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Research Article

Diel activity of foraging Eurasian red squirrels (*Sciurus vulgaris*) in the winter revealed by camera traps

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Abstract

Animals are adapted to a range of activity patterns, from diurnal to nocturnal. Under normal conditions, the 24-hour rhythm is entrained by changes in light intensity during twilight, i.e. the light and dark cycle. Many rodent species exhibit predator avoidance by adjusting their activity in relation to space or time, which is weighed against the need for food. Hence, an individual's foraging activity consists of a compromise between foraging and predation risk, in addition to competition. Our study species, the Eurasian red squirrel, is diurnal and utilises dense forest habitats. In the present study, we used non-invasive camera traps to model diel activity during the winter months in 2014–2015 (December to February 24-hour day). We found that the Eurasian red squirrels exhibited a strictly diurnal feeding activity pattern and the shape of the modelled activity curve was unimodal and concentrated in the daylight hours, starting at sunrise and peaking in the morning.

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Introduction

Almost all life forms display a biological timing, and such time-regulated behaviour can be expressed through annual (Goldman, 2001), tidal (Morgan and Christy, 1995), lunar-related (DeCoursey, 1983) and daily rhythms (Pittendrigh, 1993; DeCoursey et al., 2000). Many organisms possess an endogenous circadian pacemaker to time their daily activity and physiological processes (DeCoursey et al., 2000; Halle and Stenseth, 2012). Under normal conditions, the 24-hour rhythm is defined by changes in light intensity during twilight, i.e. differences in the amount of light between the light and dark periods, hereafter termed the "LD cycle" (Ashby, 1972; Halle and Stenseth, 2012). Animals are adapted to different grades of light sensitivity, exhibiting patterns of activity ranging from totally diurnal to totally nocturnal. The majority of mammalian species are either crepuscular or nocturnal (Ashby, 1972). In prey species, these adaptations may have occurred to avoid predation, however, the same adaptation in predators may have occurred to improve hunting success, as predation is one of the strongest selective forces over evolutionary time (Lima and Dill, 1990).

The strategies used by organisms to minimise predation risk are numerous and differ among animal groups (Cooper and Vitt, 1985; van Schaik and van Noordwijk, 1989; Treves and Chapman, 1996). Many rodent species exhibit predator avoidance by adjusting their activities in relation to space or time (Halle, 1993; Edut and Eilam, 2003; Suselbeek et al., 2014). However, this must be weighed against the need for food acquisition and, thus, an individual's foraging activity consists of a compromise between optimal foraging and reduced risk of predation (Suselbeek et al., 2014). Consequently, animals spend time being vigilant to minimise predation risk (e.g. Lendrem, 1983; Tchabovsky

et al., 2001). Predation risk influences decision making during an animal's lifetime and affects temporal feeding behaviour (Lima and Dill, 1990).

Animals' daily activity have fascinated scientists for decades (e.g. Ashby, 1972; Tonkin, 1983; Wauters et al., 1992; Halle, 1993; Edut and Eilam, 2003; Pita et al., 2011; Suselbeek et al., 2014), and knowledge about an animal's temporal niche is important to understand ecological interactions (Halle and Stenseth, 2012), further it is essential for the timing of surveys of a given animal (viz. nocturnal vs. diurnal). Hence, this knowledge is important for habitat and population management.

In recent years, new technology has made it easier to observe the activity of animals. Camera trapping is a flexible technique and applicable to terrestrial as well as arboreal animals (Di Cerbo and Biancardi, 2013). Camera traps have been demonstrated to provide information on activity and ranging patterns that coincides with telemetry data (Noss et al., 2003). In addition, it is a non-invasive method (i.e. does not require animal handling) which reduces stress and potential capture-induced mortality associated with traditional techniques (O'Farrell et al., 1994; Place and Kenagy, 2000; Fletcher and Boonstra, 2006; Sullivan and Sullivan, 2013) and potentially allows large-scale studies of wider distributions (Gompper et al., 2006).

In the present study, we used camera traps during the winter months to monitor the Eurasian red squirrel (*Sciurus vulgaris*) around the clock (24-hour day). The Eurasian red squirrel is preyed upon by hawks (Accipitriformes), owls (Strigiformes), red fox (*Vulpes vulpes*), and the European pine marten (*Martes martes*) (Petty et al., 2003). To avoid encounters with mammalian predators and reduce its visibility to birds of prey, the Eurasian red squirrel makes use of dense forest habitats, and often avoids foraging in forest edges (Petty et al., 2003). They tend to avoid using areas with minimal cover, such as clear-cuts. The Eurasian red squirrel inhabits all types of coniferous and deciduous wood-

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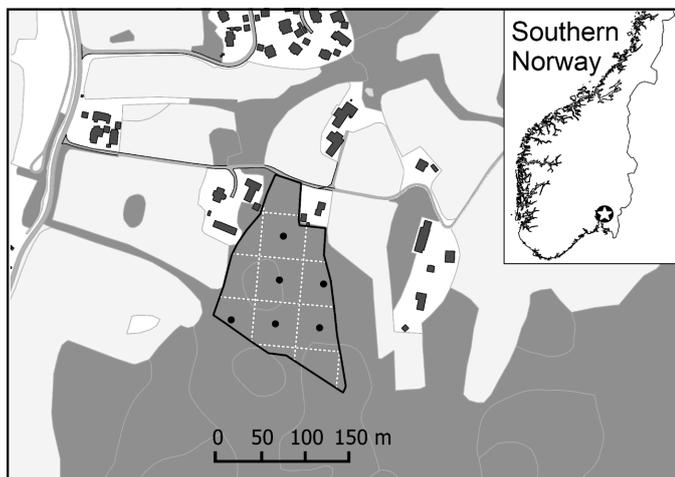


Figure 1 – Camera trap study area for Eurasian Red Squirrel was located on a small forest property in southern Norway, Ås municipality, (2 ha, denoted with black frame) during December 2014 to February 2015. Six sites (denoted with dot-plots) were chosen randomly within square grids of 50 m (denoted with white-dashed lines). Two camera traps were used simultaneously and rotated randomly between the six sites. The white area indicates open field/settlement, light grey is cropland and pasture, dark grey is forest and small dark grey squares represent buildings.

lands that provide enough edible seeds and shelter (Bosch and Lurz, 2012). Their diet mainly consists of plant tissue, including seeds, berries, mushrooms, nuts and green plants, but animal matter such as eggs, pupae and larvae may also be included as well as food from human litter and garbage (Bosch and Lurz, 2012). Food items that are suitable for storing are hoarded, which is suggested to increase the availability for food during periods of scarcity, and to lower the risk for naive foragers to find the cached food (Wauters et al., 1995). Even though Eurasian red squirrels have an endogenous basis, as many other organisms, their daily activity does vary annually due to environmental factors such as day length, temperature, snowfall, snow storms, severe winds, and food availability (Pulliainen, 1973; Tonkin, 1983; Gurnell, 1987; Wauters et al., 1992).

The aim of this study was to model diel activity of Eurasian red squirrels during the winter months using camera traps. During this time of year, we expected a short duration of activity, as the lowest level of mobility for this species is found to be during the shortest and coldest days of the year (Pulliainen, 1973; Tonkin, 1983; Wauters et al., 1992). With this study, we wanted to assess if a non-invasive method gives reliable activity estimates. Combined with advanced statistical treatment using the cosinor method (Nelson et al., 1979; Pita et al., 2011), we intended to do high-resolution temporal modelling of diel activity.

Methods

Study area

The study site was located in Ås (59°38'45.2" N 10°48'12.4" E), in the southern part of Norway. Six sites were randomly selected using grid intersects (each grid 50×50 m) within an old growth, dense spruce forest of Norway spruce (*Picea abies*) (2 ha) (Fig. 1). Each site was baited with a seed mixture (sunflower, *Helianthus annuus*; common oat, *Avena sativa*; common wheat, *Triticum aestivum*; and millet, *Panicum miliaceum*), in addition to groundnut (*Arachis hypogaea*) and peanut butter. The site was re-baited one to three times each day at randomly allocated times over the course of the day/night cycle. The high frequency of baiting and the amount of food supplied ensured the presence of food at all times (including the darkest hours). Since the sites were baited, they are points of attraction to forage, meaning we observed a temporal pattern of response to a supplemented feeding source, which we use as an index of temporal pattern of “activity”. Hence, we do not take into account time spent on other activities not associated with foraging.

Camera traps and Observations

The feeding sites were monitored by Reconyx PC900 HyperFire™ camera traps with No-glow™ high-output covert infrared technology (Reconyx Inc., WI, USA), being classified as high end device (Rovero et al., 2013). The camera traps were customised for close-up footage at a distance of ≈0.75 m from the bait. The camera traps have passive infrared sensors (PIR) that respond to heat energy emitted from animals in motion. The camera trap captured still images during movements at the feeding site (the camera has a “rapid fire” function enabling up to 2 images per second, with no delay, which means it captured images as long as there was movements). The high-definition images were stored to a 32 GB Secure Digital (SDHC®) Memory Card (Fig. 2 displays an image example).

The two camera traps were rotated among the six sites in a random progression. Each site was monitored for two periods, from last part of December to the beginning of February 2014–2015 for a total monitoring time of 1641 hours, with 274±31 hours (mean±SD) at each site. Images from the camera trap were processed using Windows Photo Viewer (Microsoft Corp., Redmond, WA), and we separated images of Eurasian red squirrels for further analyses. The feeding sites were also visited by mice, (*Apodemus* spp.), voles (*Clethrionomys* spp., *Microtus* spp.), passerines (Passeriformes), and occasionally by European roe deer (*Capreolus capreolus*). The monitoring time is the same as the time cameras was switched on at the given locality, from this we created a data frame with the onset and termination for each bout to create a time sequence for the hourly monitoring. These data were recorded and scored as to whether or not squirrels had attended a site for a given hour-block for a given day and month. The post-processing of the data was performed in Program R version 3.1.0 (R Development Core Team, 2015), where we created a time frame of the monitoring period, and separately used the file.info package to create a time frame of Eurasian red squirrels observations (images of squirrels); finally, we merged the two data frames.

To control for ambient temperature as entrainment on diel activity (Steen, 2017), we obtained hourly ambient temperature (°C) from the eKlima web-portal (www.eklima.no) and using the nearest weather station available (distance ≈3.0 km). During our study, the average temperature was -2.7 °C (±0.13 SE, range=-17.7 to 7.2).

Statistics

Statistical analysis was performed using Program R, version 3.1.0 (R Development Core Team, 2015). The analysis of diel activity rhythms was based on linear mixed effects regression models (Pinheiro and Bates, 2000) within the lme4 package (R Development Core Team, 2015), in which the periodic component of time series was represented by pairs of sine and cosine functions (Nelson et al., 1979; Pita et al.,



Figure 2 – Image from the camera trap showing the feeding site and a Eurasian red squirrel (*Sciurus vulgaris*), January 2015 in southern Norway, Ås municipality.

2011). As an index of activity around the clock, the response variable was whether there were any images of Eurasian red squirrels within an hour-block for each site for every hour for each day being monitored. The response variable had two outcomes per observed hour block: “no squirrels” or “squirrels”, which we modelled using logistic regression with a binomial distribution (Galyean and Wester, 2010). The fixed explanatory variable “time of the day” was fitted using the cosinor method (Nelson et al., 1979; Pita et al., 2011) with 24 hours as the fundamental period and with two harmonic components (1st and 2nd) to modulate the signal, as both unimodal and bimodal activity pattern has been reported in previous studies (Tonkin, 1983; Wauters and Dhondt, 1987; Wauters, 2000). Temperature was treated as a co-variable to control for possible entrainment on diel activity patterns. In all tests, each observed hour was the sample unit and “site ID” was included as a random factor to account for repeated measurements at the same site (Pinheiro and Bates, 2000). The mixed effect model fitted using the cosinor method is advantageous as it can include multiple variables that might be important entrainments (“Zeitgeber”, termed by Aschoff, 1954), in addition to the 24-hour rhythm influenced by changes in light intensity during twilight (e.g. temperature; see Pita et al., 2011 for other examples). Further, it allows for specifying a random effect to control for repeated measurements and possible variation associated with each site (Pinheiro et al., 2000). The activity models were specified as:

$$M_0 : \text{logit}(f(x)) = a_0 + \epsilon$$

$$M_1 : \text{logit}(f(x)) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + \epsilon$$

$$M_2 : \text{logit}(f(x)) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + (a_2 \cos \frac{2 \cdot 2\pi x}{24} + b_2 \sin \frac{2 \cdot 2\pi x}{24}) + \epsilon$$

$$M_3 : \text{logit}(f(x)) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{d24}) + (a_2 \cos \frac{2 \cdot 2\pi x}{24} + b_2 \sin \frac{2 \cdot 2\pi x}{24}) + (a_3 \cos \frac{3 \cdot 2\pi x}{24} + b_3 \sin \frac{3 \cdot 2\pi x}{24}) + \epsilon$$

$$M_4 : \text{logit}(f(x)) = a_0 + t + \epsilon$$

$$M_5 : \text{logit}(f(x)) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + t + \epsilon$$

$$M_6 : \text{logit}(f(x)) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + (a_2 \cos \frac{2 \cdot 2\pi x}{24} + b_2 \sin \frac{2 \cdot 2\pi x}{24}) + t + \epsilon$$

$$M_7 : \text{logit}(f(x)) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{d24}) + (a_2 \cos \frac{2 \cdot 2\pi x}{24} + b_2 \sin \frac{2 \cdot 2\pi x}{24}) + (a_3 \cos \frac{3 \cdot 2\pi x}{24} + b_3 \sin \frac{3 \cdot 2\pi x}{24}) + t + \epsilon$$

with x as “time of day”, t as “temperature” and ϵ as the random effect “site ID”. The Akaike’s Information Criterion (AIC) was calculated in turn for each model (Burnham and Anderson, 1998; Burnham, 2002) using AICcmodavg, which produces model selection tables based on the AIC and the second-order AIC (AICc). For more details about cosinor mixed-model specifications, see Pita et al. (2011).

Each model fit (M_1 – M_7) was evaluated by comparing the AICc values with the model that included only the random term (M_0). Hence, the zero-amplitude AICc comparison determined whether a given harmonic term was included in the final model, i.e. whether it contributed statistically to the characterization of the waveform (Refinetti et al., 2007). The model fits were ranked according to their AICc values, with the lowest AICc value being considered the “best”. Models in which the difference in AICc relative to AICcmin is <2 can be considered to have substantial support (Burnham and Anderson, 1998; Burnham, 2002), although we selected the most parsimonious model with as few predictor variables as possible. Graphical presentations were constructed

Table 1 – Model selection table with number of parameters (K), AICc, delta AICc, AICc weights, cumulative weight and log-likelihood (LL).

Model	K	AICc	Δ AICc	AICcWt	Cum. Wt	LL
M_2	6	546.16	0.00	0.40	0.4	-267.06
M_3	8	546.93	0.76	0.27	0.68	-265.42
M_6	7	547.63	1.47	0.19	0.87	-266.78
M_7	9	548.45	2.29	0.13	1.00	-265.17
M_1	4	559.37	13.21	0.00	1.00	-275.67
M_5	5	561.06	14.90	0.00	1.00	-275.51
M_0	2	942.84	396.67	0.00	1.00	-469.41
M_4	3	943.00	396.83	0.00	1.00	-468.4

Table 2 – Parameter estimates from the best-fitted model (number of observations: 1641; random effect: 6 sites).

Fixed Effects	Estimate	Std. Error	z-value	$p(> z)$
(Intercept)	-20.50	5.68	-3.61	<0.001
$I(\cos(2\pi \cdot \text{Hour}/24))$	-26.03	7.86	-3.31	<0.001
$I(\sin(2\pi \cdot \text{Hour}/24))$	5.14	2.36	2.18	0.029
$I(\cos(2 \cdot 2\pi \cdot \text{Hour}/24))$	-6.72	2.26	-2.97	0.003
$I(\sin(2 \cdot 2\pi \cdot \text{Hour}/24))$	1.81	1.43	1.27	0.205

with the package `graphics`. The 95% confidence intervals of the fitted line were computed by model-based parametric bootstrapping for mixed models (`bootMer` function, 1000 simulations, `lme4` package). From the cosinor model, we were particularly interested in the global acrophase, the time point in the cycle of highest global amplitude (i.e. describing a peak in activity), and which part of the day that the activity was higher than the average cycle value (MESOR). The global acrophases correspond to the time interval at which the fitted function had peak value (Pita et al., 2011). The time of day that the modelled activity was above MESOR could be defined as the main activity period (Navarro et al., 2013).

Results

The hourly frequency of Eurasian red squirrels, as a function of time of the day, indicated strongly a diurnal feeding activity pattern during the winter months (December to February) as shown by the raw data displayed in Fig. 3. This was confirmed by the best-fitted multi-cosinor model shown as the fitted line in Fig. 3, which verifies a diel pattern in feeding activity, with Δ AICc >371.1 relative to the null model including the random term only. The most parsimonious model was based on the 1st harmonic component (12-h), in addition to the fundamental period (24-h). Adding the 2nd harmonic (8-h) did not improve fits, nor did the co-variable “ambient temperature” (Tab. 1). The parameter estimates of the best-fitted model are given in Tab. 2.

The activity pattern was unimodal and concentrated in the daylight hours, starting with sunrise and peaking in the morning (09.00–10.00 and 10.00–11.00 hour-blocks, i.e. the global acrophase) and ceasing during afternoon (Fig. 4). The mean of the modelled activity curve (MESOR) was found to be 0.17 (model M_0 , including only intercept and random effect term).

Discussion

The Eurasian red squirrels exhibited a strictly diurnal feeding activity pattern during the winter months (December to February). This is in line with previous studies based upon telemetry and direct observations (Tonkin, 1983; Wauters et al., 1992; Wauters, 2000). The activity pattern was unimodal and concentrated in the daylight hours, starting with sunrise and peaking in the morning. A unimodal activity pattern has been reported in previous studies during winter, although the activity pattern is found to change over the course of the year, from unimodal winter to bimodal in the summer (Tonkin, 1983; Wauters et al., 1992; Wauters, 2000).

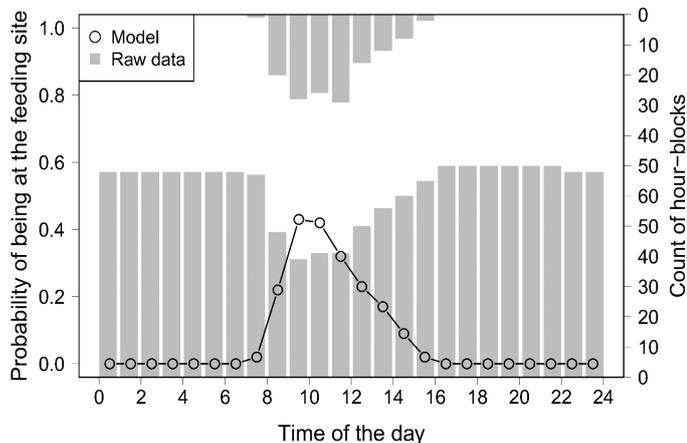


Figure 3 – Modelled diel winter activity of the Eurasian red squirrel from camera trap data, with the probability of the Eurasian red squirrel visiting the site within an hour-block (denoted with dot-plot connected with line), based upon the best-fitted model (parameter estimates given in Tab. 2, n=1641; random effect=6). The upper bars are the count of hour-blocks with “squirrels” (n=142) and lower grey bars are the count of hour-blocks with “no squirrels” (n=1499). Study conducted during December 2014 to February 2015 in southern part of Norway, Ås municipality.

The time of day that the activity of the squirrels increased from below the MESOR to above the MESOR (i.e. upward crossing) was during hour-block 07–08 and the time of day that the modelled activity decreased from above the MESOR to below the MESOR was by the end of hour-block 13–14 (i.e. downward crossing). Hence, 4–5 hours represents the relative width of the main active period, with its emphasis on the mid-morning to right after noon. Such short activity time during winter, with an onset of activity shortly before sunrise has also been reported in UK, Belgium and Switzerland (Tonkin, 1983; Wauters and Dhondt, 1987; Wauters et al., 1992; Bosch et al., 2015).

The period from no feeding activity to the curve upward crossing the MESOR was about one hour, indicating a fast onset of activity at sunrise. In the afternoon, the period from the curve downward crossing the MESOR to no activity was longer (from hour-block 14–15 to 16–17) and the activity ceased out before sunset. Similar to other studies, the onset of activity seems to be more consistent compared with the conclusion of activity (Tonkin, 1983; Wauters, 2000). A fast onset of activity at sunrise might be observed because of food acquisition is of particular interest when the squirrels are hungry after the long night and then change to other activities once satiated (S. Halle, *pers. comm.*, 2016). The pattern could also be related with non-synchronous activity peaks

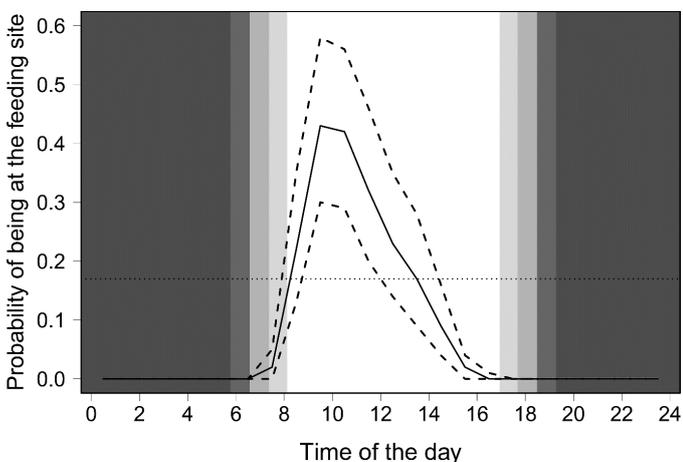


Figure 4 – Graph with grey shading in accordance to the three types of twilight: astronomical, nautical and civil (dark to light, respectively, with the white area showing the daylight), and the modelled winter activity of the Eurasian red squirrel from camera trap data (fitted line in solid and upper and lower 95% CI in dashed lines), the MESOR is indicated with a dotted line and parameter estimates are given in Tab. 2 (n=1641; random effect=6). Study conducted during December 2014 to February 2015 in southern part of Norway, Ås municipality.

of different animals. Wauters et al. (1992) found that individual animals sometimes had two peaks in winter activity in deciduous forest but that these short peaks often did not coincide, resulting in an apparent unimodal pattern at population level.

As the food sources at each site were stable and predictable throughout the 24 h cycle, we stress that the LD cycle is an important entrainment (“Zeitgeber”) of activity patterns of the Eurasian red squirrels (Halle and Stenseth, 2012). Temperature was not included in the most parsimonious model; this may be due to the restricted timeframe of our study during the winter months, when temperatures are coldest (with an average temperature of -2.7°C during our study). Annual activity patterns are likely driven by both temperature and photoperiod length (Pulliainen, 1973; Wauters and Dhondt, 1987).

The activity pattern of the Eurasian red squirrel in the present study consists of time spent at the feeding site, which may have been altered by food availability in the area, competition, and the risk of predation (Halle and Stenseth, 2012 and references therein), although we did not observe any predators at the images captured by the camera. Feeding sites are point of attractions and may induce aggressive encounters, e.g. preferential access to food of dominant animals (Wauters and Dhondt, 1992; Rice-Oxley, 1993), and influencing space use (Magris, 1998). Furthermore, we did not take into account time spent for other activities, although Wauters et al. (1992) found that the Eurasian red squirrel spent as much as 75.8% of their total activity foraging during winter in a coniferous forest, followed by travelling (12.1%), grooming (2.3%) and resting (3.3%). When not being active, the Eurasian red squirrel is found to spend a total of 18–19 hours in the drey during winter (Wauters and Dhondt, 1987), which are essential for thermoregulation by this species during the winter (Pulliainen, 1973).

Some of the variation around the modelled probability of being at the feeding site could be addressed to the fact that several Eurasian red squirrels used the feeding site. During our study, a minimum of three different individuals were observed in our study area, although we were not able to identify individuals from the camera trap images, less variation is expected than when following unique individuals. Camera trapping is a non-invasive method that could give insight to diel activity as it can easily monitor for extended periods. This method can give more information about the Eurasian red squirrels throughout the year, and contribute to better understanding of the temporal scales, in addition to spatial, at which animals’ acts is important for management (Kremen, 2005).

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplemental material S1 Time-lapse video example of squirrel in activity.