decrease with the increase of hours of light per day (Fig. 3) and fall is predicted as the season with highest percentages of daily activity.

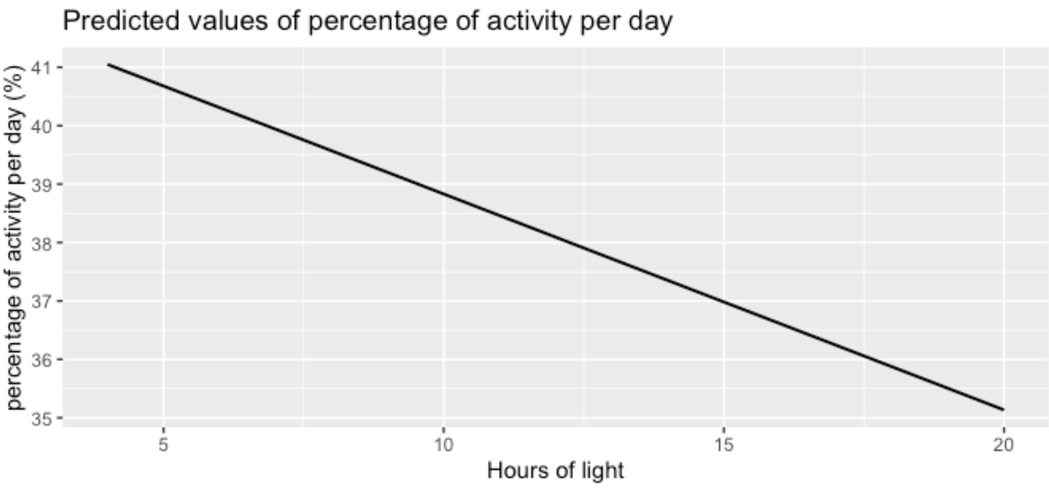


Fig. 3: Model 1 predicted values taking into consideration increase of number of hours of light per day.

Distribution of activity during the day

On average, the number of total recordings of activity (5 minute interval values > 27) per day were 113.5, while the number of total recordings of inactivity (5 minute interval values <= 27) per day were 172.6, out of 288 recordings each day. Looking into the different phases of the daily cycle, the highest percentage of activity values was recorded during dusk (55%), followed by night (48.8%), dawn (39%) and daylight (31.5%). The candidate set of 15 GLMMTMB models with the binomial response variable Activity/Inactivity (1-0) have been ranked and selected following the method used in the previous model “Amount of activity per day” (Tab. 3). The best model (Model 1 from now on) was selected as the one with the lowest AIC value. Model 1 has the explanatory variables: Hour of the day (Hour Sin and Hour Cos: $p > 0.05$), Phase of the day (called Lightfactor in the model, has dawn: $p > 0.05$; daylight: $p > 0.05$; dusk: $p > 0.05$; night: $p > 0.05$) and Mean Wind Speed ($p > 0.05$); it also includes the Individual ID and the temporal correlation factor (ar1) on Date (*Corr* = 0.39) as random factors. With regards to Model 1, predicted values and the different phases of a day, lynx were predicted to be more active during dusk, closely followed by night, while dawn and daylight were the two daily times where lynx were less active. Furthermore, the number of activity recordings (fix value > 27) was generally predicted to increase by each hour of the day starting from midnight. The same increasing trend in activity is seen following an increase of mean wind speed per hour .

	cond((Int))	disp((Int))	cond(Season)	cond(sLight_times)	cond(sAir_T)	cond(sMoon_times)	cond(sMean_Wind_Speed)	cond(Date)	family	df	logLik	AICc	delta	weight
m1	37.48846	+	+	−2.104203	NA	NA	NA	NA	gaussian(identity)	9	−20844.48	41707.00	0.000000	5.222804e−01
m2	37.50473	+	+	−2.141235	0.04761529	NA	NA	NA	gaussian(identity)	10	−20844.22	41708.49	1.490075	2.479352e−01
m3	37.48766	+	+	−2.104802	NA	0.013071802	NA	NA	gaussian(identity)	10	−20845.06	41710.16	3.165825	1.072639e−01
m4	37.49846	+	+	−2.105867	NA	NA	0.05914801	NA	gaussian(identity)	10	−20845.06	41710.17	3.171886	1.069393e−01
m5	−14.26365	+	+	−2.033154	NA	NA	NA	0.003473061	gaussian(identity)	10	−20847.31	41714.66	7.665679	1.130636e−02
m6	−14.28015	+	+	−2.033864	NA	0.018809117	NA	0.003474106	gaussian(identity)	11	−20847.89	41717.83	10.831275	2.322321e−03
m7	38.46100	+	+	NA	−0.97612108	NA	0.12522285	NA	gaussian(identity)	10	−20850.30	41720.65	13.652784	5.665515e−04
m8	38.47423	+	+	NA	−0.94115114	0.017696311	NA	NA	gaussian(identity)	10	−20850.44	41720.92	13.918596	4.960427e−04
m9	39.49751	+	+	NA	NA	NA	NA	NA	gaussian(identity)	8	−20852.48	41720.98	13.980232	4.809887e−04
m10	−14.23380	+	+	−1.991627	−0.05628256	0.019869655	0.03405228	0.003470038	gaussian(identity)	13	−20848.22	41722.51	15.510286	2.238143e−04
m11	38.45943	+	+	NA	−0.97735092	0.019548908	0.12548777	NA	gaussian(identity)	11	−20850.88	41723.81	16.809482	1.168883e−04
m12	−15.30502	+	NA	−2.505928	0.73397251	NA	NA	0.003641917	gaussian(identity)	8	−20855.41	41726.84	19.840248	2.568317e−05
m13	39.50690	+	+	NA	NA	0.004078122	0.04901456	NA	gaussian(identity)	10	−20853.65	41727.33	20.335861	2.004600e−05
m14	−16.85802	+	+	NA	NA	NA	NA	0.003777116	gaussian(identity)	9	−20854.80	41727.63	20.635285	1.725872e−05
m15	−15.30475	+	NA	−2.505754	0.73361421	0.004459600	NA	0.003641889	gaussian(identity)	9	−20855.99	41730.00	23.007534	5.270857e−06

Tab. 2: Percentage of activity per day model selection.

	cond((Int))	disp((Int))	cond(Hour_cos)	cond(Hour_sin)	cond(Light_factor)	cond(sAir_T)	cond(sMean_Wind_Speed)	family	df	logLik	AICc	delta	weight
m1	−1.2329282	+	0.2220838	0.8175392	+	NA	0.01361672	binomial(logit)	10	−938965.6	1877951	0.000000	0.8718101637
m2	−1.2292966	+	0.2215445	0.8184973	+	0.015624411	0.01200362	binomial(logit)	11	−938966.6	1877955	3.867845	0.1260462788
m3	−1.2297528	+	0.2218167	0.8188024	+	0.022246268	NA	binomial(logit)	10	−938971.8	1877964	12.329490	0.0018327672
m4	−1.2353300	+	0.2226860	0.8174143	+	NA	NA	binomial(logit)	9	−938974.6	1877967	15.878417	0.0003107903
m5	−0.5000258	+	NA	NA	+	NA	0.02098204	binomial(logit)	8	−952582.7	1905181	27230.087314	0.0000000000
m6	−0.5010144	+	NA	NA	+	−0.003538301	0.02134531	binomial(logit)	9	−952586.7	1905191	27240.130406	0.0000000000
m7	−0.5037214	+	NA	NA	+	NA	NA	binomial(logit)	7	−952611.3	1905237	27285.414715	0.0000000000
m8	−0.5012703	+	NA	NA	+	0.008216923	NA	binomial(logit)	8	−952614.6	1905245	27293.911809	0.0000000000
m9	−0.9081348	+	0.2986947	0.6707269	NA	−0.466547685	0.02238604	binomial(logit)	8	−960484.9	1920986	43034.472404	0.0000000000
m10	−0.9090113	+	0.2992887	0.6712685	NA	−0.452172747	NA	binomial(logit)	7	−960515.6	1921045	43094.014163	0.0000000000
m11	−0.9139780	+	0.3000509	0.6936933	NA	NA	−0.03649890	binomial(logit)	7	−963795.3	1927605	49653.279192	0.0000000000
m12	−0.9130286	+	0.2990305	0.6938822	NA	NA	NA	binomial(logit)	6	−963894.5	1927801	49849.827511	0.0000000000
m13	−0.4723965	+	NA	NA	NA	−0.521997720	0.03486889	binomial(logit)	6	−974636.9	1949286	71334.621633	0.0000000000
m14	−0.4732439	+	NA	NA	NA	−0.499484905	NA	binomial(logit)	5	−974720.4	1949451	71499.501372	0.0000000000
m15	−0.4627404	+	NA	NA	NA	NA	−0.02965518	binomial(logit)	5	−978730.0	1957470	79518.763943	0.0000000000

Tab. 3: Activity/Inactivity model selection.

Overlap analyses

Light, and the distribution of it during the day, was identified as the main factor affecting variation in daily activity of lynx (Fig.4). This result is in line with previous studies (see Heurich *et al.*, 2014). For this reason, the overlap analyses between camera and collar data were made while accounting for seasonal changes in the distribution of daylight during the year, and the subsequent change in activity pattern. Hence, 3 subsets of the accelerometer dataset and 3 subsets of the camera trap dataset were made, as well as 3 different overlap analyses, considering: from 5 to 7 hours of light per day (Fig. 5a), from 11 to 13 hours of light per day (Fig. 5b) and from 17 to 19 hours of light per day (Fig. 5c). The analyses of data within the interval from 5 to 7 hours of light per day gave an estimate of overlap of 0.90 (CI 95%: 0.87 - 0.93). While the analyses of data from 11 to 13 hours of light per day had an estimate of overlap of 0.95 (CI 95%: 0.92 - 0.97). Finally, the analyses of data from 17 to 19 hours of light per day had an estimate of overlap of 0.96 (CI 95%: 0.93 - 0.99).

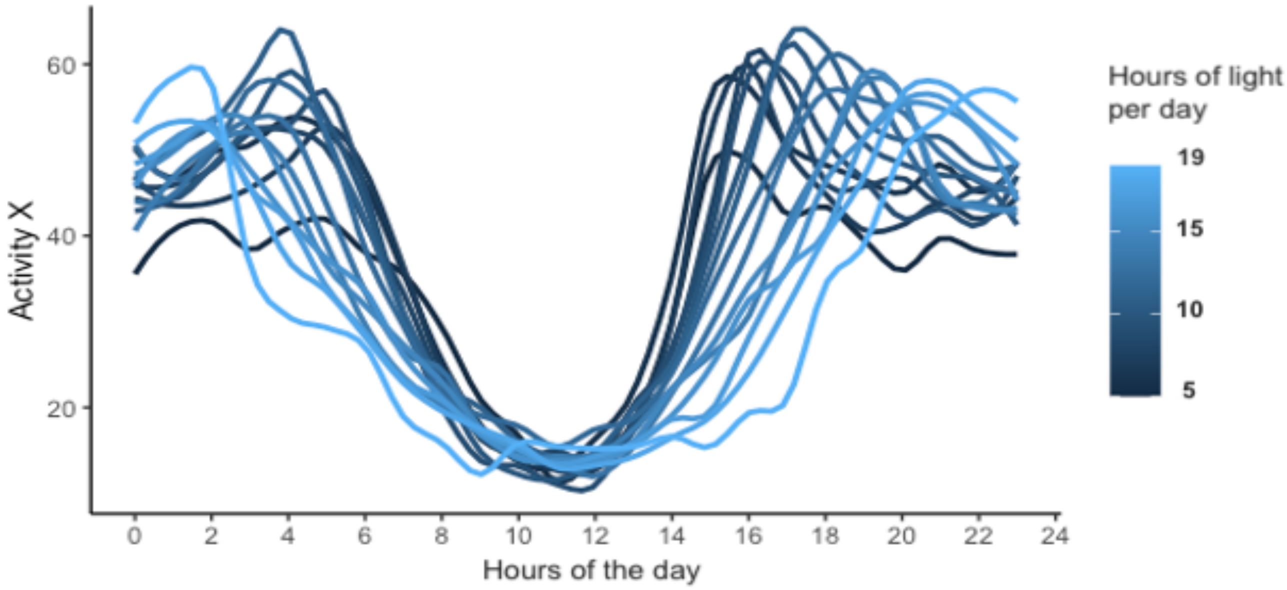
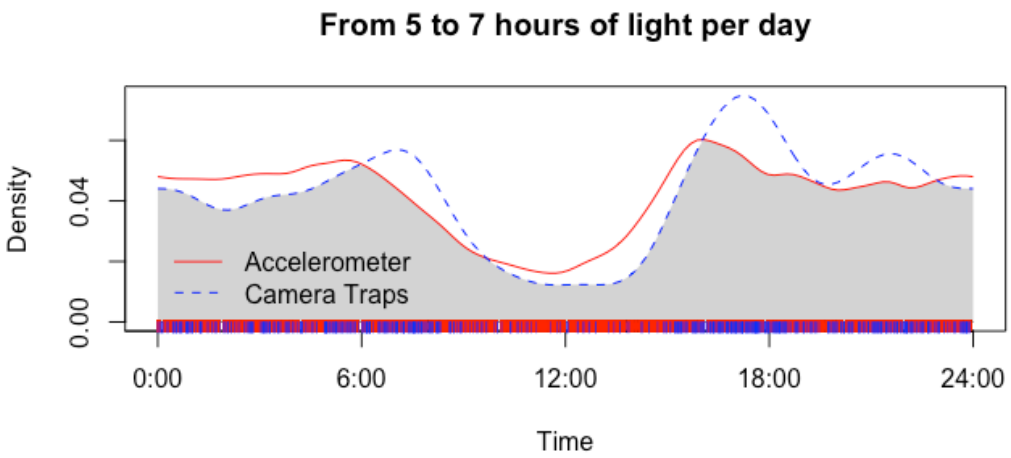
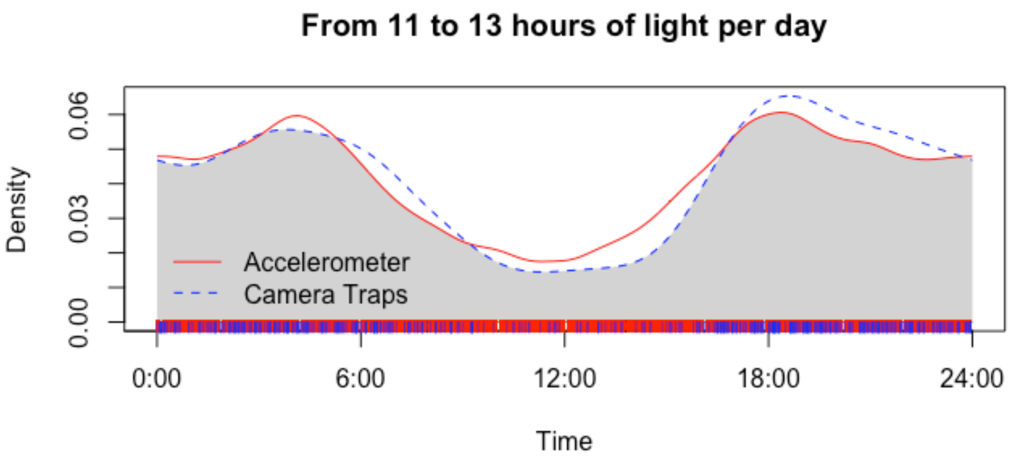


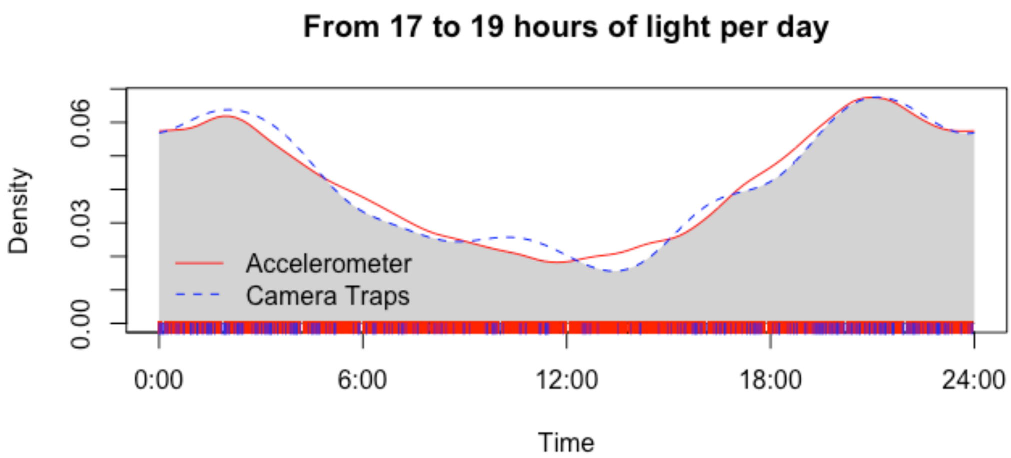
Fig. 4: Using accelerometer dataset: plot of activity X values over the day (averaged across all individuals) in relation with hours of light per day.



5a.



5b.



5c.

Fig. 5: Overlap analyses between accelerometer and camera traps data within the interval: from 5 to 7 hours of light per day (5a), from 11 to 13 hours of light per day (5b) and from 17 to 19 hours of light per day (5c).

Determining how many camera traps are needed to produce reliable estimates of activity pattern

When considering the full camera trap dataset and the down-sampled camera traps datasets with 50%, 40%, 30% and 20% of camera traps used, estimates of overlap showed a general stable trend, ranging from 0.88 to 0.96. On the other hand, the overlap estimates decreased consistently using 10% and 5% of camera traps from the original dataset (i.e. 33 and 16 total number of camera traps used respectively), ending with the lowest estimate of 0.73 within the interval 17 to 19 hours of light (Tab. 4 and Fig. 6). All the overlap graphs results can be found in Appendix I.

Hours of light per day	Percentage of camera traps dataset used	Number of detections	Estimate of overlap	%95 C.I.
5 to 7	Full dataset (327 camera traps)	639	**0.90**	0.87 - 0.93
11 to 13	Full dataset (327 camera traps)	552	**0.95**	0.92 - 0.97
17 to 19	Full dataset (327 camera traps)	333	**0.96**	0.93 - 0.99
5 to 7	50% (162 camera traps)	312	**0.89**	0.85 - 0.93
11 to 13	50% (162 camera traps)	332	**0.93**	0.89 - 0.97
17 to 19	50% (162 camera traps)	165	**0.91**	0.86 - 0.96
5 to 7	40% (130 camera traps)	294	**0.88**	0.84 - 0.92
11 to 13	40% (130 camera traps)	290	**0.90**	0.86 - 0.94
17 to 19	40% (130 camera traps)	157	**0.91**	0.86 - 0.96
5 to 7	30% (98 camera traps)	116	**0.90**	0.83 - 0.95
11 to 13	30% (98 camera traps)	118	**0.93**	0.87 - 0.98
17 to 19	30% (98 camera traps)	52	**0.92**	0.83 - 0.99
5 to 7	20% (65 camera traps)	141	**0.90**	0.85 - 0.95
11 to 13	20% (65 camera traps)	130	**0.92**	0.86 - 0.97
17 to 19	20% (65 camera traps)	96	**0.91**	0.83 - 0.97
5 to 7	10% (33 camera traps)	67	**0.90**	0.76 - 0.92
11 to 13	10% (33 camera traps)	47	**0.91**	0.81 - 0.98
17 to 19	10% (33 camera traps)	35	**0.83**	0.70 - 0.94
5 to 7	5% (16 camera traps)	24	**0.77**	0.62 - 0.90
11 to 13	5% (16 camera traps)	35	**0.84**	0.72 - 0.94
17 to 19	5% (16 camera traps)	11	**0.73**	0.48 - 0.92

Tab. 4: Summary of overlap analyses on full camera trap dataset and using reduced camera trap datasets.

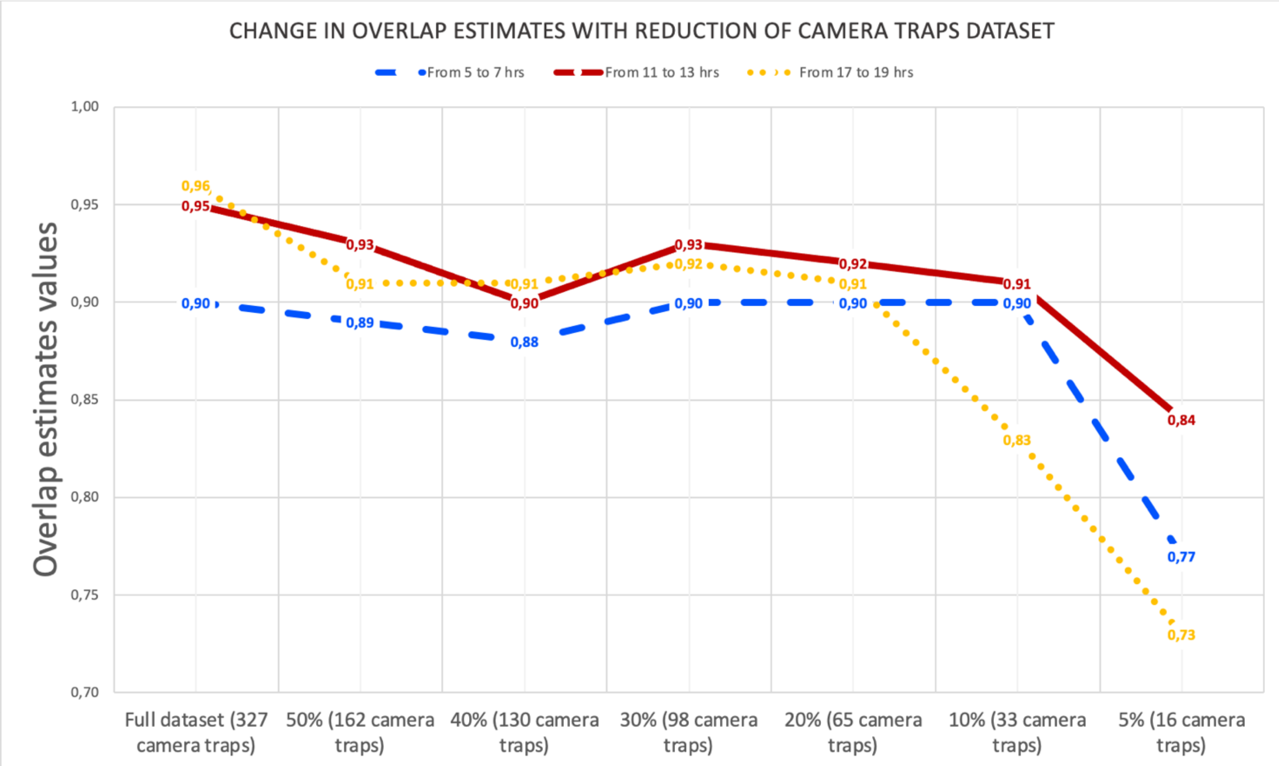


Fig. 6: Graph of overlap estimates with full camera trap dataset and reduced camera trap datasets.

Discussion

Studying the activity pattern of lynx using accelerometer data

Accelerometer recordings open a world of opportunities for remotely studying behaviors of hard-to-observe cryptic wildlife in detail (Kays *et al*., 2015; Brown *et al*., 2013; Gervasi *et al*., 2006). Differentiating fine scaled behavioural activities using activity sensor data requires a training dataset (i.e. direct observations) that can be used to calibrate the interpretation of the sensor values (Gonzales *et al*., 2014). A recently published paper on Canadian lynx *Lynx canadensis* presents a first study that attempts to classify four major behavioural activities (chewing, not moving, grooming and walking) from accelerometer data based on direct observations of the animals in the wild (Studd *et al*., 2021). For Eurasian lynx, an observational study involving accelerometer has still not been published, however a study made by Podolski *et al*. mentions an unpublished preliminary study with a captive lynx that allowed the definition of a threshold to discriminate between activity and resting values (Podolski *et al*., 2013). In this l study, accelerometer values were divided in two main categories: values from 0 to 27 as inactive behaviour, values from 28 to 255 as active behaviour. This preliminary differentiation took into account the sensitivity of the accelerometer and the fact that some light head shakings or movement of the collars were recorded with values above 0. Thanks to the threshold defined by Podolski *et al*., it is possible to model accelerometer values for obtaining an overview of factors that influence this species diel activity (Krop-Benesch *et al.,* 2013).

In this study, two models have been developed for analyzing factors that affect firstly the amount of daily activity and secondly the distribution of the activity over the day of Eurasian lynx in southeastern Norway.

The first model assessed the impact of some variables on the change of the amount of activity per day. The explanatory variables considered were: hours of light per day, moon phases, season, mean air temperature, mean wind speed. With regards to the weather variables, it is challenging to find weather data uninterruptedly collected over long period, such as the period of GPS collars data collection in this study (8 total years), with a temporal resolution of days or hours and good accuracy. However, it might be interesting for future studies to investigate more potential weather factors, than the ones considered here, affecting daily amount of lynx activity.
Nevertheless, from my best model I have obtained results that are in line with previous studies identifying the duration of daylight as an important factor impacting lynx activity (Heurich *et al*., 2014; Podolski *et al*., 2013). My analyses showed that activity changed following the duration of daylight: the amount of daily activity has been previously predicted to decrease with the increase of hours of light. Lynx have a fundamental nocturnal and crepuscular activity rhythm (Heurich *et al*., 2014; Schimdt, 1999) so that an increase of the duration of daylight leads to shorter periods of darkness and hence results in a limitation of their potential activity time. According to the best model, seasonality was also a factor influencing the change in amount of activity, which is not surprising since it co-varies with change in duration of daylight. However, season also embraces other changes such as the presence of snow, changes in availability and distribution of prey, and the life-cycle of lynx. Moreover, fall was the season that recorded highest percentages of daily activity. This result is in line with a previous study conducted by Heurich *et al*., where they hypothesized that the increase of activity related to fall was due to a higher hunting effort (Heurich *et al*., 2014). In fact, despite the fact that lynx are expected to increase their activity in the mating season (from February to March), dispersion of prey might have a bigger impact on daily movements and activity of this species in northern Europe (Heurich *et al*., 2014). In winter, snow can be an obstacle to prey movements which leads to their clustering around supplementary feeding stations, or patches of dense forest with less snow, hence being more easily found by lynx (Heurich *et al*., 2014). However, more studies are needed for a deeper investigation of how lynx movements and daily activity are related to snow depth and prey movements.

The second model studied the distribution of lynx activity across the day, using a more fragmentated response variable where each record from the accelerometer was considered as an inactivity or activity value (0-1). An alternative way of formulating the response variable could have been aggregating or averaging the record values. Although, this would have implied the loss of the extraordinary temporal resolution provided by the accelerometer (a recording of activity value every 5 minute). As in the previous model, the explanatory variables used (phase of the day, hour of the day, mean air temperature and mean wind speed) were limited compared to the total number of factors that might affect the distribution of lynx activity during the day.

For example, factors like gender differences, reproductive season, reproductive status, predation events and human disturbances could significantly impact the time the lynx is active during the day (Heurich *et al*., 2014; Podolski *et al*., 2013; Schmidt *et al*., 1999). Some major differences between sex could occur during the mating season, when males cover larger areas and travel longer, hence being active for longer periods over the day compared to females (Heurich *et al*., 2014; Schimdt, 1999). It has also already been shown that reproductive females with kittens are less nocturnal than adult males (Heurich *et al*., 2014; Schimdt, 1999). Furthermore, the reproductive status affects the amount and distribution of activity over the day. Females with kittens are active for longer time over the days from May to August compared to females without kittens (Schimdt, 1999). Also predation events could impact lynx activity during the day as shown by Podolski *et al*.: lynx are less active in days with kills compared to days without kills (Podolski *et al*., 2013). Finally, lynx might show different activity patterns if closer to humans, this could be explained as an avoidance behaviour carried out by lynx (Podolski *et al*., 2013). In a study that screened nocturnal activity of 62 wildlife mammal species (including 10 wild feline species) from 6 different continents, it has been shown how human disturbance generally increases wildlife nocturnality (Gaynor *et al*., 2018).

Therefore, the results of the model need to be considered as a first exploration of some of the factors that can potentially influence the timing of lynx activity and resting over the day. The best model included the explanatory variables “phase of the day”, “hour of the day” and “mean wind speed”. Phase of the day is a variable based on the change of light during the day (with the categories: dawn, daylight, dusk and night), suggesting that lynx activity pattern is modulated depending on light and specifically that lynx are more active during dusk and night time. This result is again in line with previous studies (Heurich *et al*., 2014; Podolski *et al*., 2013; Schmidt *et al*., 1999). The reason why lynx are mainly active during dusk is related mostly to the activity pattern of their main prey species in Europe, the roe deer, which are most active during crepuscular hours (Podolski *et al*., 2013). Nocturnal activity is characteristic for feline species, that have highly developed sense of sight, smell and hearing and they can take advantage of prey vulnerability during this time of the day (Podolski *et al*., 2013; Schimdt, 1999). In addition, Schimdt (1999) discussed in his study how lynx activity does not simply vary according to when the prey is active, it also depends on the type of activity the prey is displaying (Schimdt, 1999). The fact that in my model the distribution of daily activity depends on the hour of the day was expected since each hour of the day has different degrees of light and hence the lynx display different levels of activity depending on being during day time, twilight or night hours. On the other hand, taking into account mean wind speed variable, it is possible that the presence of this variable in the best model happened to be independent from biologically effects. Indeed, this specific variable, used in both this and the previous activity model, has values recorded from each meteorological station but wind speed has actually very localized change of speed depending for example from presence or absence of natural barriers or presence or absence of open spaces. For this reason, the influence of this variable is hard to assess properly. Further studies should find a more locally precise wind variable and investigate in greater detail how this environmental variable could have a direct or indirect effect on lynx behaviour. In fact, wind speed might influence lynx activity since it affects its main prey’s movements and activity: for example, roe deer flee at longer distances when walking down wind compared to when they walk up wind or with calm wind (Boer *et al*., 2004).

Another important variable which influences lynx activity but needs to be carefully interpreted is the temperature. In this study, temperature was included in both models but it did not seem to have a major effect on either the amount or the distribution of lynx daily activity. Despite my results, temperature is often mentioned in the literature as a contributor in changing lynx activity pattern (Heurich *et al*., 2014; Podolski *et al*., 2013; Rockhill *et al*., 2013). A study made in 2013 found that with an increase of 10°C of mean air temperature per day, lynx decrease their time of daily activity by 30 minutes, this might be due indirectly to the impact that temperature has on roe deer activity and directly being a strategy that lynx adopt for decreasing energetic cost of movements in periods of very warm weather (Podolski *et al*., 2013). Temperature may also influence the way in which prey scent is carried, which may influence their detectability by lynx (Eriksen *et al*., 2011).

In summary, the models derived in this study have not found or investigated new factors affecting lynx activity compared to literature. However, they closely confirm what other studies had already found: that the duration and timing of daylight periods have a major impact on daily activity of Eurasian lynx in northern Europe (Heurich *et al*., 2014; Podolski *et al*., 2013; Schmidt *et al*., 1999).

Comparison of activity estimations from accelerometer and from camera traps

For the study of activity patterns, accelerometer data can be used as control data in a comparison with camera traps data since they record activity continuously with an averaged value every 5 minute, which allows the production of a reasonably accurate estimate of diel activity curve (Kays *et al*., 2015; Brown *et al*., 2013; Gervasi *et al*., 2006). Seeing the nature of accelerometer data, and the remarkable amount of them available for this study, it has been possible to investigate change in lynx daily activity throughout the year. Particularly, in period with longer daylight (from 17 to 19 hours of light) the activity curve appeared more attenuated, with a peak of activity occurring at 2-3 am (dawn) and 9-10 pm (dusk). Instead, in periods with lower duration of daylight (from to 5 to 7 hours of light) the activity curve displayed shorter intervals of low activity limited to a few central hours of the day and a longer period of activity coinciding with longer nights. Moreover, during this low light period, the change of activity (from resting to being active) is more accentuated and peaks of activity are around 5-6 am (slightly before dawn) and 3-4 pm (dusk).

Camera trap estimations produced very similar activity curves compared to those estimated from accelerometer data. For each of the three overlap analyses made considering change of daylight, camera traps detections followed the patterns estimated by accelerometers with high coefficients of overlap: 0.90 (from 5 to 7 hours of light), 0.95 (from 11 to 13 hours of light) and 0.96 (from 17 to 19 hours of light). It is crucial to remember that in this study we had an abundance of camera traps placed (327 total camera traps) from which we obtained more than 2200 detections of lynx over a long period of time (11 years). In wildlife studies it is not always affordable to place that many camera traps as well as monitor them regularly (for example considering personnel required for changing batteries and downloading / classification of pictures) over long periods and large areas. In addition, taking into consideration camera traps placement, it is important to assess the design of camera trapping studies since it affects the reliability of activity estimations (Lashley *et al*., 2018). Previous studies that tested the activity estimations obtained from camera traps, claimed that it would be preferable to randomly place camera traps for estimating activity curves, however, in wildlife studies it is common to choose specific camera traps location in order to maximize the detection probability of elusive species, such as Eurasian lynx (Lashley *et al*., 2018; Rowcliffe *et al*., 2014) because random placement will result in too few detections to analyse.

Despite the practical issues related to conducting camera trapping studies (i.e. number of camera traps, camera traps placement, length of the study, effort required for checking and placing camera traps and classifying images), the data obtained have major differences compared to collar activity sensor data, and these differences need to be discussed in detail. First of all, camera traps aim to detect all the individuals present in a specific area, in this way averaging activity pattern estimations over a population (Edward *et al*., 2020; Lashley *et al*., 2018; Frey *et al*., 2017). GPS collars, and relative activity sensors, record data on a specific individual, throughout its whole home range, resulting in a more comprehensive and location independent picture of activity from a sub-sample of individuals (Edward *et al*., 2020; Lashley *et al*., 2018; Frey *et al*., 2017). Secondly, some camera traps may capture animals only when outside of cover and/or moving close to the camera trap, this results in a bias since animals that are active in areas where the camera traps are not placed cannot be sampled (Lashely *et al*., 2018; Rowcliffe *et al*., 2014). Moreover, while camera traps can potentially collect data of activity over a population, they cannot easily track individual differences in activity pattern, as GPS collars do. In fact, if the target species do not allow for individual identification, variation within individuals cannot be taken into account in activity estimations obtained from camera traps. Some Eurasian lynx individuals photographed by camera traps can be identified thanks to specific spot pattern that varies between individuals, although, the identification is often challenging due to blurry photographs (especially when using infra-red flash) and incomplete detections (Avgan *et al*., 2014). Even when individual identification is possible, determination of other individual traits such as sex, age and reproductive status, are not always feasible (Avgan *et al*., 2014). Another important difference that occurs in activity estimation obtained from camera traps or from GPS collars, relies on the type of activity recorded from these two methodologies: accelerometers continuously record data resulting in a value from 0 to 255 for all 5 minutes interval, while camera traps exclusively record the animal when it is moving. Hence, camera traps mostly detect activity associated with a few specific behaviours such as walking or running, cutting out a wide range of activities that the animals perform on a daily basis (resting, grooming, eating, etc). Furthermore, the way camera traps collect data on activity (i.e. only detecting the animal while it is moving) do not easily allow for more challenging analysis of the activity pattern through, for example, statistical modelling that accounts for factors of impact. As a matter of fact, the data obtained from camera traps do not give any information on the activity displayed when the animal is not captured, which means: you only get data of a subset of activity (i.e. activities such as walking or running) but you do not get any data on other type of activities, but most important, you do not have data from periods of non-activity. For this reason, defining parameters such as amount or distribution of daily activity from camera traps detection, and how some environmental variables impact them, becomes difficult.

How many camera traps do you need to produce reliable estimates?

The choice of down sampling the number of camera traps used instead of down sampling the number of detections has been made taking into consideration the fact that randomly reducing the number of detections implies losing the pattern describe by the distribution of the detections over the day. Furthermore, defining the number of camera traps needed for obtaining reliable activity estimations might be a more useful information from a practical point of view when planning budgets and field logistics.

It is important to know how the activity estimations might change due to the number of detections used and therefore assess the accuracy of the estimations evaluating this aspect as well. Related to this, another key element to consider is how the probability of detection can vary and the fact that this affects the number of detections overall (Lashley *et al*., 2018). Activity pattern estimations from camera traps depend on the number of detections you are working with, indeed a bigger number of detections increase your probability of getting more accurate activity curves. The probability of detecting an animal through camera traps relies on several factors: the most important being an appropriate camera trapping technique that accounts for the ecology and status of the target species (Lashley *et al*., 2018).

In this study, the comparison between accelerometer estimations and down sampled camera trap datasets estimations was made taking into account the change in activity that occurs with the change of light during the year, i.e. when there are from 5 to 7 hours of daylight or from 11 to 13 hours of daylight or from 17 to 19 hours of daylight. The number of detections varied too between these latter three categories, the interval from 17 to 19 hours of daylight (falling within the summer season) has generally fewer detections compared to the other daylight categories. The reason why lynx are less captured by camera traps during the summer season might be related to seasonal variation in this species' activity. For example, between May and August, females with kittens are more active but move over smaller territories because they become entra-place foragers when kittens are so small as to have reduced mobility (Schimdt, 1999). As previously mentioned, males generally move over larger territories during the mating season compared to the rest of the year.

Overall, activity estimations from camera traps showed high coefficients of overlap with accelerometer estimations using at least 65 camera traps (20% of the original number of camera traps). With 65 camera traps the overlap estimates were: 0.90 (from 5 to 7 hours of daylight), 0.92 (from 11 to 13 hours of daylight) and 0.91 (from 17 to 19 hours of daylight) with numbers of detections ranging from 96 to 141. Instead, using the down sampled datasets with 33 (10% of the original number of camera traps) and 16 (5% of the original number of camera traps) camera traps showed a prominent decrease in values of overlap, ranging from 0.83 to 0.91 in the first case and from 0.77 to 0.84 in the second case. The number of detections using 33 total camera traps ranged from 35 to 67, while the number of detections using 16 total camera traps ranged from 11 to 24. The confidence intervals also dropped consistently from using 65 camera traps (CI 95%: 0.76 – 0.92; 0.81 – 0.98; 0.70 – 0.94) to 33 camera traps (CI 95%: 0.62 – 0.90; 0.72 – 0.94; 0.48 – 0.92). For this reason, using less than 65 camera traps and/or working with less than 96 detections is discouraged because it might led to inaccurate activity pattern estimations from camera traps. This result, only with regards to the number of the detections, is similar to what Lashley *et al*. found from the comparison between activity pattern estimations obtained from active and passive camera traps and GPS collars positions (Lashley *et al*., 2018). Although, another important aspect that has to be considered when assessing activity estimation is the shape that the activity curve displays. In matter of fact, even in the case where coefficients of overlap with accelerometer estimations were remarkably high, some relevant differences between the shape of the two curves occurred. See for example the difference in activity curve estimations obtained from 130 (40% of the original number of camera traps) and from 98 (30% of the original number of camera traps) total camera traps during the frame from 17 to 19 hours of light, the peaks of activity have different intensities and the curve that describes the activity during the day shows two slightly different patterns.

Conclusion

- New statistical methods have produced robust ways to compare different estimates of activity patterns derived from different field techniques that vary greatly in the degree of invasiveness and their impact on animal welfare;
- Accelerometer and activity sensors in GPS collars are a robust method for studying general activity pattern of wildlife with the potential of investigating behaviours at a very fine temporal scale;
- Camera traps can be used to estimate overall activity curves with comparable estimations to the ones obtained from accelerometers, however, it requires a large number of camera traps and proper camera trapping study design while keeping in mind the fundamental differences that occur between data collected from these two methodologies;
- A lower number of camera traps, and consequently a lower number of detections, results in a less accurate activity estimation from camera traps. This is particularly evident when using less than 65 camera traps and/or working with less than 96 detections.

Acknowledgement

This study has been possible thanks to the support of SCANDLYNX project and SCANDCAM project that have provided data of accelerometer and camera traps. I thank my first supervisor John Linnell, for helping formulate my thesis and reviewing my work step by step and for the language revision, and my other supervisors John Odden and Morten Odden for the support. I thank Jenny Mattisson for the helpful consultation. Last but not least I thank Olivier Devineau for the help in the statistical analyses.

References

Arnemo, J. M., Evans, A., & Fahlman, Å. (n.d.). *Biomedical Protocols for Free-ranging Brown Bears, Wolves, Wolverines and Lynx*. 14.

Avgan, B., Zimmermann, F., Güntert, M., Arıkan, F., & Breitenmoser, U. (2014). The first density estimation of an isolated Eurasian lynx population in southwest Asia. *Wildlife Biology*, *20*(4), 217–221. https://doi.org/10.2981/wlb.00025

Beltran, J. F., & Delibes, M. (1994). Environmental Determinants of Circadian Activity of Free-Ranging Iberian Lynxes. *Journal of Mammalogy*, *75*(2), 382–393. https://doi.org/10.2307/1382557

Boer, H. Y., Breukelen, L., Hootsmans, M. J. M., & Wieren, S. E. (2004). Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biology*, *10*(1), 35–41. https://doi.org/10.2981/wlb.2004.007

Brown, D. D., Kays, R., Wikelski, M., Wilson, R., & Klimley, A. (2013). Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry*, *1*(1), 20. https://doi.org/10.1186/2050-3385-1-20

Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2157–2162. https://doi.org/10.1098/rstb.2010.0107

Edwards, S., Noack, J., Heyns, L., & Rodenwoldt, D. (2021). Are camera traps a reliable method for estimating activity patterns? A case study comparing technologies for estimating brown hyaena activity curves. *Remote Sensing in Ecology and Conservation*, *7*(2), 129–138. https://doi.org/10.1002/rse2.175

Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H. P., Arnemo, J. M., Gundersen, H., Liberg, O., Linnell, J., Milner, J. M., Pedersen, H. C., Sand, H., Solberg, E. J., & Storaas, T. (2011). Activity patterns of predator and prey: A simultaneous study of GPS-collared wolves and moose. *Animal Behaviour*, *81*(2), 423–431. https://doi.org/10.1016/j.anbehav.2010.11.011

Frank, J. & Tovmo, M. 2021. Inventering av lodjur 2021. Bestandsovervåking av gaupe i 2021. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien. Nr 2-2021. 33 s. Grimsö och Trondheim, juni 2021

Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing in Ecology and Conservation*, *3*(3), 123–132. https://doi.org/10.1002/rse2.60

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Gervasi, V., Brunberg, S., & Swenson, J. E. (2006). An Individual-Based Method to Measure Animal Activity Levels: A Test on Brown Bears. *Wildlife Society Bulletin*, *34*(5), 1314–1319. https://doi.org/10.2193/0091-7648(2006)34[1314:AIMTMA]2.0.CO;2

Gervasi, V., Nilsen, E. B., Odden, J., Bouyer, Y., & Linnell, J. D. C. (2014). The spatio-temporal distribution of wild and domestic ungulates modulates lynx kill rates in a multi-use landscape. *Journal of Zoology*, *292*(3), 175–183. https://doi.org/10.1111/jzo.12088

González, L. A., Bishop-Hurley, G. J., Handcock, R. N., & Crossman, C. (2015). Behavioral classification of data from collars containing motion sensors in grazing cattle. *Computers and Electronics in Agriculture*, *110*, 91–102. https://doi.org/10.1016/j.compag.2014.10.018

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson, J., Odden, J., Persson, J., Rauset, G. R., Schmidt, K., & Linnell, J. D. C. (2014). Activity Patterns of Eurasian Lynx Are Modulated by Light Regime and Individual Traits over a Wide Latitudinal Range. *PLoS ONE*, *9*(12), e114143. https://doi.org/10.1371/journal.pone.0114143

Hofmeester, T. R., Thorsen, N. H., Cromsigt, J. P. G. M., Kindberg, J., Andrén, H., Linnell, J. D. C., & Odden, J. (2021). Effects of camera-trap placement and number on detection of members of a mammalian assemblage. *Ecosphere*, *12*(7). https://doi.org/10.1002/ecs2.3662

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Kelly, M. J., & Holub, E. L. (2008). Camera Trapping of Carnivores: Trap Success Among Camera Types and Across Species, and Habitat Selection by Species, on Salt Pond Mountain, Giles County, Virginia. *Northeastern Naturalist*, *15*(2), 249–262. https://doi.org/10.1656/1092-6194(2008)15[249:CTOCTS]2.0.CO;2

Krop-Benesch, A., Berger, A., Hofer, H., & Heurich, M. (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. https://doi.org/10.1080/11250003.2012.725777

Lashley, M. A., Cove, M. V., Chitwood, M. C., Penido, G., Gardner, B., DePerno, C. S., & Moorman, C. E. (2018). Estimating wildlife activity curves: Comparison of methods and sample size. *Scientific Reports*, *8*(1), 4173. https://doi.org/10.1038/s41598-018-22638-6

Lee, A. (2010). Circular data: Circular data. *Wiley Interdisciplinary Reviews: Computational Statistics*, *2*(4), 477–486. https://doi.org/10.1002/wics.98

Linnell, J. D. C., Broseth, H., Odden, J., & Nilsen, E. B. (2010). Sustainably Harvesting a Large Carnivore? Development of Eurasian Lynx Populations in Norway During 160 Years of Shifting Policy. *Environmental Management*, *45*(5), 1142–1154. https://doi.org/10.1007/s00267-010-9455-9

Löttker, P., Rummel, A., Traube, M., Stache, A., Šustr, P., Müller, J., & Heurich, M. (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. https://doi.org/10.2981/08-014

Lynam, A. J., Jenks, K. E., Tantipisanuh, N., Chutipong, W., Ngoprasert, D., Gale, G. A., Steinmetz, R., Sukmasuang, R., Bhumpakphan, N., & Grassman, L. I. (2013). *TERRESTRIAL ACTIVITY PATTERNS OF WILD CATS FROM CAMERA-TRAPPING*. 10.

Manfredi, C., Lucherini, M., Soler, L., Baglioni, J., Vidal, E. L., & Casanave, E. B. (2011). Activity and movement patterns of Geoffroy's cat in the grasslands of Argentina. *Mammalian Biology*, *76*(3), 313–319. https://doi.org/10.1016/j.mambio.2011.01.009

Meredith, M., & Ridout, M. (2021). *Overview of the overlap package*. 9.

Podolski, I., Belotti, E., Bufka, L., Reulen, H., & Heurich, M. (2013). Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx lynx* in relation to availability of kills. *Wildlife Biology*, *19*(1), 69–77. https://doi.org/10.2981/12-049

Roberts, C. P., Cain, J. W., & Cox, R. D. (2016). Application of activity sensors for estimating behavioral patterns. *Wildlife Society Bulletin*, *40*(4), 764–771. https://doi.org/10.1002/wsb.717

Rockhill, A. P., DePerno, C. S., & Powell, R. A. (2013). The Effect of Illumination and Time of Day on Movements of Bobcats (Lynx rufus). *PLoS ONE*, *8*(7), e69213. https://doi.org/10.1371/journal.pone.0069213

Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, *5*(11), 1170–1179. https://doi.org/10.1111/2041-210X.12278

Schmidt, K. (n.d.). *Variation in daily activity of the free-living Eurasian lynx (Lynx lynx) in Bia□owiezÇa Primeval Forest, Poland*. 9.

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, *56*(4), 740–749. https://doi.org/10.1111/aje.12557

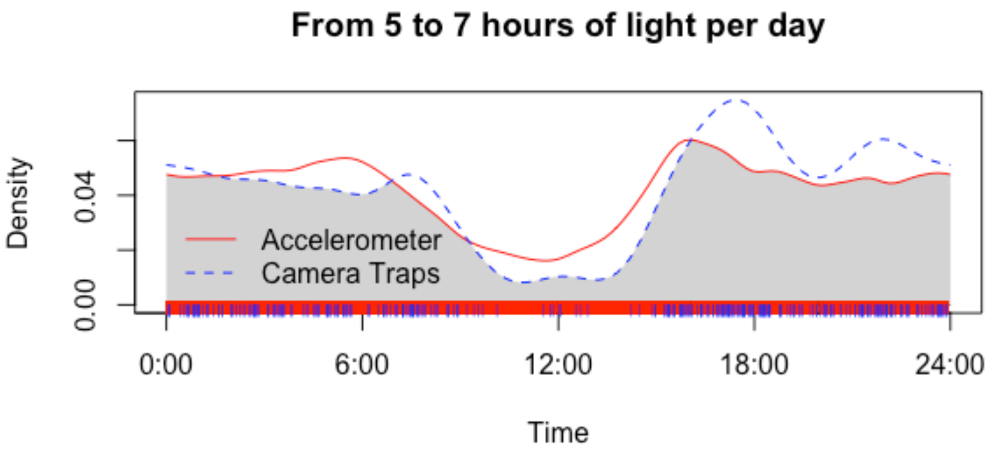
Sollmann, R., Furtado, M. M., Gardner, B., Hofer, H., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2011). Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation*, *144*(3), 1017–1024. https://doi.org/10.1016/j.biocon.2010.12.011

Studd, E. K., Derbyshire, R. E., Menzies, A. K., Simms, J. F., Humphries, M. M., Murray, D. L., & Boutin, S. (2021). The Purr-fect Catch: Using accelerometers and audio recorders to document kill rates and hunting behaviour of a small prey specialist. *Methods in Ecology and Evolution*, *12*(7), 1277–1287. https://doi.org/10.1111/2041-210X.13605

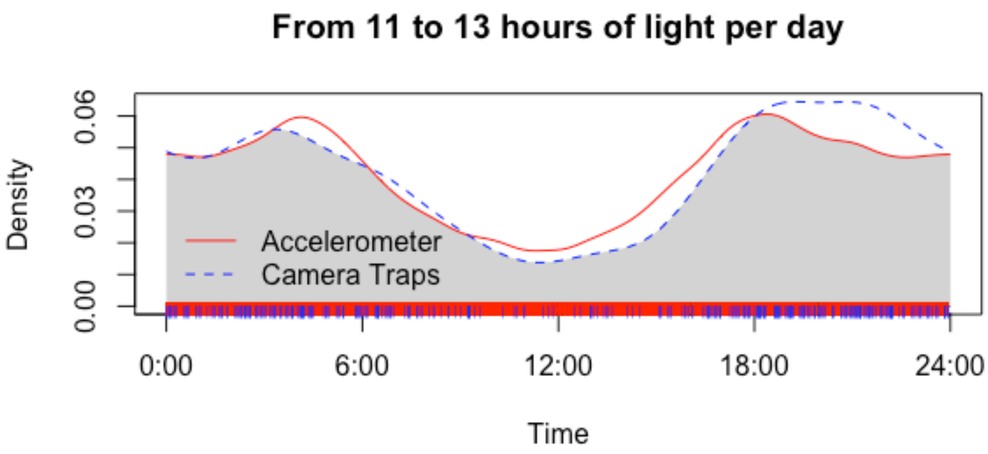
Tambling, C. J., Minnie, L., Meyer, J., Freeman, E. W., Santymire, R. M., Adendorff, J., & Kerley, G. I. H. (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology*, *69*(7), 1153–1161. https://doi.org/10.1007/s00265-015-1929-6

Wang, Y., Nickel, B., Rutishauser, M., Bryce, C. M., Williams, T. M., Elkaim, G., & Wilmers, C. C. (2015). Movement, resting, and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements. *Movement Ecology*, *3*(1), 2. https://doi.org/10.1186/s40462-015-0030-0

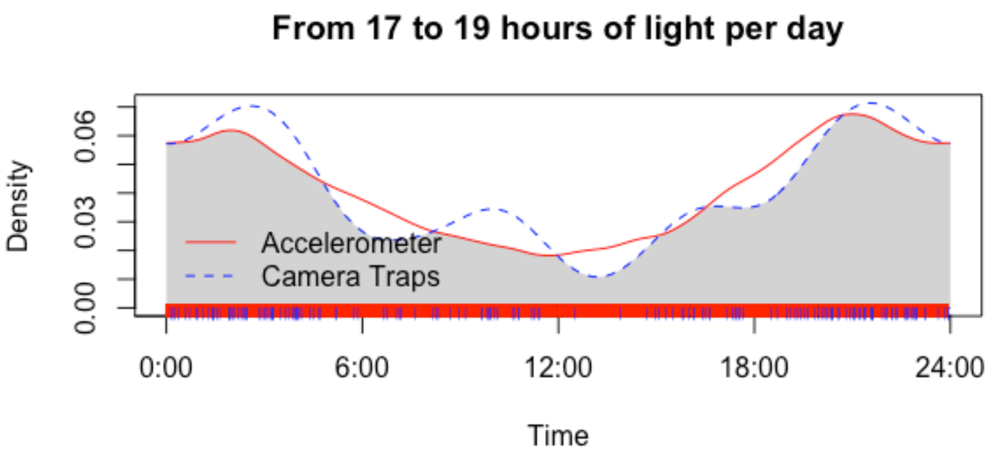
Appendix I



1a.

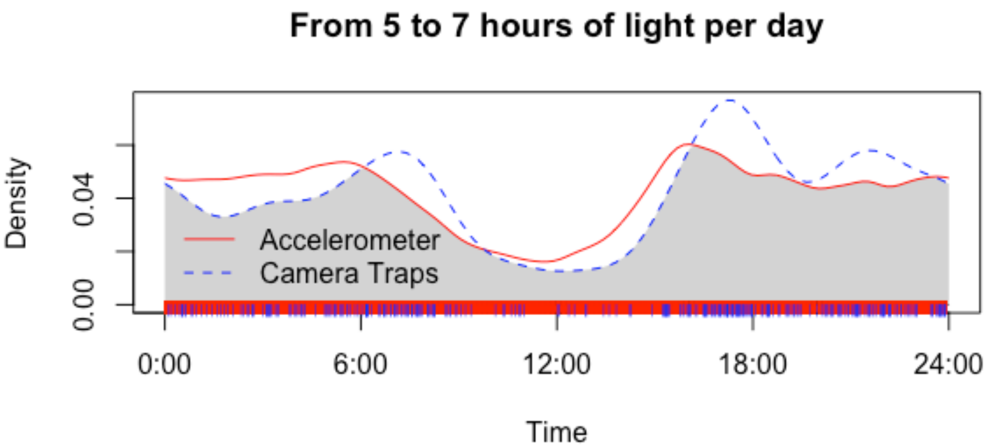


1b.

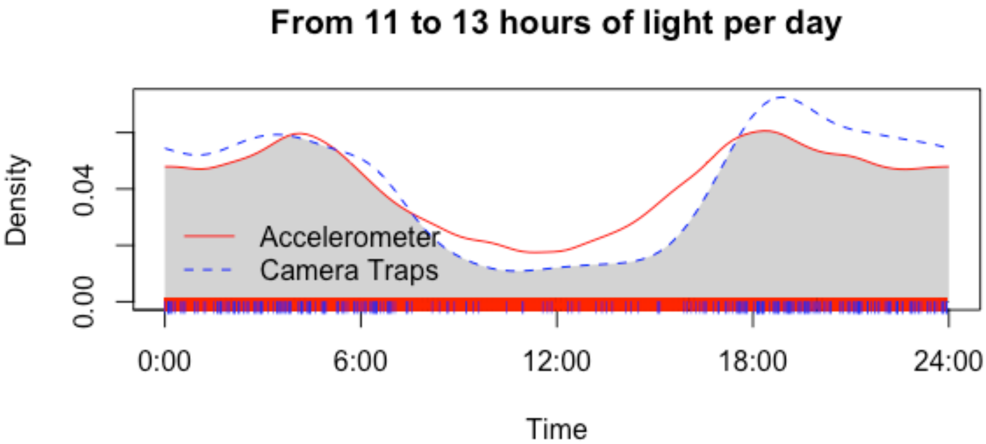


1c.

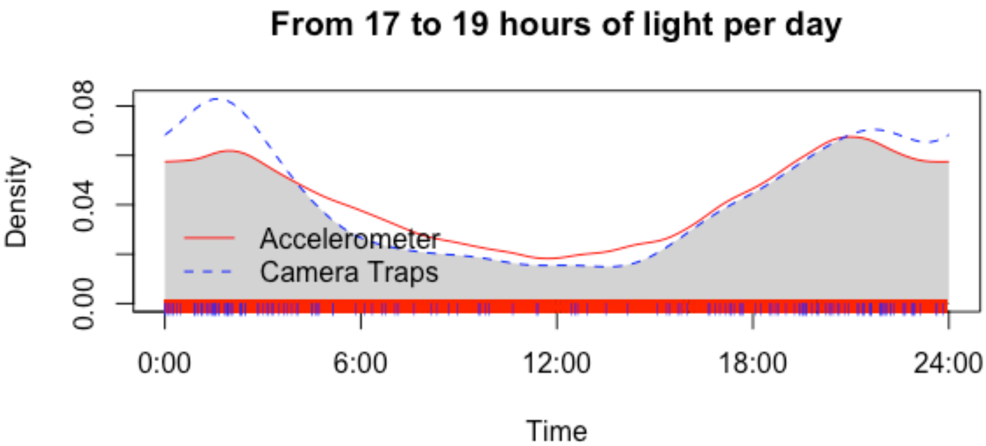
Fig. 1: Overlap analyses between accelerometer and 50% camera traps data (162 total number of camera traps used) within the interval: from 5 to 7 hours of light per day (1a), from 11 to 13 hours of light per day (1b) and from 17 to 19 hours of light per day (1c).



2a.

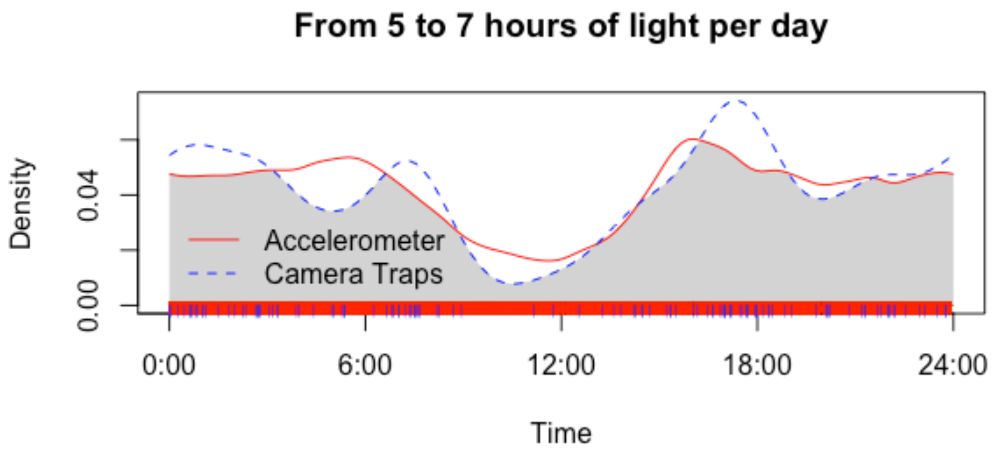


2b.

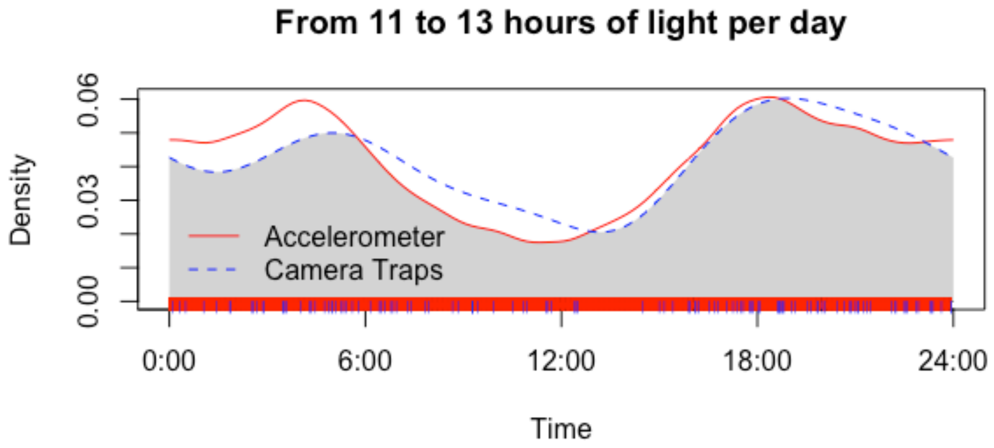


2c.

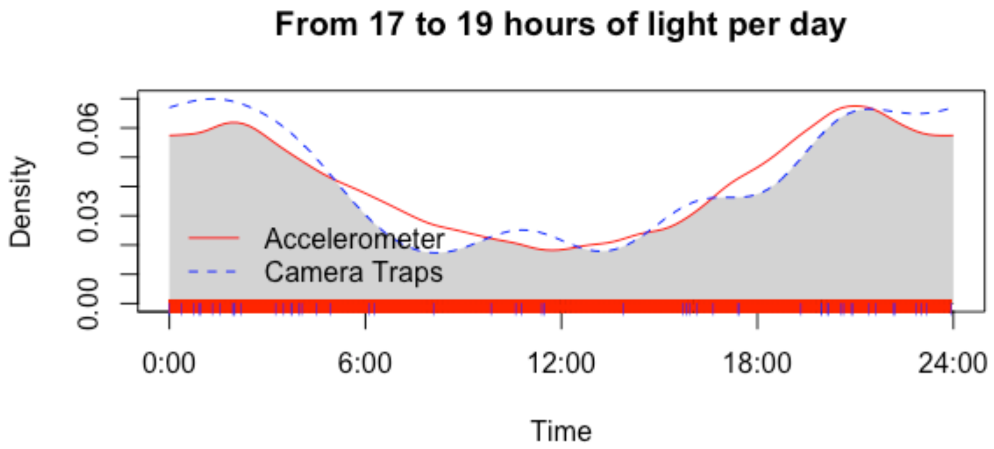
Fig. 2: Overlap analyses between accelerometer and 40% camera traps data (130 total number of camera traps used) within the interval: from 5 to 7 hours of light per day (2a), from 11 to 13 hours of light per day (2b) and from 17 to 19 hours of light per day (2c).



3a.

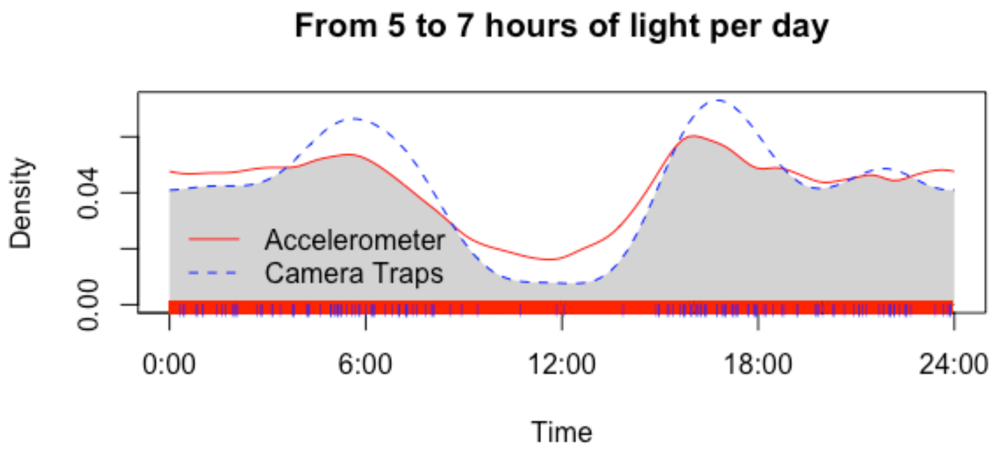


3b.

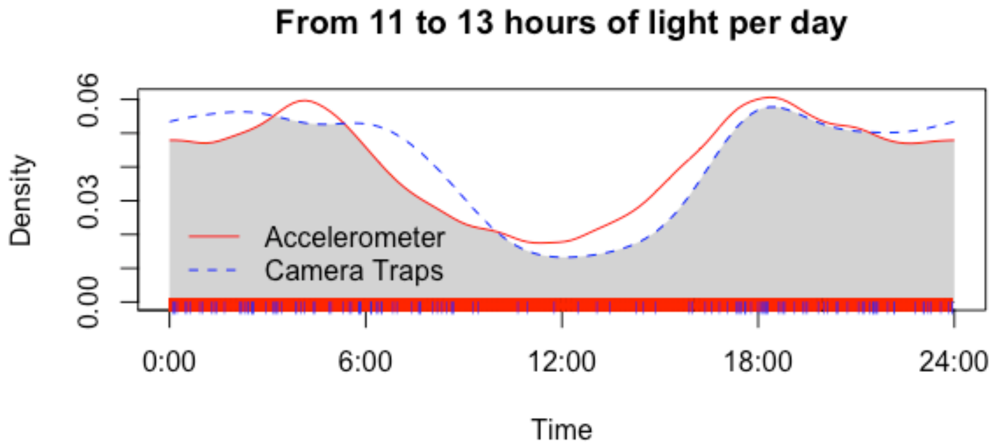


3c.

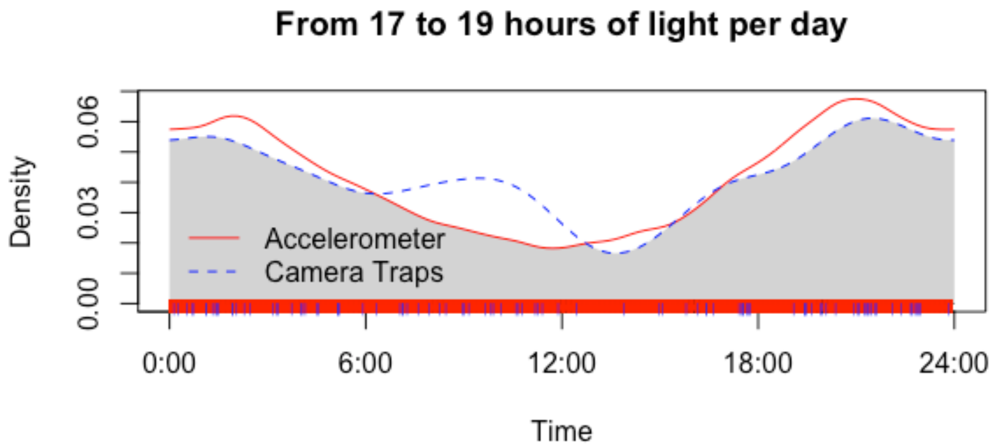
Fig. 3: Overlap analyses between accelerometer and 30% camera traps data (98 total number of camera traps used) within the interval: from 5 to 7 hours of light per day (3a), from 11 to 13 hours of light per day (3b) and from 17 to 19 hours of light per day (3c).



4a.

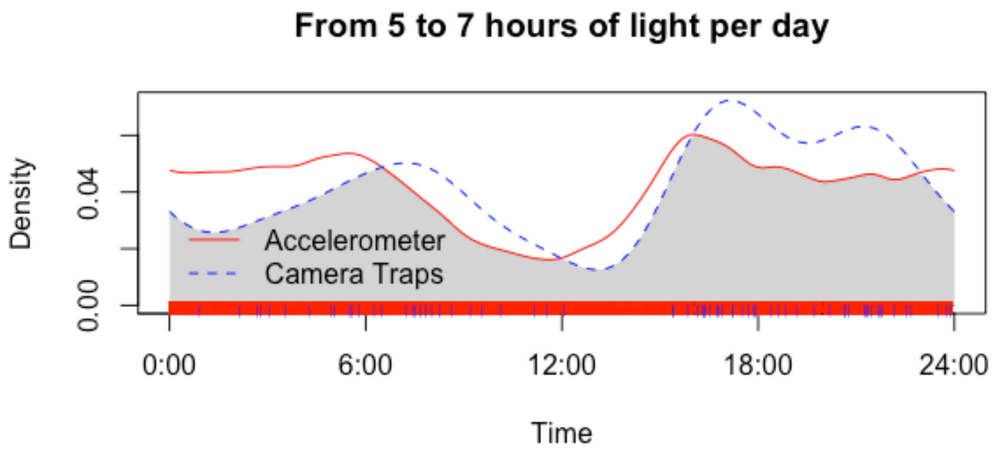


4b.

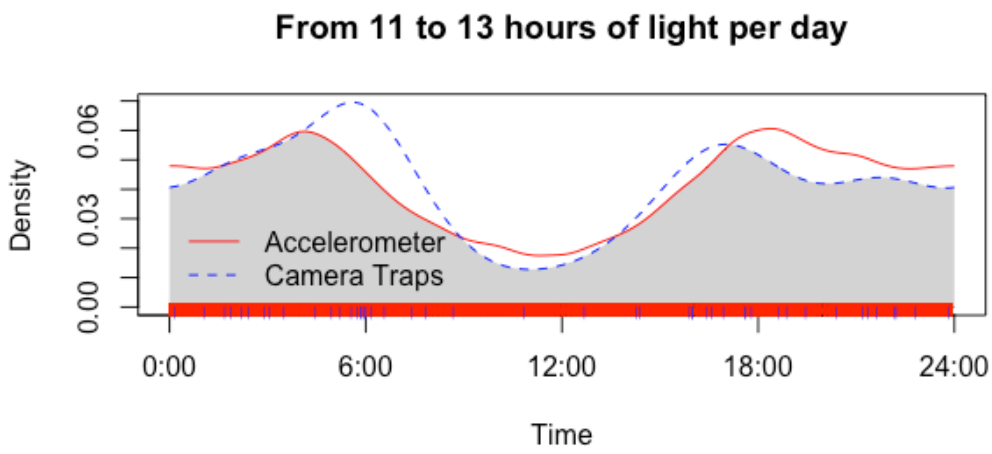


4c.

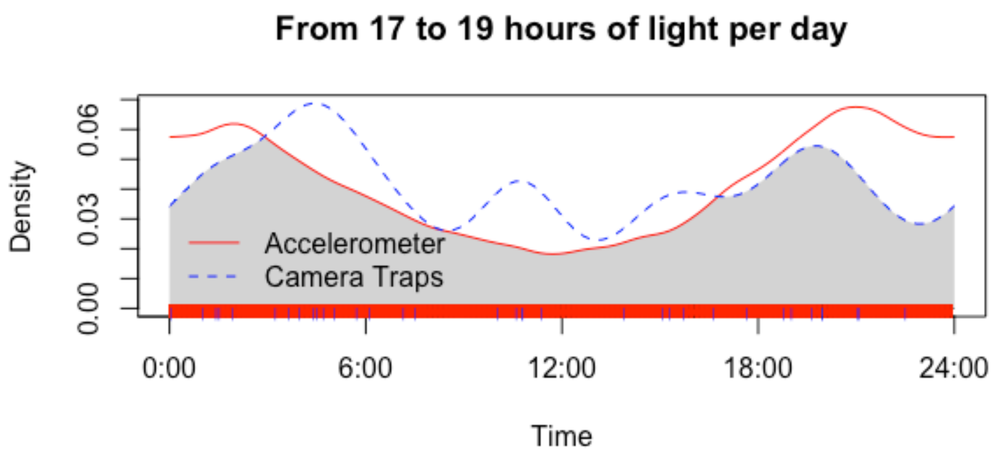
Fig. 4: Overlap analyses between accelerometer and 20% camera traps data (65 total number of camera traps used) within the interval: from 5 to 7 hours of light per day (4a), from 11 to 13 hours of light per day (4b) and from 17 to 19 hours of light per day (4c).



5a.

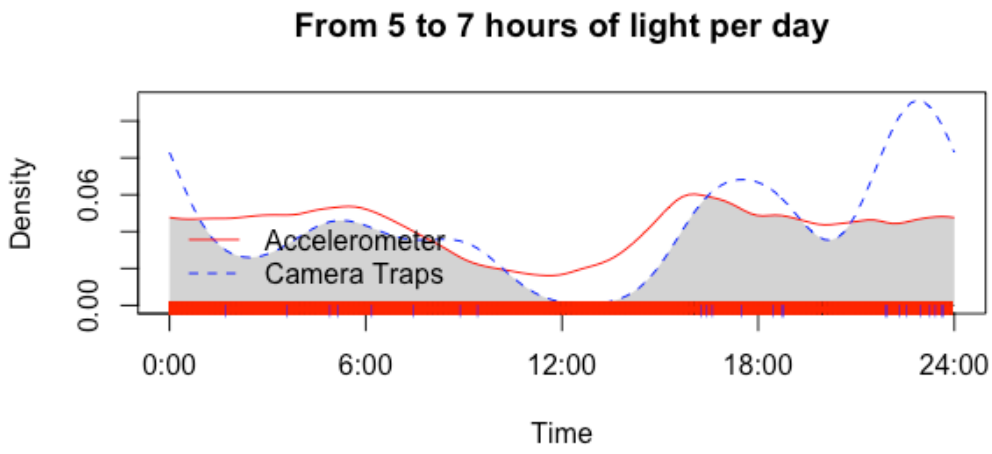


5b.

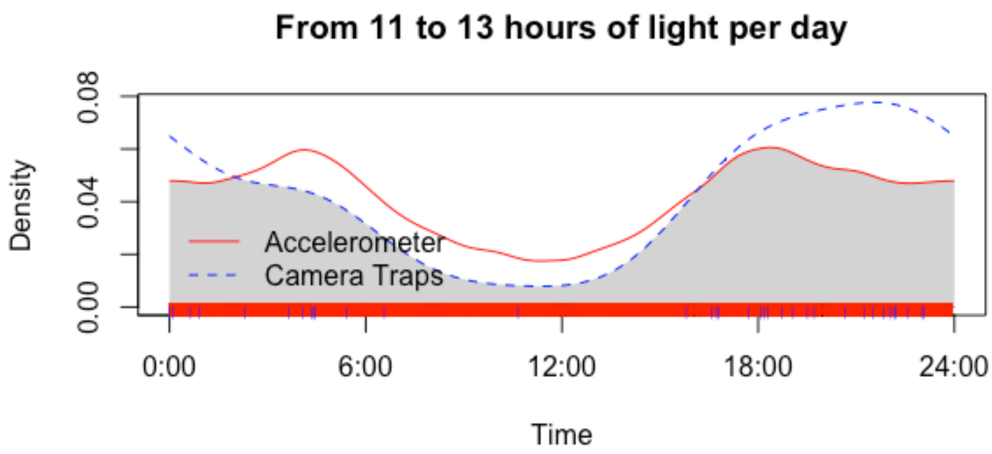


5c.

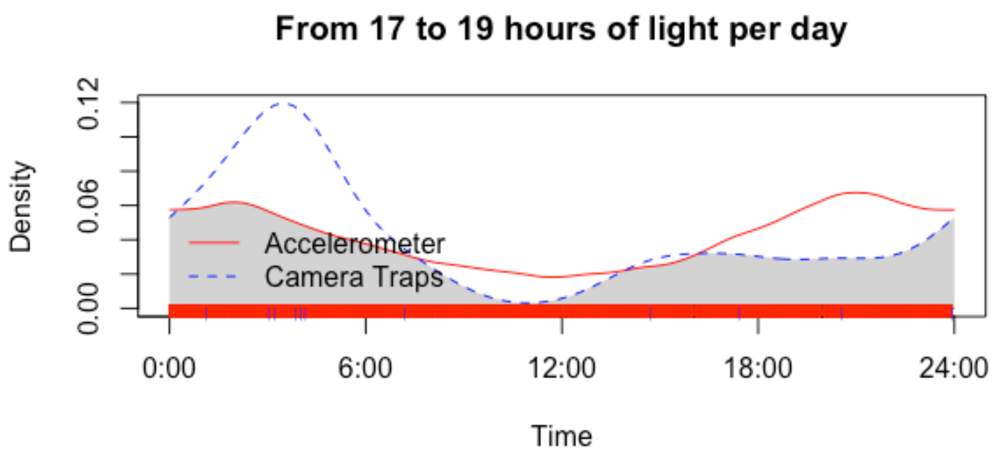
Fig. 5: Overlap analyses between accelerometer and 10% camera traps data (33 total number of camera traps used) within the interval: from 5 to 7 hours of light per day (5a), from 11 to 13 hours of light per day (5b) and from 17 to 19 hours of light per day (5c).



6a.



6b.



6c.

Fig. 6: Overlap analyses between accelerometer and 5% camera traps data (16 total number of camera traps used) within the interval: from 5 to 7 hours of light per day (6a), from 11 to 13 hours of light per day (6b) and from 17 to 19 hours of light per day (6c).