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Disentangling the drivers of European badger (*Meles meles*) activity at multiple temporal scales

Laura Bartra Cabré
Master of Science in Ecology

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ABSTRACT

Animals shape their activity in response to several processes that take place at different timescales. It stands to reason that the assessment of activity at multiple temporal scales will enhance the understanding of its patterns and determinants than studies that focus on a single scale. This thesis aimed to explore the patterns and drivers of the activity of the European badger (*Meles meles*) at three temporal scales: annual, seasonal and diel. I fitted occupancy models to data from camera traps collected continuously from different latitudes in Norway between 2015 and 2018. The results showed that activity patterns of the badgers were influenced by seasonality more significantly than by photoperiod, revealing plasticity in their temporal patterns to variation in environmental conditions. Season, temperature and time of the day had the strongest effect on activity levels, with badgers being more active in spring, during cold but not freezing days, and during night-time. Further, badgers in this study selected sites at lower latitude and altitude, and also closer to fields and human settlements. Overall, this study showed that scale is important for understanding the activity of species both in the long and short term. Further development of models considering both multiple temporal and spatial scales would offer more opportunities for enhancing the knowledge related to management and conservation of species.

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1. Introduction

The ability of animals to shape their activity patterns as a response to multiple processes occurring at different temporal scales is fundamental to maximize fitness (e.g. Halle and Stenseth, 2012). Most studies focus on a single timescale when investigating species behaviour, assuming a constant rate of activity at other (ignored) timescales. It can be argued that a multi-scale approach might explain hidden interactions between ecological processes that are acting at different timescales and explain the activity and time niche of a species.

The budgeting of activity over a year and during a day varies among mammals and is a response to key environmental factors such as weather and photoperiod as well as human disturbance. Annual and diel activity patterns are an adaptive behaviour resulting from a trade-off related to energy requirements, social needs, competition and changing environmental factors such as seasonality (Davimes *et al.*, 2017), temperature (Stokes, Slade and Blair, 2001) or day-night length (Halle and Stenseth, 2000). These factors vary over and within a year or a day, and animals might be required to present some plasticity in their activities and temporal niches, masking the effect of other variables in the environment. This is particularly noticeable in more variable environments such as in high latitudes, with large variation in climatic conditions during the year. Moreover, these patterns might change depending on the habitat (Sasidhran *et al.*, 2016) or other site conditions such as human disturbance (Klar *et al.*, 2008).

Seasonal flexibility has been noticed in some species affecting both activities during the year as well as diel activity patterns. For example, the Arabian oryx (*Oryx leucoryx*) showed more crepuscular activity during the colder months in spring and summer, and more nocturnal patterns during the warmer months in summer. This species also showed more daytime inactivity during the warmer months (Hetem *et al.*, 2012). Another study on the same species showed that there was also a temporal niche variation, with more diurnal activity in the winter and more crepuscular activity in the summer (Davimes *et al.*, 2017).

Annual and diel activities of many mammals are affected by weather (van Tienderen, 1997; Vieira *et al.*, 2009). For instance, the temperature can alter foraging patterns (Zhou *et al.*, 2011) and precipitation influences predator-prey interactions (Grindal *et al.*, 1992). Cold temperatures contribute to high costs of energy for thermoregulation, hence several mammals reduce their activity during winter to subsist (Kitao *et al.*, 2009; Zub *et al.*, 2009). Moreover, day length is an important ecological constraint for nocturnal mammals, since it restricts the duration of the activity and it oscillates according to season (Halle and Stenseth, 2000).

Therefore, seasonal changes in daylight can affect vital activities (Cresswell and Harris, 1988; Fowler and Racey, 1988). The climatic conditions due to seasonality have also been found to interact with diel activity shifts, with even complete temporal niche inversions of nocturnal animals turning diurnal during extreme weather periods.

To predict the consequences of environmental changes it is important to understand how species may adapt to changing environmental conditions. In this thesis, I investigate the patterns and determinants of the activity of the European badger (*Meles meles*; Linnaeus 1758) at three different temporal scales: annual, seasonal and diel. I will use occupancy models to analyse camera trap data from a camera trapping project in Norway, the northern margin of the species' distribution (Johnson, Jetz and Macdonald, 2002). The inability to detect every individual present in the study area, together with heterogeneous detection probability, has direct consequences for the reliability of inferences drawn from camera trap surveys (Archaux, Henry and Gimenez, 2012; Guillera-Arroita and Lahoz-Monfort, 2012). Occupancy models, which account for imperfect detection when estimating parameters (MacKenzie *et al.*, 2002, 2017), have been selected for this work due to their suitability to address questions about ecological processes, particularly the ones that display at large spatial scales.

In recent years, the number of camera trap studies have increased, and they have been used for evaluating populations' densities and occupancy, measuring the behaviour of individuals or species interactions (McCallum, 2013; Bischof, Hameed, *et al.*, 2014; Burton *et al.*, 2015; Wang, Allen and Wilmers, 2015). Camera traps are a non-invasive method to study terrestrial mammals, in particular those species that are otherwise difficult to study, for example, nocturnal or crepuscular carnivores (Burton *et al.*, 2015), and it allows long-term studies minimizing the in-situ effort and the disturbance of the species (Kays and Slauson, 2008).

The badger is a species that rarely is the target of long-term studies using camera traps. Nevertheless, badgers offer a good model for studying the effects of day length and weather due to their adaptability to different climatic conditions and wide geographical range. Moreover, badgers are central place foragers, which means that movement ecology is linked to their sett spots (Roper, 2010). Thus, they do not present wide migratory movements, making them more exposed to daylight shifts, weather and climatic changes (Byrne *et al.*, 2015). Badgers are mostly inactive during daylight, especially during winter (Pyšková *et al.*, 2018). Also, badgers are mainly nocturnal, with a significant increase of detections by camera traps after dusk, and a decrease of detections around dawn. Moreover, these patterns varied with the season (Caravaggi *et al.*, 2018). Hence, variability in weather and climate and daylight length

seasonality conditions increases the need to assess how badger populations occupying the north of their range might alter their activity patterns.

In this thesis, I hypothesize badger's annual, seasonal and diel activity patterns are determined by:

H1) The year's environmental conditions. Other studies have shown that badgers activity differs between consecutive years, due to inter-annual climatic conditions variations, affecting biological responses as well as behavioural routines (Noonan *et al.*, 2014).

Therefore, the associated predictions are:

P1.1) Annual activity rhythms will show differences between years, not only with differences in the amount of activity but also the patterns. Badgers will probably be more active during warmer years. Moreover, they will be more active during wetter days due to a higher earthworm availability (Elliott, O'Brien and Hayden, 2015) and a reduced sense of smell for possible threats (Byrne *et al.*, 2015).

P1.2) Not all seasons' activity will be affected the same way by the year's conditions. Winter may be the season with more differences between the years as it is the season with harsher weather conditions for badgers.

H2) The seasonality and its temperature conditions. It is well known that the activity of the badgers has a peak in the spring as well as before winter hibernation (Bevanger and Lindstrom, 1995; Goszczynski *et al.*, 2005). Also, its foraging strategy is only possible during the snow-free season (Pyšková *et al.*, 2018). Hence, the badger is thought to hibernate at northern latitudes. Therefore, the associated predictions are:

P2.1) Badgers will be more active during the warmest seasons of the year, as well as inactive during winter.

P2.2) Badgers will be more active during the warmer days of each season.

P2.3) Badgers will be more active during rainy periods due to food availability but will avoid harsh precipitation days.

H3) Daylight length. Many studies have confirmed that badgers are strictly nocturnal (Harris, 1982; Arroyo *et al.*, 2002). For example, another camera trap study recorded more than 85% of badgers' detections between 19:00 and 06:00 (Caravaggi *et al.*, 2018). Maurel and Boissin (1983) found that the daily activity patterns of the badgers were correlated with the duration of the night, with the start synchronized with sunset time. Also, Tanaka

(2005) observed differences in daily activity between months, with a peak in activity before midnight during the summer months, and a longer peak from after to before midnight during the late summer and autumn months. Therefore, the associated predictions are:

- P3.1) Badgers will be most active during night-time.
- P3.2) Badgers' activity period gets reduced during the short nights in the summer and increases with the longer nights at the end of the autumn and the beginning of spring. Also, the peak of activity will vary with seasonality and changes in daylight length.

2. Material and methods

2.1. Study species

Badgers (*Meles sp.*) are distributed almost worldwide and are highly adaptable to different biomes and ranges of temperature (Sato et al. 2012). In this thesis, I study the European badger, a species occurring in most of Europe, from Portugal to the west until Russia to the east and all the way north until the Scandinavian countries (Proulx and San, 2016; Macdonald, Newman and Harrington, 2017; Kinoshita *et al.*, 2020). The European badger is classified as an omnivore and opportunistic forager (Roper, 2010; Gomes *et al.*, 2020). In Scandinavia, badgers are considered earthworm specialists (Bevanger and Lindstrom, 1995). In the most northern range of their distribution, badgers have established populations everywhere except in mountainous locations, close to fjords or above the Arctic Circle (Roper, 2010). In Norway, badgers are known to be found from the southern part until the arctic circle latitude (Bevanger and Lindstrom, 1995b). However, there have been observations of badgers registered even in further north latitudes of Norway (<https://artsdatabanken.no>).

2.2. Study area

The study area extends across Norway from the southmost region (58°N) up to 68°N of latitude (Figure 1). Norway's landscape is dominated by boreal forests, mainly deciduous forests of birch (*Betula pendula*), ash (*Fraxinus excelsior*), linden (*Tilia cordata*), maple (*Acer platanoides*), elm (*Ulmus glabra*) and hazel (*Corylus avellana*). Coniferous forests, which are

dominated by pine (*Pinus sp.*) and Norway spruce (*Picea abies*), are common at the eastern coast and central and northern valleys of the country (Fremstad, 1998).

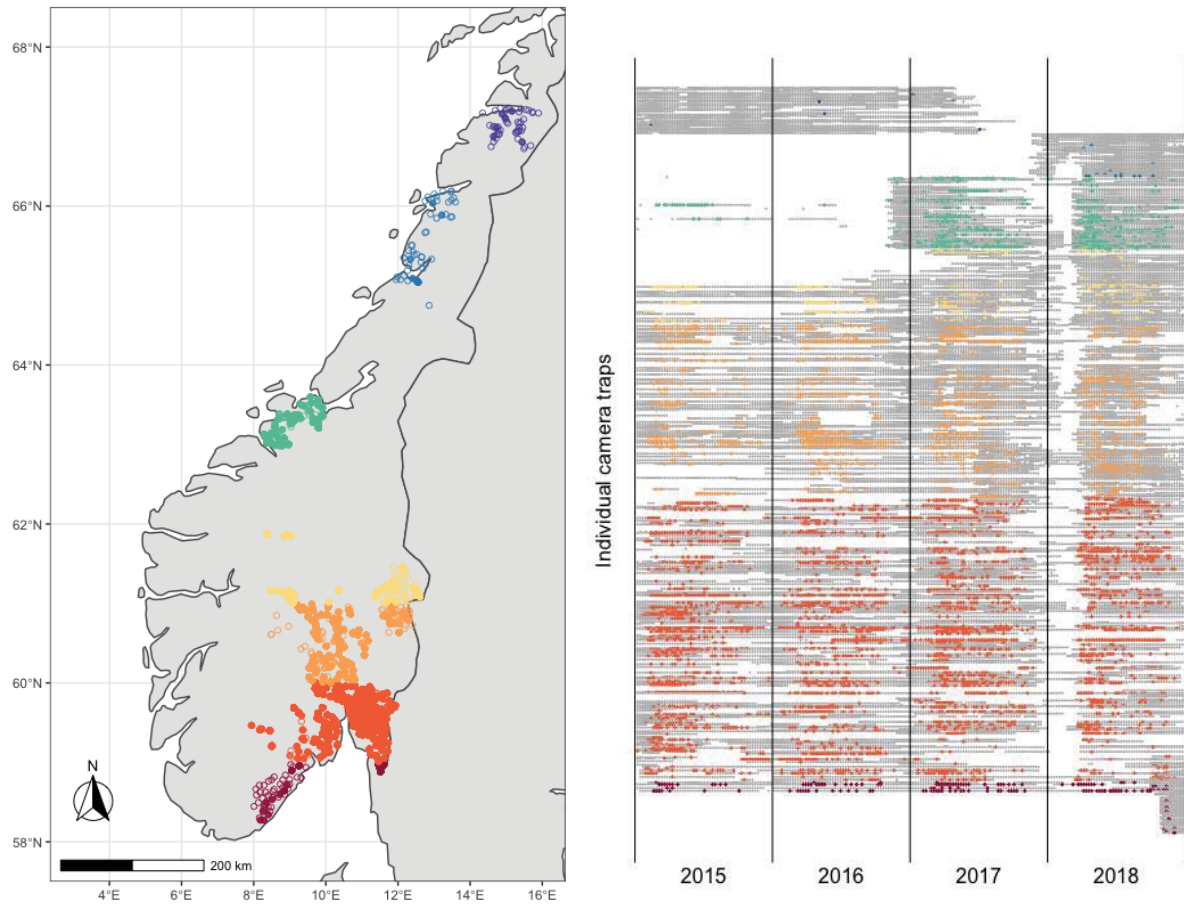


Figure 1. On the left, the map shows the location of the camera trap stations in Norway (solid grey lines: country borders). Locations with empty circles indicate no photographic captures of the European badger (*Meles meles*), full circles indicate at least one photographic capture of badgers at the study (2015-2018). On the right, the survey effort of the study: each row in the graph represents the history of one camera trap station (ordered by latitude), with grey horizontal lines indicating time periods (each point is a day) during which each station was active, and coloured points representing at least one photographic capture of badger the corresponding day. Grey vertical lines separate years.

The climate differs from coastal to continental, with large variations in temperature, which is quite different between latitudes and continentality. In Bodø (Nordland, north coastal town) there is a mean temperature of 15.4°C in July and of -1.6°C in January, in Grimstad (Aust-Agder, southern coastal town) the mean temperature is 20.6°C in July and -0.1°C in January, while in Innbygda (Hedmark, continental town), the mean temperature in July is 19.2°C and -8.9°C in January (<http://yr.no>, data from July 2018 and January 2019).

The shortest day length is approximately 49 minutes in Bodø (December 21) and 6 hours and 20 minutes in Grimstad (December 21) while in the summer, the sun is up all day in Bodø from June 1 until July 12 and the longest day lasts 18 hours and 17 minutes in Grimstad (June 21) (<http://www.timeanddate.com/sun/norway/oslo>).

2.3. Camera traps and data collection

The camera trap data were collected by the Norwegian Institute of Nature Research's (NINA) as part of the wildlife camera project SCANDCAM (<https://scandlynx.nina.no>). The main objective of the project is to monitor the lynx population (*Lynx lynx*), thus cameras are located in places to maximize the probability of capturing a picture of this species. Camera density in all areas is one per 50 km². The first years of the study (2011-2014) only contain camera traps from the south of Norway (up until Oppland county). From 2015 onwards, more cameras were situated in the centre and north of Norway (Møre, Romsdal, Trøndelag and Nordland counties; Figure 1). The camera models the project uses are Reconyx© wildlife cameras (address: 3828 Creekside Ln, Ste 2, Holmen, WI 54636): HC500 HyperFire Semi-Covert IR, HC600 HyperFire High Output Covert IR, PC800 Hyperfire Professional Semi-Covert IR, PC900 HyperFire Professional Covert IR and PC850 HyperFire Professional White Flash LED. The five models have a 0.20 seconds trigger speed (<http://www.reconyx.com/>). The cameras were mounted by employees and volunteers in a standardized way: attached to trees, around 30 cm above the ground, depending on the terrain slope and the snow coverage, facing north or, if not possible, the best angle for the optimal picture capturing.

For this study, only the active cameras' data from 2015 until 2018 were used, to include data from all the regions of the study. The camera stations were located from a minimum latitude of 58°16'27" N until a maximum latitude of 68°57'43"N (Figure 1).

2.5. Data analysis

All statistical analyses were performed in R version 3.6.1 (R Development Core Team, 2019). All camera stations capture data were combined and organized in a binary system to structure the detection histories: 1 = at least a badger picture was taken, 0 = camera active but badger not detected. "NA" indicated that the camera station was not active (Figure 2). Only the cameras up to 68°N were included in the models, as no badgers were detected by camera traps above this latitude.

To investigate badger temporal activity at multiple scales, likelihood-based single-season occupancy models were used (MacKenzie *et al.*, 2006, 2017) with different grain and extent detection matrices as inputs (Figure 2). Preliminary analysis, using dynamic occupancy models, showed year was not an explanatory variable for colonization and extinction probabilities in the sites (AIC of the model including year = 23175.12, AIC of the model not including year = 23168.24). Therefore, occupancy was assumed to be constant within years and static single-season occupancy models were used. Also, differences in the abundance of badgers between years and/or seasons were not considered in the analysis of this study (MacKenzie *et al.*, 2002; Nielsen *et al.*, 2005). The function ‘colect’ from the R package ‘unmarked’ was used for all analysis (MacKenzie *et al.*, 2006; Fiske and Chandler, 2011). Using the occupancy model framework the probability of species presence/absence was estimated while accounting for imperfect detection, based on detection/non-detection data collected at repeated visits to multiple sites (MacKenzie *et al.*, 2002). As badgers can have quite large and variable home ranges, multiple camera sites might be covered by a single home range (Kruuk, 1978). Therefore, the assumption of a closed population (i.e. no changes in occupancy in the same site), would be incorrect due to the presence at the site being temporary. Thus, depending on the scale of the occupancy analysis, it was assumed that instead of estimating the absolute occupancy (ψ), presence-absence or site use would be estimated (MacKenzie *et al.*, 2017). Also, the probability of detection (p) would be assumed as an estimate of the relative variability between activity levels at different times for a given site (Rowcliffe *et al.*, 2014) and camera sensitivity affected e.g. by the weather (Meek, Ballard and Fleming, 2015).

Depending on which scale the occupancy analysis was conducted, relative differences in activity were reflected in differences in occupancy and detection probability, or only as detection probability (see more details in the sections below: 2.6. Annual scale analysis, 2.7. Seasonal scale analysis, 2.8. Diel scale analysis). However, in the methods part, those parameters will still be referred to as “occupancy” and “detection”, consistent with the nomenclature in the occupancy framework.

The predictors of detection and occupancy probability were selected following a two-step methodology (Kéry and Chandler, 2012). This consisted of modelling detection probability first as a function of environmental explanatory variables that may affect badger activity (based on the knowledge of survey design and the previous knowledge on the species; Table 1) while keeping constant occupancy. The top model was obtained based on the Akaike Information Criterion (AIC; Akaike, 1998) with only explanatory variables for the detection and a constant

occupancy, starting with the global model, and performing a backward elimination manually. The top models arising from this selection were updated with explanatory variables biologically likely to affect occupancy, followed by backward elimination of the occupancy variables. Covariate effects were considered significant when 95% confidence intervals (CI) of the beta coefficient estimates did not overlap 0 (Richmond, Hines and Beissinger, 2010). The selected explanatory variables used to create the candidate models varied according to the objectives of each time scale analysis (Tables 2, 4 and 6).

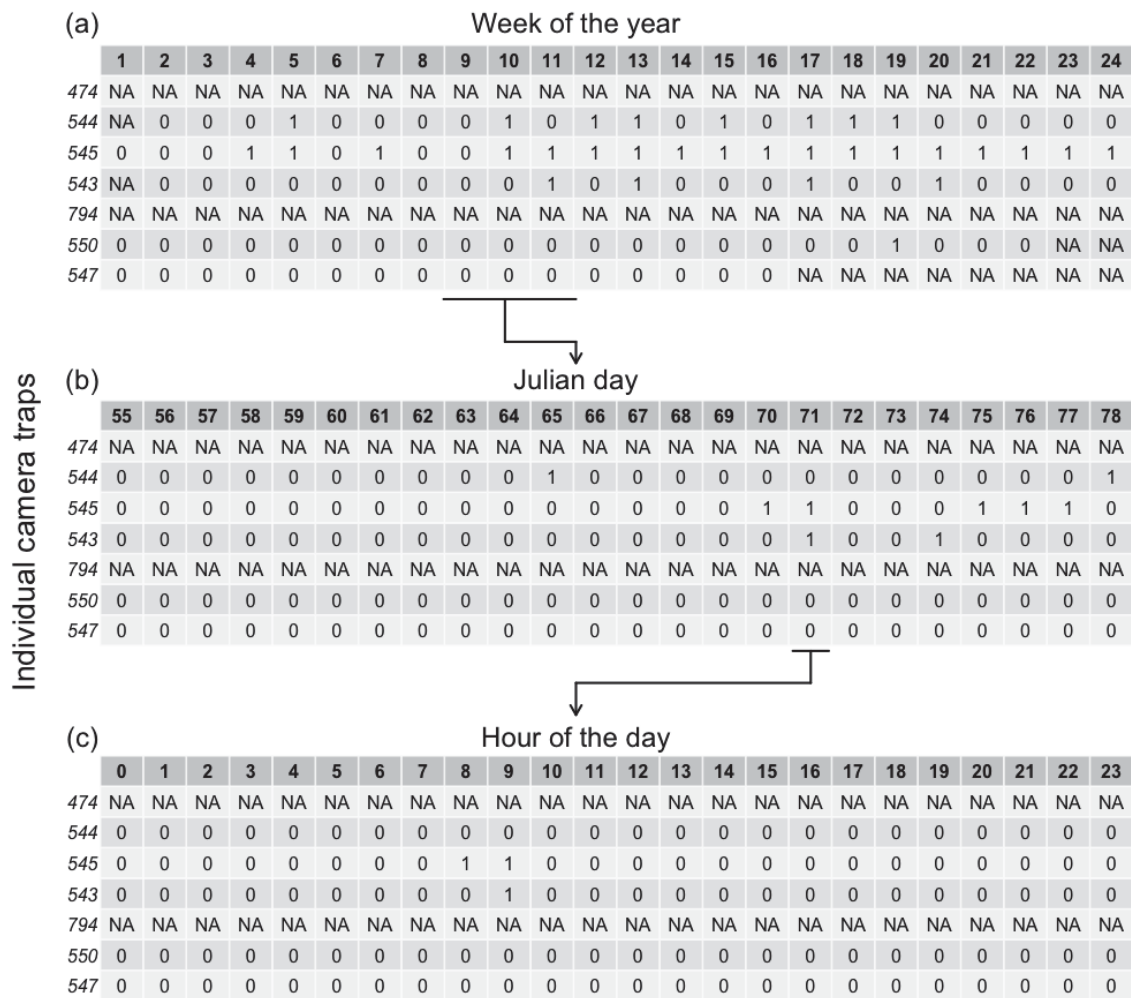


Figure 2. Visualization of the data organization for each occupancy analysis at different temporal scales to analyse activity patterns of European badgers (*Meles meles*) from camera trap data. The tables display a subset of the camera trap detection history of year 2017 showing the setup of the matrices for (a) the annual scale analysis, (b) the seasonal scale analysis and (c) the diel scale analysis. Matrices are made of time scale as columns and camera trap stations as rows.

2.5. Explanatory variables

I selected time-varying predictors depending on the scale of the analysis: year, week, season, Julian day (i.e. day of the year, from 1 to 365) and/or hour of the day, and the site or environmental predictors based on the availability of these variables and factors known to be important to badger's ecology: latitude (Noonan *et al.*, 2014), elevation (Johnson, Jetz and Macdonald, 2002), forest type (Prigioni and Deflorian, 2005), land use (proportion of fields around the site, Broseth, Knutsen and Bevanger, 1997), distance to settlement (Elliott, O'Brien and Hayden, 2015) and local weather (Rosalino *et al.*, 2019). Polynomial effects were considered for variables that might not have linear effects: week, Julian day, hour of the day, latitude, and temperature.

Table 1. Environmental variables considered to explain badger (*Meles meles*) site use and activity patterns using occupancy models

Explanatory variables	Code	Description	Units	Range (min to max)	Source
Latitude	Lat	Measure from the south (low) to north (high)	°N	58.27 to 67.19	Camera site GPS location
Elevation	Elev	The vertical distance from sea level	m	0.05 to 839.8	Measure at site
Proportion of fields	Prop. fields	The proportion of area covered with fields on a buffer zone of 1km around the camera site	Proportion	0.0 to 0.8	AR5 (NIBIO) *
Forest type	Forest	4 categories: • Coniferous forest (CF): at least 50% of the wooded area is covered with conifers. • Mixed forest (MF): Between 20-50% of the wooded area is covered by conifers. • Deciduous forest (DF): Less than 20% of the wooded area is covered by conifers. • Non-forest (NF)		Number of sites: CF: 583 MF: 55 DF: 91 NF: 90 Not mapped: 7	AR5 (NIBIO)*
Distance to house	Dist. H	Linear distance from camera site to the nearest human house	m	0.0 to 7191.8	Norwegian FKB data (FKB road)
Temperature	T	Daily mean temperature	°C		Measure at site
Precipitation	Precip	Daily precipitation. Interpolated rainfall in a grid of 1 km distance from camera site without correction of catch failure for observations.	mm		Measure at site

*Reference: <https://www.nibio.no/tema/jord/arealressurser/arealressurskart-ar5>

To avoid multicollinearity, I evaluated the relationships between the explanatory variables using Spearman's correlation test. To check the correlation of the continuous environmental covariates (temperature, precipitation and snow) the maximum, mean and minimum value for each variable for each of the sites was calculated. There were no strongly correlated variables ($r < 0.7$, Kozak, 2009), except for temperature and snow, that were negatively correlated ($r = -0.78$). Therefore, as for some of the seasons and sites, snow data was not available, it was excluded from the analysis.

2.6. Annual scale analysis

For this analysis, the occupancy was assumed to be presence/absence. Also, relative differences in detection probability between weeks and years were assumed to be at least in part related to the difference in activity levels.

To evaluate the annual relative activity rhythms and the effect of spatial covariates (Table 1) on the activity patterns and site use of badgers, a single-season static occupancy analysis was used, including the four years of the study and all of the camera trap stations. Capture histories at each camera site were pooled into consecutive 7-days sampling events (occasions: 52 weeks per year) to generate the detection matrix of detection histories, resulting in a 741x208 matrix (741 sites x 208 weeks, Figure 2a). For the year 2016, observations on the 31st of December were removed (so all years would include the same number of days).

The global model for detection probability included the season or the week number (to a maximum of a fourth-degree polynomial) and year, assuming that the climatic conditions of each year would be reflected. Explanatory variables for the occupancy parameter were latitude, elevation, distance to the nearest house, the proportion of fields and forest type were included (Table 2).

2.7. Seasonal scale analysis

For this analysis, it was assumed that the relative differences in occupancy between seasons were related to seasonal differences in activity levels. The variation in detection probability was at least in part assumed to be related to differences activity levels between season and year, as well as driven by the weather explanatory variables included in the models.

To explore further the variability in activity patterns between and within seasons, and to check for the relative influence of weather variables (i.e. temperature and precipitation, Table 1) on the activity of badgers, the previous data was divided into four seasons: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February). For the winter season, a continuous winter season was used instead of the winter months of each year, meaning that the winter season of each year included the last month of the previous year and the first two months of the actual year (e.g. winter 2015 included captures from December 2014 and from January and February of 2015, and winter 2018 included captures from December 2017 and January and February of 2018). Each Julian day was one survey occasion, resulting in four matrices with four time periods of data collecting including 92 occasions each in both spring and summer, 91 occasions in the autumn and 90 occasions in the winter (Figure 2b).

The global model for detection probability (activity) included explanatory variables: year, temperature (up to a second-degree polynomial) and precipitation. Explanatory variables for occupancy model, included latitude, elevation, distance to the nearest house, the proportion of fields and forest type (Table 4).

2.8. Diel scale analysis:

For this analysis, it was assumed that the relative differences in occupancy between seasons were related to seasonal differences in activity levels. The variation in detection probability was, at least in part, assumed to be related to differences in between activity levels between the hour of the day, the Julian day and the year.

To explore the diel activity of badgers, and also compare between and within seasons, the same data sets as for the previous analysis (seasonal scale) was used, but with each hour of the day as one survey occasion, resulting in four matrices with four periods of data collection including 92x24 occasions each in the spring and the summer, 91x24 occasions each in the autumn and 90x24 occasions each in the winter (24 being the hours of the day, Figure 2c). For the year 2016, observations on the 31st of December were removed (so all years have the same number of days).

Because the data sets were very large, using all of the data for the analysis presented some computing limitation (i.e. not all of the explanatory variables desired could be included in the model). To solve that, a compromise was made, and only the camera sites between 59°N and

61°N of latitude were used (dark orange dots in Figure 1). This way, the difference in activity between latitudes was assessed (confirmed in the two previous analysis) as well as the difference between daylight length between latitudes, that could alter the diel activity patterns of the badgers (Vazquez *et al.*, 2019). Thus, for this analysis, more attention was given on the variance of the diel activity between seasons and days of the years, instead of between the different camera sites (i.e. based on their location).

Also, to simplify the models even more, in this part of the study, constant occupancy was assumed. Therefore, the model did not include any explanatory variables for the occupancy parameter. For detection explanatory variables, the hour of the day up to a second-degree polynomial, Julian day up to a second-degree polynomial, year, and the interaction between the hour and Julian day were included (Table 6).

3. Results

3.1 General results

During the 4-year study period, the 741 cameras were active for a total of 333,446 trapping days (with a mean of 427 ± 361 trapping days per camera site). A total of 12,474 badger pictures were captured, with a mean of 30 ± 64 pictures per camera site (examples of photography captures in Figure 3). The proportion of sites with badger captures was 0.64 (477 cameras with recordings of badgers out of the total number of sites).

An average of $3,119 \pm 478$ photographs were captured per year (2,818 in 2015, 2,804 in 2016, 3,818 in 2017 and 3,034 in 2018). During the four-year period, 6,182 pictures were captured during spring, 3,204 during summer, 1,538 during autumn and 1,550 during the winter season.



Figure 3. Example of European badgers (*Meles meles*) camera trap photos: (a) a badger captured at 5°C of temperature in the summer, (b) a group of badgers captured during a summer day at 19°C of temperature, and (c) a badger captured during a winter night at -5°C of temperature and with snow cover.

3.2. Annual scale analysis

The most parsimonious model based on AIC comparison included week as a fourth-degree polynomial and year as explanatory variables of detection probability (activity; Table 2). Besides, the top model included latitude as a quadratic polynomial, elevation, proportion of fields and forest type as explanatory variables for occupancy (presence/absence).

Week as a fourth-degree polynomial had a significant effect on detection probability (Table 3), with relatively higher detection probability occurring between week 16 and 17 (corresponding to mid-April, mean detection probability = 0.318, 95% CI = 0.303 to 0.334; Figure 4b), and relatively lower detection probability during the first week of the years (mean detection probability = 0.001, 95% CI = 0.001 to 0.002; Figure 4b). Year 2015 had a significantly higher detection probability than years 2016, 2017 and 2018 (mean detection probability in 2015 =

0.174, 95% CI = 0.163 to 0.186; in 2016 = 0.159, 95% CI = 0.149 to 0.170; in 2017 = 0.161, 95% CI = 0.152 to 0.171; in 2018 = 0.143, 95% CI = 0.134 to 0.152; Table 3 and Figure 4a).

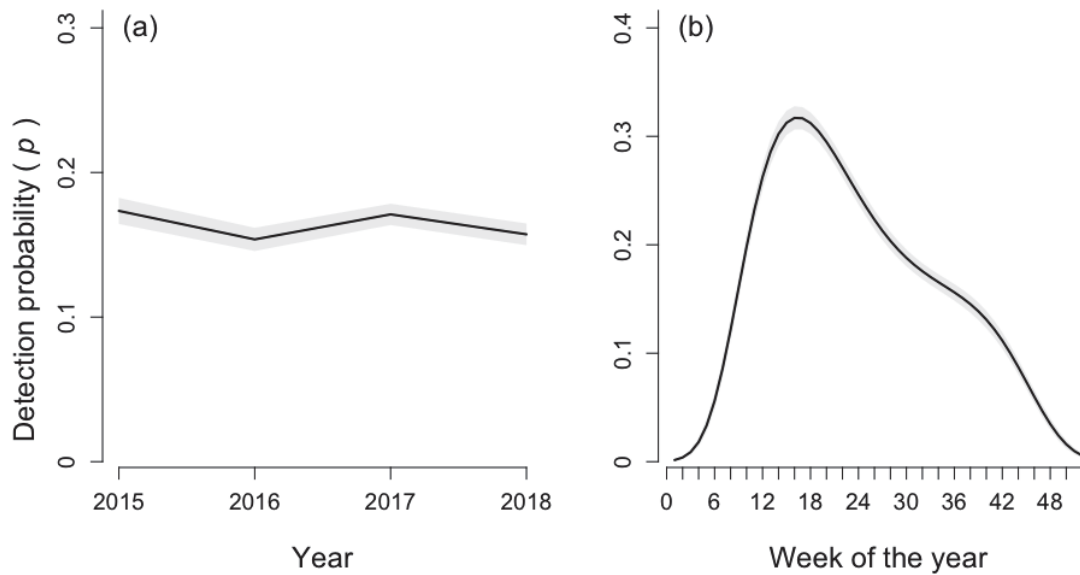


Figure 4. Predictions for (a) years and (b) the week of the year detection probabilities of badger (*Meles meles*) from the annual scale analysis (grey shadows show 95% confidence intervals).

Latitude as a quadratic polynomial was included in the top-ranked model as an occupancy parameter, but the quadratic term was not significant (Table 3). Elevation, distance to the nearest house, proportion of fields and forest type were also included in the top-ranked model and significant explanatory variables for the occupancy parameter. Badgers chose to occupy sites at lower latitudes and altitudes (Figure 5a and b). Also, site use was significantly higher in sites closer to houses and surrounded by more fields (Figure 5c and d). Site use was significantly higher at deciduous forests sites (mean occupancy probability at DF = 0.706, 95% CI = 0.462 to 0.851; at CF = 0.556, 95% CI = 0.315 to 0.735; at MF = 0.620, 95% CI = 0.354 to 0.804, at NF = 0.546, 95% CI = 0.298 to 0.734; Table 3 and Figure 5e).

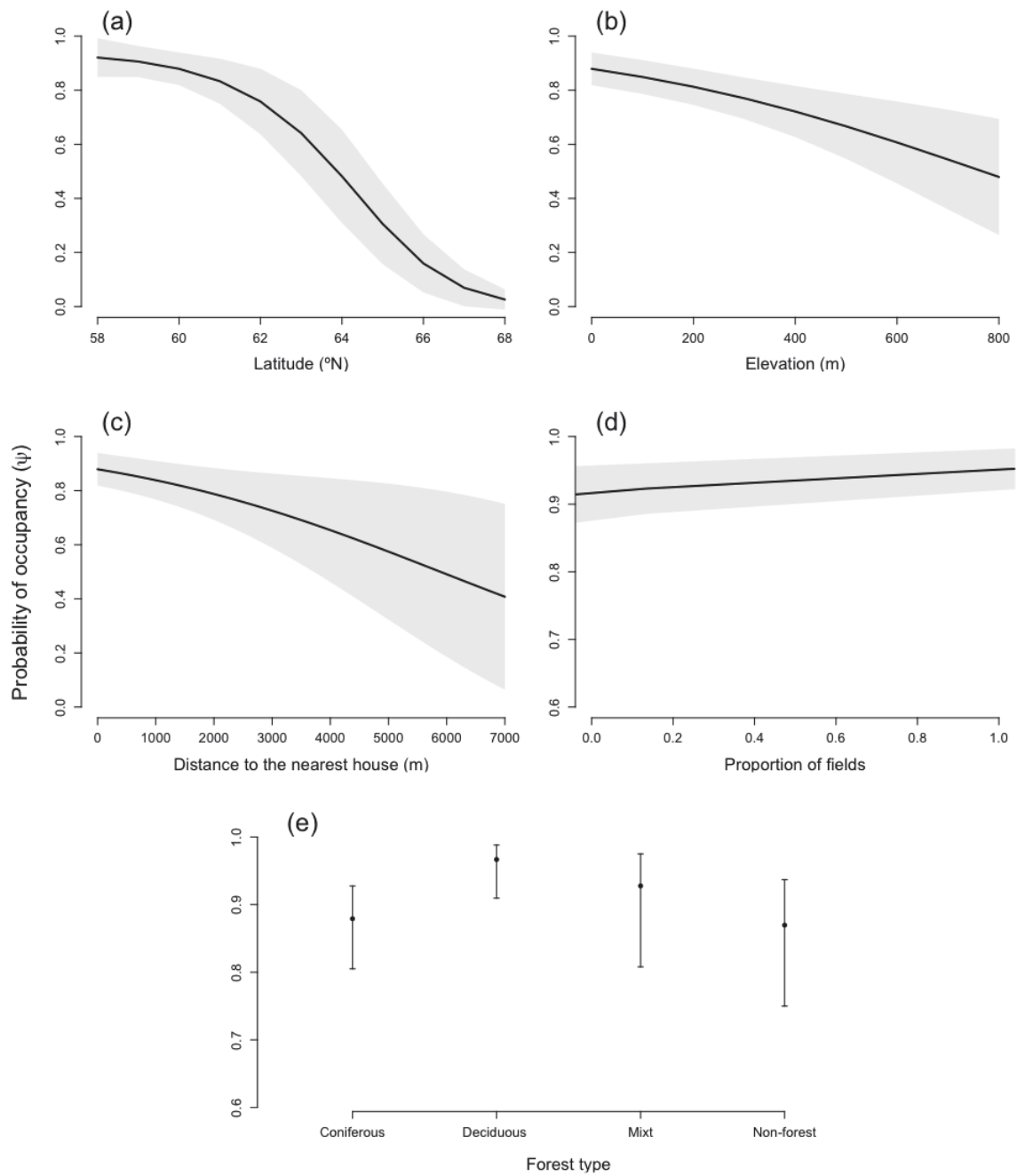


Figure 5. Predictions for covariate effect on site use (occupancy) of badger (*Meles meles*) from the annual scale analysis (grey shadows on the top plots and vertical lines in the bottom plot show 95% confidence intervals).

Table 2. Candidate models for the annual scale analysis of badger (*Meles meles*) activity. Only models with $\Delta AIC < 6$ and the top model with constant occupancy are shown. The top model based on AIC evaluation (most parsimonious model) is in bold. Explanatory variables abbreviations are presented in Table 1. p : probability of detection; ψ : probability of occupancy; df: degrees of freedom, AIC w: Akaike weight.

Candidate models	df	ΔAIC	AICw
$\psi(\text{Lat} + \text{Lat}^2 + \text{Elev} + \text{Dist. H} + \text{Prop. fields} + \text{Forest}) p(\text{Week} + \text{Week}^2 + \text{Week}^3 + \text{Week}^4 + \text{Year})$	18	0.00	0.65
$\psi(\text{Lat} + \text{Elev} + \text{Dist. H} + \text{Prop. fields} + \text{Forest}) p(\text{Week} + \text{Week}^2 + \text{Week}^3 + \text{Week}^4 + \text{Year})$	17	1.26	0.35
$\psi(.) p(\text{Week} + \text{Week}^2 + \text{Week}^3 + \text{Week}^4 + \text{Year})$	9	192.53	0.00

Table 3. Annual scale analysis and seasonal scale analysis top models' coefficients on the logit scale. Number of sites = 572. Significant estimates are in bold. 95% CI in parentheses. Explanatory variables abbreviations are presented in Table 1. p : probability of detection; ψ : probability of occupancy.

Parameter	Explanatory variables	Estimate (CI)
ψ	Lat	-0.99 (-1.45,-0.53)
	Lat ²	-0.24 (-0.51,0.03)
	Elev	-0.42 (-0.65,-0.19)
	Prop. fields	0.56 (0.20,0.92)
	Dist. H	-0.34 (-0.55,-0.12)
	Forest	CF (intercept) 1.10 (0.78,0.42)
		DF 1.39 (0.44,2.33)
		MF 0.57 (-0.46,1.59)
		NF -0.08 (-0.73,0.57)
p	Week	-0.90 (-0.99,-0.82)
	Week ²	0.38 (0.23,0.53)
	Week ³	0.46 (0.39,0.52)
	Week ⁴	-0.68 (-0.76,-0.60)
	Year	2015 (intercept) -1.14 (-1.22,-1.07)
		2016 -0.11 (-0.206,-0.02)
		2017 -0.10 (-0.18,-0.01)

2018

-0.25 (-0.34,-0.16)

3.3. Seasonal scale analysis

The season-specific analysis revealed that site use and the level of activity were determined by the explanatory variables in a slightly different way between seasons (Table 4). Also, contrarily the previous analysis, occupancy and detection probabilities during winter were significantly different from zero when considered in isolation (mean occupancy probability = 0.041, 95% CI = 0.021 to 0.104; mean detection probability = 0.010, 95% CI = 0.007 to 0.014).

For all seasons, the temperature had a significant effect on detection probability (Table 5). The temperature for maximum detection probability were around 0°C in the spring and 3 °C in the autumn (maximum detection probability in spring = 0.104, 95% CI = 0.098 to 0.111; in autumn = 0.062, 95% CI = 0.055 to 0.069; Figure 6). In the winter, the top-ranked model included the temperature as a quadratic polynomial, but no significant effect of this variable's quadratic term was detected (Table 5), with higher detection probability at higher temperatures (Table 5, Figure 6). In the summer, the pattern reversed, with detection probability decreasing with temperature (Table 5 and Figure 6).

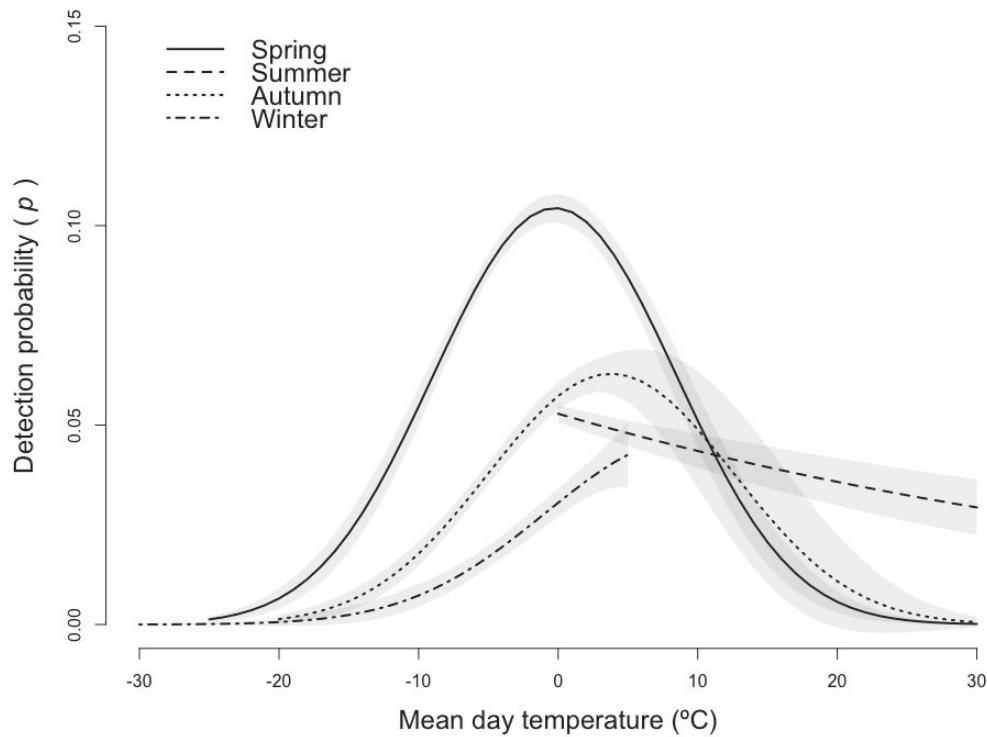


Figure 6. Influence of mean daily temperature on detection probabilities of badger (*Meles meles*) each season (grey shadows show 95% confidence intervals).

All top models included year as an effect on detection probability during spring, summer and winter, but the effect was only significant during spring and winter (Table 4). In spring, there was significantly higher detection probability (activity) in 2015 (mean detection probability = 0.043, 95% CI = 0.039 to 0.049, Table 5 and Figure 7h), and it was significantly lower in 2016 (mean detection probability = 0.036, 95% CI = 0.032 to 0.040, Table 5 and Figure 7h). In the winter, the also in 2015 the detection probability was significantly higher (mean detection probability = 0.014, 95% CI = 0.011 to 0.020; Table 5 and Figure 7k), and lower in 2016 and 2018 (mean detection probability in 2016 = 0.010, 95% CI = 0.007 to 0.014; in 2018 = 0.001, 95% CI = 0 to 0.003; Table 5 and Figure 7k). Precipitation was not included in any of the top-ranked models (Table 4).

Latitude and elevation were included in the top-ranked models of all seasons as predictor variables for the occupancy parameter (Table 4). As in the annual scale analysis, higher latitude and higher altitude sites experienced lower site use (Table 5 and Figure 8a, e, i and m). During autumn, site use was less probable in the lowest latitudes, with the maximum occupancy at latitude 60°N (mean occupancy probability = 0.476, 95% CI = 0.225 to 0.718; Figure 8i). Also, distance to settlement was a significant covariate for site use in all seasons, with badgers

selecting to use more sites closer to human settlements (Figure 8c, g, k and o). However, in the winter the site use probability decreased faster than in the other seasons, with site use probability = 0.006 (95% CI = 0 to 0.065) in sites around 5 km away from a house (Figure 8o).

In spring, summer and autumn, site use was also significantly influenced by the proportion of fields with, as in the annual scale analysis, badgers selecting for sites with more fields around (Tables 4-5 and Figure 8d, h and l).

Forest type was only a significant explanatory variable of site use in the spring (Table 4). Badgers significantly selected for sites with deciduous and mixed forests more than coniferous forests or non-forested sites (mean occupancy probability at DF = 0.725, 95% CI = 0.492 to 0.862; at CF = 0.521, 95% CI = 0.290 to 0.704; at MF = 0.613, 95% CI = 0.362 to 0.794, at NF = 0.519, 95% CI = 0.282 to 0.710; Table 5 and Figure 9).

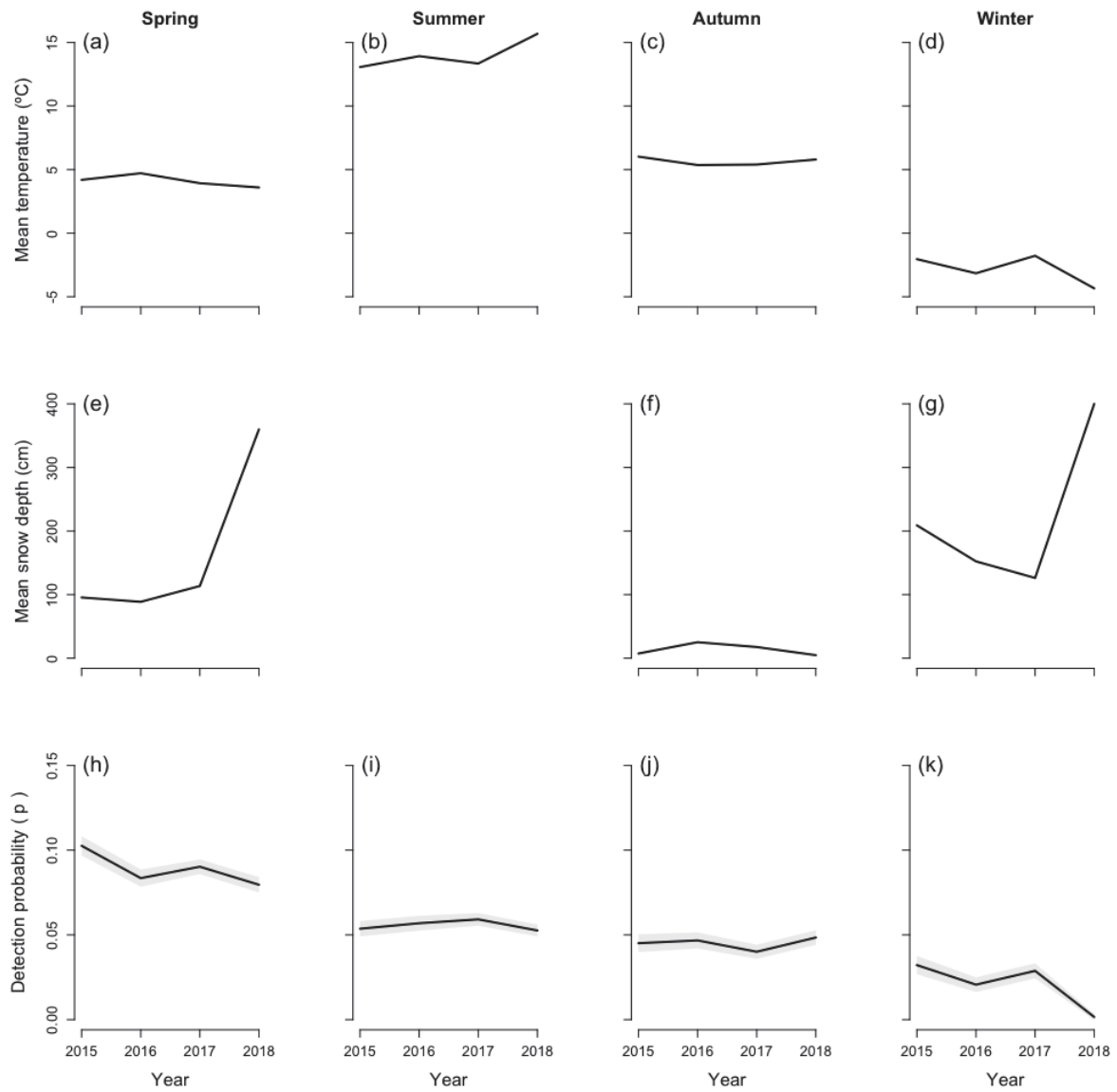


Figure 7. Average (a-d) mean daily temperature and (e-g) snow depth for each season of each year and (h-k) predictions of detection probability of badger (*Meles meles*) for each season of each year (grey shadows show 95% confidence intervals). Snow depth data in the summer was unavailable or zero in most of the sites.

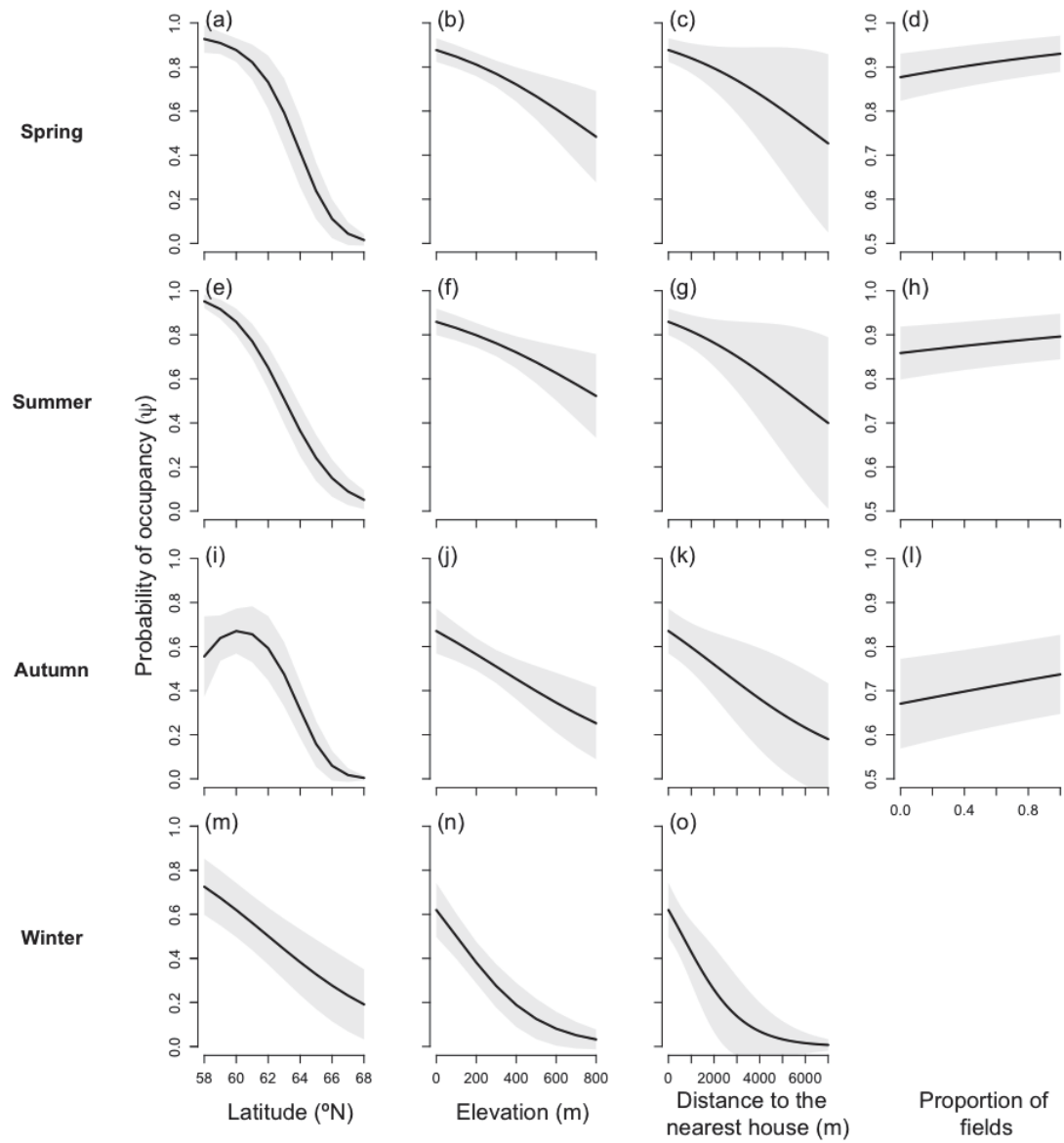


Figure 8. Predictions of occupancy (site use) of badger (*Meles meles*) in each season, from the seasonal scale analysis (grey shaded bands show 95% confidence intervals).

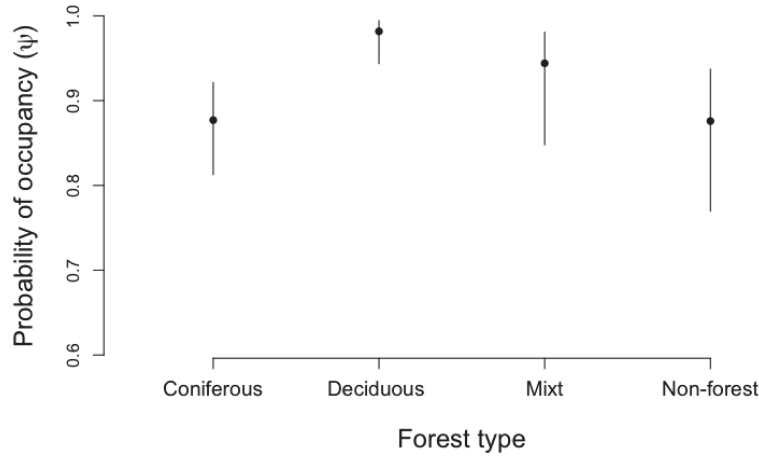


Figure 9. Estimates of badger (*Meles meles*) site use in spring in different forest types, from the seasonal scale analysis (vertical lines: 95% confidence intervals).

Table 4. Candidate models for the seasonal scale analysis of badger (*Meles meles*) activity. Only models with $\Delta AIC < 6$ and the top model with constant occupancy are shown. The most parsimonious model of each season in bold. Explanatory variables abbreviations are presented in Table 1. p : probability of detection; ψ : probability of occupancy

Season	Candidate models	df	ΔAIC_c	AIC _w
Spring	$\psi(\text{Lat} + \text{Lat}^2 + \text{Elev} + \text{Dhouse} + \text{Pfields} + \text{Forest}) p(\text{T} + \text{T}^2 + \text{Year})$	16	0.00	0.63
	$\psi(\text{Lat} + \text{Elev} + \text{Dhouse} + \text{Pfields} + \text{Forest}) p(\text{T} + \text{T}^2 + \text{Year})$	15	1.04	0.37
	$\psi(.) p(\text{T} + \text{T}^2 + \text{Year})$	7	192.33	0.00
Summer	$\psi(\text{Lat} + \text{Elev} + \text{Dhouse} + \text{Pfields}) p(\text{T} + \text{Year})$	10	0.00	0.47
	$\psi(\text{Lat} + \text{Lat}^2 + \text{Elev} + \text{Dhouse} + \text{Pfields}) p(\text{T} + \text{Year})$	11	0.23	0.42
	$\psi(\text{Lat} + \text{Elev} + \text{Dhouse}) p(\text{T} + \text{Year})$	9	4.27	0.056
	$\psi(\text{Lat} + \text{Elev} + \text{Dhouse} + \text{Pfields} + \text{Forest}) p(\text{T} + \text{Year})$	14	5.48	0.03
	$\psi(.) p(\text{T} + \text{Year})$	6	166.7	0.00
Autumn	$\psi(\text{Lat} + \text{Lat}^2 + \text{Elev} + \text{Dhouse} + \text{Pfields}) p(\text{T} + \text{T}^2 + \text{Year})$	12	0.00	0.94
	$\psi(\text{Lat} + \text{Lat}^2 + \text{Elev} + \text{Dhouse} + \text{Pfields} + \text{Forest}) p(\text{T} + \text{T}^2 + \text{Year})$	16	5.37	0.064
	$\psi(.) p(\text{T} + \text{T}^2 + \text{Year})$	7	99.54	0.00
Winter	$\psi(\text{Lat} + \text{Elev} + \text{Dhouse}) p(\text{T} + \text{T}^2 + \text{Year})$	10	0.00	0.37
	$\psi(\text{Lat} + \text{Lat}^2 + \text{Elev} + \text{Dhouse}) p(\text{T} + \text{T}^2 + \text{Year})$	11	0.24	0.33
	$\psi(\text{Lat} + \text{Elev} + \text{Dhouse} + \text{Pfields}) p(\text{T} + \text{T}^2 + \text{Year})$	11	1.95	0.14
	$\psi(\text{Lat} + \text{Lat}^2 + \text{Elev} + \text{Dhouse} + \text{Pfields}) p(\text{T} + \text{T}^2 + \text{Year})$	12	2.19	0.12
	$\psi(.) p(\text{T} + \text{T}^2 + \text{Year})$	7	55.78	0.00

Table 5. Seasonal scale analysis top models' coefficients on the logit scale. Significant estimates are in bold. 95% CI in parentheses. Explanatory variables abbreviations are presented in Table 1. p: probability of detection; ψ : probability of occupancy. *Intercept of the model

Param.	Explanatory variables	Spring (n sites = 595)	Summer (n sites = 572)	Autumn (n sites = 632)	Winter (n sites = 547)
Ψ	Lat	-1.13 (-1.58,0.66)	-1.35 (-1.64,-1.06)	-0.43 (-0.78,-0.07)	-0.59 (-0.848,-0.26)
	Lat ²	-0.25 (-55,0.04)		-0.54 (-0.92,-0.17)	
	Elev	-0.41 (-0.6,-0.18)	-0.35 (-0.57,-0.13)	-0.37 (-0.61,-0.13)	-0.80 (-1.15,-0.55)
	PFields	0.62 (0.26,0.98)	0.35 (0.07,0.65)	-0.32 (0.09,0.55)	
	D house	-0.31 (-0.54,-0.07)	-0.31 (-0.55,-0.08)	-0.21 (-0.57,-0.06)	-0.77 (-1.32,0.22)
	Fores' CF*	0.62 (0.30,0.94)			
	DF	2.02 (0.95,3.08)			
	MF	0.87 (-0.18,1.91)			
	NF	-0.01 (-0.67,0.65)			
P	Year 2015*	-2.12 (-2.18,-2.06)		-3.05 (-3.17,-2.92)	-3.56 (-3.76,-3.37)
	2016	-0.20 (-0.29,-0.11)		0.15 (-0.01,0.31)	-0.37 (-0.65,-0.10)
	2017	-0.06 (-0.14,0.02)		-0.07 (-0.23,0.09)	-0.07 (-0.30,0.17)
	2018	-0.0 (-0.18,0.00)		-0.12 (-0.04,0.27)	-2.79 (-3.95,-1.62)
	T	0.20 (0.16,0.24)	-0.10 (-0.14,-0.06)	0.46 (0.39,0.53)	0.72 (0.40,0.71)
	T ²	-0.18 (-0.21,-0.15)		-0.19 (-0.92,-0.17)	-0.17 (-0.22,0.01)

3.4. Diel scale analysis

During the 4-year study period and in latitudes below 62°, 433 cameras were active for a total of 1156 trapping days (with a mean of 481.4 ± 411.9 trapping days per camera site). A total of 10,181 badger pictures were captured (with a mean of 33.4 ± 71.2 pictures per camera site).

During all seasons the majority of pictures were captured at night, with a slightly different proportion (Table 6). A total of 8,486 pictures were taken at night, 1,369 pictures at daylight, 283 pictures at dusk and 43 pictures at dawn.

Table 6. Proportion of camera trap pictures of European badgers (*Meles meles*) at each period of the day. n: number of pictures.

Period of the day	Spring (n = 4,811)	Summer (n = 2,684)	Autumn (n = 1,327)	Winter (n = 1,359)
Dusk	0.027	0.027	0.041	0.020
Dark	0.854	0.794	0.787	0.884
Dawn	0.002	0.006	0.008	0.004
Daylight	0.117	0.174	0.164	0.091

Applying the simplest model, assuming constant probability of occupancy across sites and no other explanatory variables as parameters of detection probability but the hour of the day, Julian day and year, differences in activity between years were found, as in the previous analysis (Table 7-8). Also, in all seasons except in the summer, there is a change of activity level with Julian day (Table 7). There was not a significant increase in activity from the beginning of the spring, but a significant decrease in activity at the end of this season (Figure 10). In the autumn, there was a significant decrease in activity with Julian day. In contrast, activity relatively increased at the end of the winter (mean detection probability the first day of winter = 0.001, 95% CI = 0 to 0.002; the last day of winter = 0.005, 95% CI 0.004 to 0.007; Figure 10-11). In the summer, Julian day was included in the top-ranked model but was not significant (Table 8).

Moreover, the pattern of diel activity (reflected as the interaction between hour of the day and Julian day) changed with Julian day in all seasons. In the winter, activity length decreased with Julian day, both with the probability of detection increasing slower and decreasing faster at the end of the winter (Figure 11a). Both in the autumn and the summer, activity length decreased with Julian day, with the activity decreasing earlier in the morning the last days of the seasons (Figure 11c and d). In the spring, the activity period had a relatively little increase at the end of the season (Figure b).

As in the previous analysis, the camera trap sites used in this analysis showed a higher detection probability in the mid-spring months (Figure 10), and relatively lower detection probability the beginning of the winter, as well as the end of autumn (Figure 10).

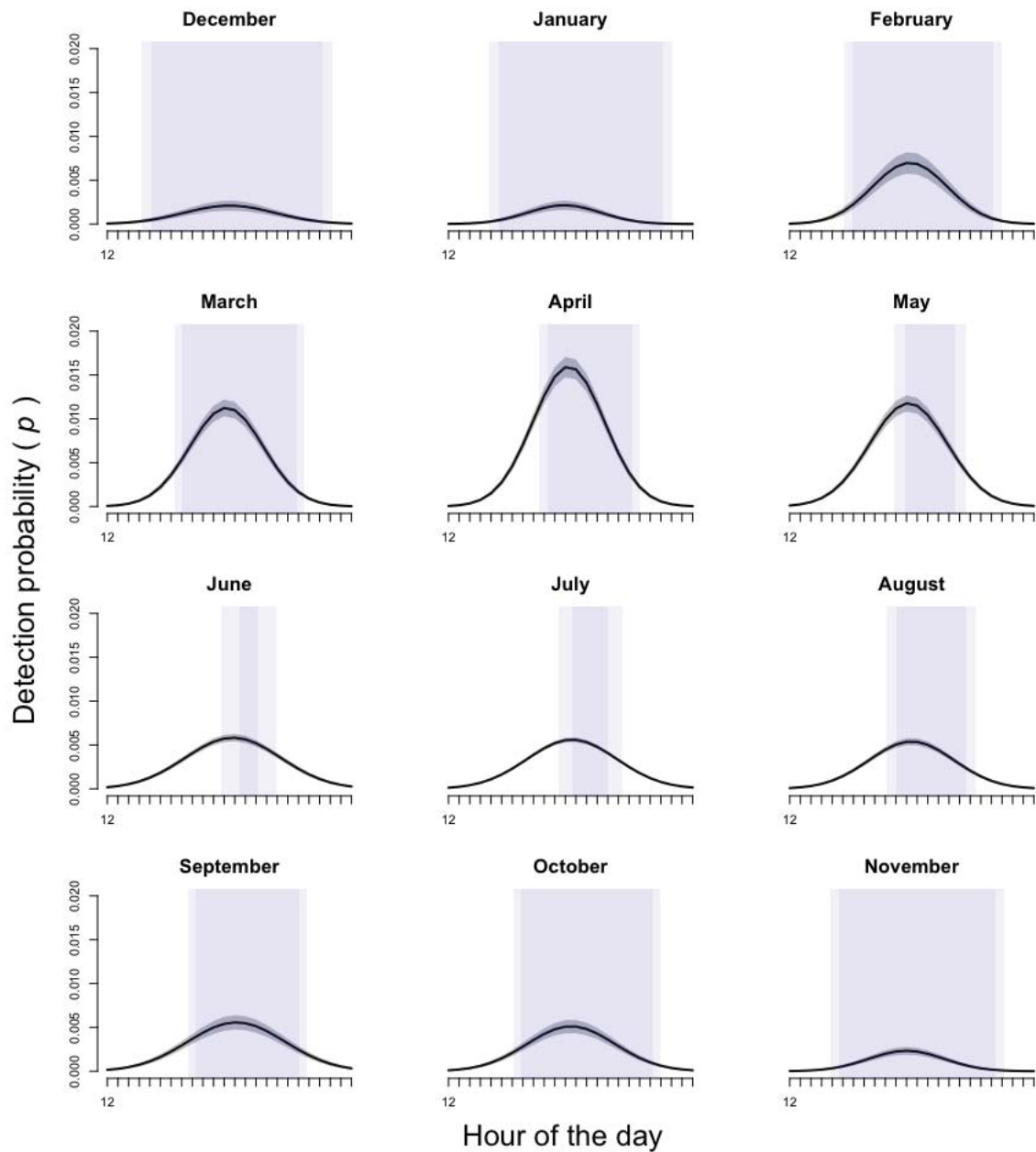


Figure 10. Predictions for monthly diel activity patterns (detection probabilities) of badger (*Meles meles*) in each season (grey shadows: 95% confidence intervals, blue shadow: night period including twilight, darker blue shadows: night period).

In the winter and the spring, there was relatively higher activity before midnight, starting to decrease after midnight (mean detection probability at 23 h in spring = 0.011, 95% CI = 0.010 to 0.012; in winter = 0.003, 95% CI = 0.002 to 0.004; Figure 10). In the summer and the autumn, the activity length was longer, with a peak of activity at midnight, decreasing slower than in the winter and the spring (mean detection probability at 24 h in summer = 0.006, 95% CI =

0.005 to 0.006; in autumn = 0.005, 95% CI = 0.004 to 0.006; Figure 10). The autumn presented a similar pattern of activity as the summer the first days of the season, shifting until having a similar pattern as in the winter the last days of the season (Figure 10 and Figure 11).

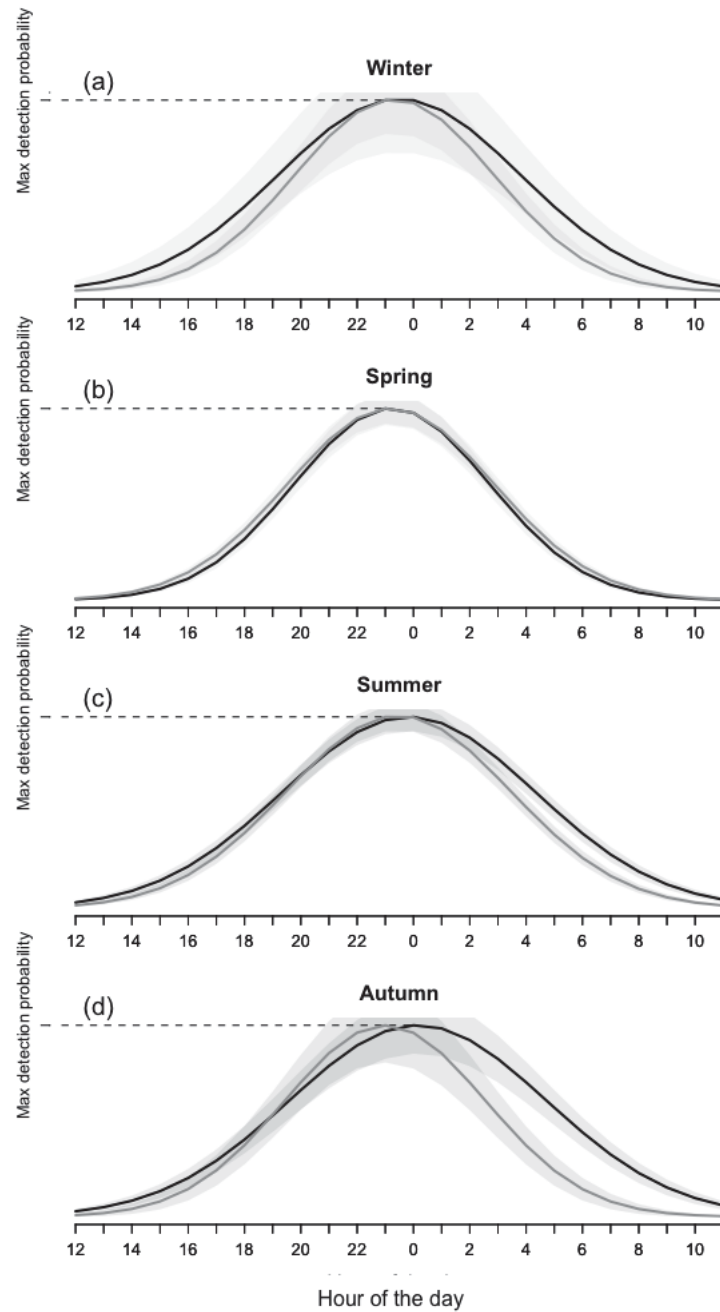


Figure 11. Comparison of the shape of the detection probability curves the first month of each season (black curve) vs the last month of the season (grey curves) for each season (grey shadows: 95% confidence intervals).

Table 6. Candidate models for the diel scale analysis of badger activity. Only models with $\Delta AIC < 6$ and the top model with constant probability of occupancy (ψ) are shown. The most parsimonious model of each season is shown in bold. p : probability of detection; ψ : probability of occupancy

Season	Candidate models	df	ΔAIC	AICw
Spring	$\psi(.)$ $p(\text{Hour} + \text{Hour}^2) * (\text{Julian} + \text{Julian}^2) + \text{Year}$	13	0.00	0.50
Summer	$\psi(.)$ $p(\text{Hour} + \text{Hour}^2) * \text{Julian}$	7	0.00	0.96
	$\psi(.)$ $p(\text{Hour} + \text{Hour}^2) * (\text{Julian} + \text{Julian}^2)$	10	7.74	0.02
	$\psi(.)$ $p(\text{Hour} + \text{Hour}^2) * \text{Julian} + \text{Year}$	10	8.61	0.01
Autumn	$\psi(.)$ $p(\text{Hour} + \text{Hour}^2) * (\text{Julian} + \text{Julian}^2) + \text{Year}$	13	0.00	0.94
	$\psi(.)$ $p(\text{Hour} + \text{Hour}^2) + \text{Julian} + \text{Julian}^2 + \text{Year}$	9	5.47	0.06
Winter	$\psi(.)$ $p(\text{Hour} + \text{Hour}^2) * (\text{Julian} + \text{Julian}^2) + \text{Year}$	13	0.00	0.53

Table 7. Diel scale analysis top models' coefficients on the logit scale. For all models, probability of occupancy (ψ) was assumed constant. Significant estimates are in bold. 95% CI limits in parentheses. Explanatory variables abbreviations are presented in Table 1. p : probability of detection.

Param.	Explanatory variables	Spring (n sites = 368)	Summer (n sites = 356)	Autumn (n sites = 354)	Winter (n sites = 343)
p	Year	2015* -4.12 (-4.20,-4.05)		-5.29 (-5.44,-5.14)	-6.13 (-6.38,-5.88)
		2016 -0.19 (-0.29,-0.10)		0.24 (0.08,0.41)	-0.37 (-0.60,-0.15)
		2017 -0.13 (-0.21,-0.04)		-0.03 (-0.20,0.14)	-0.24 (-0.46,-0.03)
		2018 -0.42 (-0.52,-0.32)		0.032 (0.16,0.48)	-4.19 (-6.64,-1.73)
	Julian	-0.01 (-0.05,0.03)	-0.03 (-0.08,0.02)	-0.42 (-0.51,-0.33)	0.59 (0.47,0.71)
	Julian ²	-0.26 (-0.31,-0.21)		-0.28 (-0.37,-0.20)	0.47 (0.34,0.60)
	Hour	-0.11 (-0.20,-0.02)	0.05 (-0.02,0.11)	0.00 (-0.13,0.13)	-0.35 (-0.70,0.00)
	Hour ²	-2.12 (-2.25,-1.99)	-1.36 (-1.44,-1.27)	-1.42 (-1.59,-1.26)	-2.01 (-2.50,-1.53)
	Hour:Julian	-0.01 (-0.07,0.06)	-0.06 (-0.12,0.01)	-0.22 (-0.36,-0.09)	-0.02 (-0.17,0.13)
	Hour:Julian ²	-0.04 (-0.11,0.04)		-0.03 (-0.16,0.09)	0.24 (0.05,0.42)
	Hour ² :Julian	0.12 (0.023,0.21)	-0.14 (-0.23,-0.06)	-0.34 (-0.52,-0.15)	-0.24 (-0.42,-0.06)
	Hour ² :Julian ²	0.17 (0.07,0.27)		-0.09 (-0.25,0.07)	0.31 (0.07,0.55)

4. Discussion

4.1. General discussion

Several factors and restrictions lead to the majority of studies investigating the activity patterns of species on a single temporal scale and only for short periods. This study is the first one that accounted for continuous 4-year activity recordings of European badgers, including all days in all years and under completely natural environmental conditions.

Overall, this study revealed that badger's activity was strongly influenced by seasonality rather than daylight, showing plasticity in their temporal patterns concerning external environmental factors. When the data were divided according to the season, subtler but intricate patterns became apparent. Temperature was an important determinant of badger activity, but there were also interesting interactions between the time of the year, season and hour of the day. Also, this study confirmed that badgers are not present at sites at high latitude and altitude, and prefer sites far from agricultural land and human settlements.

4.2. Annual scale analysis

As hypothesized (H1 and H2), badger activity was indeed partly year and season-specific. There was substantial variation between the years, with badgers' detection probability being higher in 2015. 2015 was a year with a warmer winter, indicating that, as predicted (P1.1 and P1.2), most of the differences in detection probability between years were explained by temperature, in particular temperature in the winter season. However, even though badgers usually do not experience high mortality or migrations within a year (Macdonald *et al.*, 2009), there might be a dissimilarity between the abundance, extinction and colonization rates of badgers in each site between the years of the study. Yet, I assume that at least part of the variation of the detection probability between the years could be attributed to varying levels of activity.

Regarding the seasonal patterns (change over the weeks of the year), there was a pronounced peak in the detection probability during the spring weeks and a pronounced decline in the winter weeks (P2.1). Since most of the changes in abundance of badgers might be during winter and spring, when there is higher mortality of cubs (Macdonald and Newman, 2002) and cubs are born (Page, Ross and Langton, 1994) respectively, detection patterns within a year are mostly explained by changes in activity levels during the year. In the summer, detection

probability decreased significantly compared to spring, and it remained constant over the autumn weeks. Badgers need to stock resources after winter, particularly if they were asleep for a long time (Broseth, Knutsen and Bevanger, 1997). Yet, many studies have claimed that badger activity is higher during the summer than during spring (Arroyo *et al.*, 2002; M. J. Sadlier *et al.*, 2003), related to earthworm abundance. The availability of earthworms has its peak in the spring, allowing badgers to actively forage for shorter amounts of time compared to the summer. The fact that in this study, spring detections were significantly higher could imply that the activity of badgers in the spring is not only explained by food availability but also by other vital activities, e.g. spring being the primary breeding period (Page, Ross and Langton, 1994).

In the winter, detection probability dropped almost to zero, denoting a decline in relative activity during that season. This finding is consistent with previous studies that showed that badgers in the northernmost range of their distribution hibernate (Bevanger and Broseth, 1998). Moreover, studies located in the south of their distribution also showed that badger activity was minimal due to the harsher conditions they have to overcome (Arroyo *et al.*, 2002). This study included sites from several latitudes, implying that while the badgers in the southern sites remained active during the winter (e.g. to forage or patrol their territories), the badgers in the northern sites might be inactive during the colder months, probably due to the lack of resources. However, the differences in the annual activity patterns between latitude were not tested. Further exploration of the differences in annual activity patterns differences between latitudes is needed.

In contrast to other studies (Nouvellet *et al.*, 2013; Noonan *et al.*, 2014), this study revealed that badgers are present at latitudes above the arctic circle (up to 68°), as well as in altitudes up to 700 meters, but that in such extreme locations the probability of occupancy is quite low. There were no records of badgers at higher latitudes and altitudes. The highest probability of occupancy was found at lower latitudes and elevations. Other studies have suggested that the ranging behaviour of badger is mostly a response to food availability, in particular during the coldest months of the year at northern latitudes (Bevanger and Lindstrom, 1995). In Norway, badgers mainly feed on earthworms and invertebrates (Gomes *et al.*, 2020), thus their food sources are dependent on soil temperature as well as snow-free periods. Even though badgers are generally flexible when selecting habitat, they usually select lower elevations and latitudes, with a warmer climate (Van Apeldoorn *et al.*, 1998). Therefore, the length of the snow-free season and its average temperature would potentially become the limiting factor on badgers'

site use and may explain the absence of badgers from high altitudes as well as high latitudes. Concerning older studies suggesting that badgers did not occur in such higher latitudes in Scandinavia (Broseth, Knutsen and Bevanger, 1997), these results might be caused by climate change during the last decade, allowing the badgers to expand their range further north (Bevanger and Lindstrom, 1995).

In line with other studies (Rosalino *et al.*, 2019), this study supported that badgers select for sites with a higher proportion of agricultural land. The preference for this habitat type might be given, again, as a response of food availability, as earthworm biomass is likely to be higher in cultivated fields than in forested areas (Van Apeldoorn *et al.*, 1998). This contradicts other studies that had found a lower site use of badgers in agricultural land (Broseth, Knutsen and Bevanger, 1997). However, these studies were located in Mediterranean habitats, meaning that the food requirements were different. Besides, in humid areas and high latitudes, badgers main source of food are earthworms (Remonti, Balestrieri and Prigioni, 2006; Lara-Romero *et al.*, 2012), and in drier areas at low latitudes, badgers can also prey on insects and reptiles (Kruuk and Parish, 1981; Lanszki, 2004; Li *et al.*, 2013).

Yet, non-forest habitats did not show more activity of the badgers in our study, which might be explained by the fact that most of the cameras of the study were located in forest. Regardless, I did not test if non-forest sites were agricultural fields. Badgers are often found in landscape mosaics of deciduous forests and agricultural land, avoiding wet soils where they are not able to dig deep setts (Virgós and Casanovas, 1999; Pyšková *et al.*, 2018). The results confirmed badgers actively select for deciduous forest habitats.

In this study, badgers also selected sites closer to human settlements. Badgers have previously been found to adapt to urban environments and select houses with gardens and farm buildings (Lara-Romero *et al.*, 2012), which is a common type of housing in Norway. Conversely, other studies found badger abundance to be negatively affected by human presence (Martín, Rodríguez and Delibes, 1995; Fedriani, Ferreras and Delibes, 1998). Generally, badgers avoid human infrastructures (Lara-Romero *et al.*, 2012; Silva *et al.*, 2017), but can still inhabit forests mixed with pastures and farmland (Huck, Davison and Roper, 2008). Also, at northern latitudes, badgers have shown a preference for agricultural areas (Bevanger and Lindstrom, 1995), probably because these areas offer better foraging opportunities. In the central part of European badger's distribution, the species is mostly limited by disturbance factors such as fragmentation by human constructions or habitat change (Macdonald and Newman, 2002; Macdonald *et al.*, 2010; Nouvellet *et al.*, 2013). However, in the north of their range, badgers are more affected

by climate and topographic factors that can restrict cub survival (Clarke, White and Harris, 1998), food availability (Kauhala, 1995) and habitat suitability (Virgós and Casanovas, 1999).

4.3. Seasonal scale analysis

As hypothesised (H2), the results show that badger activity (detection) is strongly influenced by temperature throughout the four seasons of the year. This study included sites from the south of Norway until up to sites above the arctic circle, therefore temperature was intrinsically related to latitude as well as to elevation. However, the relationship between temperature and latitude or elevation (i.e. change of climatic conditions) was not tested. Including both temperature and year in the analysis indicated that activity varied with temperature in all seasons. Other hidden variables intrinsic to each year possibly affected activity levels, in particular during the spring and the winter.

Contrarily to my prediction (P2.2), the optimal temperature was around 0-5°C, supportive of other studies that found badgers to have a preference for cold and moderate temperatures (Silva *et al.*, 2017; Rosalino *et al.*, 2019). Also, contrary to what was predicted (P2.1.), badgers were not inactive in all study sites during the winter. Even if the detection probability was low during winter season of all years, there were badgers active during the entire winter, and this activity was strongly correlated with temperature. As predicted (P1.1. and P2.1), badgers were not only relatively more active during warmer winters, but also the warmest days of the winter. This goes in line with cold temperatures restraining badgers more than high temperatures (Rosalino *et al.*, 2019). Moreover, badgers avoid snow (Slamka, 2016). Even though the effect of the snow was not tested in this study, snow depth was correlated to the years with relatively lower detection probability compared to other years with less snow. In particular, the winter of 2018 had comparatively lower detection probability than the rest of the years and was also the year with higher snow depth and coldest winter temperatures. Mild winters help maintain body weight and energy, thus boost the probability of survival during this season (Macdonald *et al.*, 2002). Thus, badgers might cease or reduce their activity during cold winters and avoid areas with rough climatic conditions to reduce their energy loss.

As hypothesised (H2), the activity of the badgers had a peak in the spring, following other studies (Pyšková *et al.*, 2018). Yet, badger cubs are born at the beginning of spring (Fell, Buesching and Macdonald, 2006; Pearce, 2011), indicating that the differences between spring detection probabilities were potentially not only explained by activity levels but also by an

increase or decrease on the number of offspring. However, cubs usually emerge from the sett some weeks after being born, and, when they start to go above ground, tend to stay close to the sett entrance until mid-summer (Fell, Buesching and Macdonald, 2006). Since the cameras were located randomly (i.e. not in front of badger setts), I can assume that most of the detection probability in the spring was explained by the activity levels of the badgers rather than an increase of the population. Indeed, the springs after the coldest years (2016 and 2018), were the ones with relatively lower detection probability, indicating again a reduction of activity during colder periods.

Unexpectedly, there was not a second increase in activity just after the winter. In Norway, badgers are known to hibernate from the end of October to the beginning of April (Bevanger and Broseth, 1998). However, this study shows that the badgers did not seem to hibernate consistently, at least not every year and/or at all camera sites. Even though winter activity was very close to zero, meaning that badgers remained largely in their setts, there were some observations of badgers during all the winter season. Remaining slightly active during the winter might imply that there was no need for the badgers to increase their foraging activity just before the winter. Lindsay and Macdonald (1985) results showed that the emergence of the badgers during the winter season was related to temperature, avoiding emergence only during temperatures below zero at night. However, there was no evidence of what the function of the emergences during winter nights was. In this study, this effect was not tested but might be that in some sites the temperature in the winter was not cold enough for badgers to remain in their setts during winter nights. Moreover, Gomes *et al.* (2020) found that, at least in the autumn, badgers were able to feed on domestic plants and anthropogenic food, something that it is potentially available in most of the camera sites of this study. Other studies have also found that, in areas with no availability of earthworms, badgers were able to forage on small mammals or fruits (Martín, Rodríguez and Delibes, 1995; Rosalino *et al.*, 2005) denoting high flexibility of badgers diet.

Many studies have confirmed the effect of not only temperature but also precipitation shaping badgers activity patterns (Martin *et al.*, 2017), however, contrary to predicted (P2.3) activity did not vary with precipitation in any of the seasons. Noonan *et al.* (2014), found that the autumn activity of the badgers was explained by rainfall and that the activity was also higher during wetter days. The lack of an effect from precipitation in this study might be because the effect of precipitation was reflected with some temporal delay. Other studies found that precipitation during the summer (providing more earthworm availability) was affecting the

survival of cubs during the winter (Woodroffe and Macdonald, 2000). Another hypothesis might be that in Norway, badgers are more influenced by other climatic conditions, for example, the temperature or the snowfall, or that as already mentioned, their diet does not entirely depend on earthworms (Martín, Rodríguez and Delibes, 1995; Rosalino *et al.*, 2005; Gomes *et al.*, 2020).

There were no major differences in the probability of site use between seasons. However, forest type was a significant explanatory variable in the spring. This potentially indicates that forest being a determinant in the annual scale analysis was mostly because of badgers actively selecting for deciduous forests in the spring only, when their diet mostly depends on earthworms (Gomes *et al.*, 2020).

4.4. Diel scale analysis

As expected (P3.1), European badgers in this study were mainly nocturnal. However, not all pictures of badgers were captured during the night. Contrarily to expectation (P3.2), during the summer, when nights were short, their activity curves were wider and many of their captures were during daylight. This goes in line with badgers daylight activity commonly associated with hot summers, with low food availability, or with isolated sites with low human disturbance (Clark, 2010). Moreover, summers in Norway have very short night-time, suggesting that badger might compromise nocturnality to fulfil their required activities. Other studies in Europe have also confirmed that badgers leave their setts before dark and return after sunrise in the summer days when daylight length is longer (Kowalczyk, Jedrzejewska and Zalewski, 2003; Sidorchuk and Rozhnov, 2018). Earthworms are less abundant in summer, therefore badgers need to forage for longer periods than in the spring. Also, Arroyo *et al.* (2002) found that the duration of the activity was longer during spring and summer when their activity is a compromise between foraging and nocturnality, and of shorter duration during autumn and winter when their activity is limited by the severe weather conditions. Conversely, several studies found a negative correlation between daylight length and activity duration (Cresswell and Harris, 1988; Fowler and Racey, 1988). Nonetheless, there were almost no detections during daylight in the autumn and winter, potentially because of inactivity in the colder months as well as more food availability in the autumn.

Also, as it has been suggested in other studies (Harris, 1982; Maurel and Boissin, 1983; Fowler and Racey, 1988), badger relative diel activity was characterized by a single peak of activity

around midnight. Since the variable “hour of the day” was only considered as a second-degree polynomial, in this study it was assumed the activity could only have one peak, simplifying a lot the reality of the diel activity of badgers. It appeared that there was a connection between both daylight length and ambient temperature, and this was what dictated the diel activity patterns of the badgers in this study. The main difference in diel activity between months was in the probability of being active, rather than the shape of the diel activity curves. However, a slight difference in shape was found between difference among seasons, with a maximum detection around midnight in the coldest months, and a maximum detection during sunset in the summer days, with intermediate patterns during the in-between months.

However, this part of the analysis assumed constant site use probability across the study area and did not include other environmental variables that could affect diel activity patterns of the badgers. Further suggestions could be made with a deeper examination of additional environmental variables, as well as more distinction between the characteristics of the sites included in the study.

4.5. The methodology and analysis framework

In addition to the ecological results, this study has contributed to methodological advances. Using an established analytical framework i.e. occupancy, I provided a new approach to analyse activity patterns from camera trap data, differently from the conventional methods (e.g. generalized mixed effect models or kernel densities; Bischof *et al.*, 2014; Rowcliffe *et al.*, 2014), that ignore hierarchical relationships between occupancy and detection processes. This was possible to do with European badgers because this species does not experiment major changes in abundance or mortality rates (aside from the slight increase of the population with the emergence of the offspring in late spring; Fell, Buesching and Macdonald, 2006; Macdonald *et al.*, 2009). Hence, their variation detection rates were mostly explained by their aboveground activity patterns and it was possible to link detection probabilities with relative activity levels over time. Still, a better awareness of the changes in abundance in addition to migration rates in the study area could have improved the interpretation of the results.

In the case of the methodology used in this study, hierarchical models, the differences in presence/absence between the sites to account for activity were corrected, as well as the environmental drivers that might affect each local site. Occupancy models account for temporal and spatial heterogeneity of detection probability based on explanatory variables as well as the

independence of the sites (MacKenzie *et al.*, 2006). Other simpler methodologies might not take imperfect detection into account and lead to errors in estimating activity patterns of a species (MacKenzie *et al.*, 2006; Kéry, Gardner and Monnerat, 2010). However, in this study, no spatial explanatory variables were tested for detection probability as most of the camera sites were located in the forest in order to monitor lynx (decreasing randomness to a certain degree), hence opposing the previous assumptions.

4.6. Different time scales: implications and limitations

This study shows the importance of timescale and approaches when using occupancy models as well as other methodologies. When studying activity patterns, all relevant timescales should always be considered, even if the research is focused on a smaller scale. The badgers in this study were affected not only by the conditions of the site at a certain time but also by the conditions the site was exposed before (e.g. spring detection being lower after cold winters). Reliable descriptions of temporal patterns, recognizing multiple scales differences, can provide both value in the natural history of a species perspective and be relevant for effective management and conservation decisions that will involve long-term consequences.

Further research using occupancy models inspecting activity using even more different timescales distinctions (e.g. more years or weekly scale) or adding more possible drivers that can affect presence/absence, detection and activity would be very interesting to expand the knowledge not only of badgers' ecology, but also other mammals that could be studied the same way. Moreover, addressing the fact that density variations were not identified in this study is needed, as occupancy models are developed for tasks other than providing density estimates (Parsons *et al.*, 2017). In this particular case, it is known that climate and habitat determine not only occurrence and activity levels but also density and abundance of badgers (Kruuk and Parish, 1982; Carr and Macdonald, 1986; Woodroffe and Macdonald, 1993).

Another limitation of this study is the fact that to keep the analysis simpler and focus on the change of activity over time, I did not consider spatial variables that might affect the detection probability of the badgers, but rather only their presence/absence or site-use. However, herein temporal variables have been considered to have a stronger and more important effect on detection probability than differences in activity between e.g. habitat. The development of models considering both space and time use might bring better insight into the complex effects on the activity of badgers or any other species. Further exploration of the diel activity patterns

and how this activity might be different between latitudes, different habitats or even different human disturbances is recommended.

Finally, a key weakness of the data used for this study was the distribution of the camera stations. The fact that the camera placement was meant to maximize detections of lynx, could somehow have affected the results, for example, as the camera locations were biased towards forest instead of urban areas, and might have hidden other habitats where badger's activity might differ. Moreover, most of the camera sites were located in the same latitude (59 to 61°N), leading to results masking site use and activity of badgers' variations in northern locations. To fully understand the activity of badgers in Norway, further studies with more representation of northern latitudes as well as coastal sites are needed.

5. Conclusion

The results of this thesis lend further support to multiple timescales being a necessary approach to fully understand activity of animal species (McCann, Zollner and Gilbert, 2017). There was an activity variation between years, season and time of the day. Badgers' activity was maximum during the spring season, and during night-time, with some variation within and between years. Further, temperature also had a great impact on activity during all the seasons, denoting a potential consequence of weather and climatic future shifts affecting badgers' populations. Spatial variations in detection probability due to habitat, and further explanatory variables explaining diel activity levels remains to be tested. Developing models that consider both multiple time and space use scales would provide new opportunities for exploring activity patterns of badgers and other species, offering a significant tool for increasing conservation and management of species knowledge.

7. References

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Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway