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Activity patterns of European roe deer (*Capreolus capreolus*) are strongly influenced by individual behaviour

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Abstract. With solitary-living species, such as the European roe deer (*Capreolus capreolus*), high individuality is also expected to influence activity. Here we studied the annual activity patterns of European roe deer in the Bavarian Forest National Park. We investigated the influence of age and sex, the weather, and the individuality. We used sex-specific generalized additive models with variables that considered the age of the animal and also the high-resolution site-specific parameters temperature, precipitation, and snow depth. Data from 20 males and 9 females were gathered continuously with GPS-GSM collars carrying a dual-axis acceleration sensor. Our results indicated that the main factors influencing the activity patterns of the crepuscular roe deer in the Bavarian Forest National Park are the individual, the season, and the time of day, and that weather parameters are secondary. GPS-GSM collars with a dual-axis acceleration sensor allow long-term, continuous, and remote activity monitoring of European roe deer.

Key words: animal activity, acceleration sensor, generalized additive model, individuality, National Park Bavarian Forest

Introduction

Continuous, long-term records of free-ranging individuals are required to analyse animal activity (Scheibe et al. 1999). In early studies of animal activity, the animals were directly observed. Such observations depend on the visibility of the animals, the habitat, and light. This method is often restricted to enclosures (roe deer (*Caprelus capreolus*): Ellenberg 1978, Schober et al. 1995; sika deer (*Cervus nippon*): Borkowski 2000) and data can often only be gathered during the daytime.

An indirect method that does not require direct visual contact is very high frequency (VHF) telemetry. The level of animal activity assigned by the observer is based on the assumption that moving animals pass obstacles, which results in changes in the VHF signal volume and tone. This method has been used e.g. for roe deer in Sweden (Cederlund 1981).

VHF collars were later equipped with motion sensors. The radio signal switched to a higher impulse rate when the animal moved. With this methodology, it was possible to distinguish not only active and inactive behaviour, but also different behavioural categories in red deer (*Cervus elaphus*) (Georgii 1981, Green & Bear 1990) and white-tailed deer (*Odocoileus virginianus*) (Beier & McCullough 1990).

All three methods are time consuming, labour intensive and expensive and are therefore not suitable for observing a substantial number of individuals simultaneously or for gathering activity data continuously over longer periods. These problems have been solved with the development of new tracking systems. The automatic telemetry system ETHOSYS (Scheibe et al. 1998, Berger et al. 2002, Berger et al. 2003, Pépin et al. 2006) is attached to collars and has two sensors, one for acceleration and one for tracking the position of the animal's head, i.e. up and down. ETHOSYS has been used to study the activity of, e.g. captive roe deer (Scheibe et al. 1999). Global Positioning System (GPS) telemetry, in use since the early 1990s, has become an established method in wildlife monitoring. Some GPS telemetry systems are combined with acceleration sensors to record data on animal activity (from Lotek Engineering:

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e.g. Adrados et al. 2003, Coulombe et al. 2006; from VECTRONICS Aerospace: e.g. Gervasi et al. 2006, Löttker et al. 2009, Krop-Benesch et al. 2013).

Animal activity is the result of both exogenous and endogenous factors (Aschoff 1954). Activity constantly switches between active and inactive phases. The endogenous factor driving ruminant activity, such as that of roe deer, is the capacity of their digestive system (Turner 1979), which has to ensure the more or less constant supply of nutrients for the body and results in ultradian cycles. The duration of one digestive cycle, i.e. feeding and digestion, depends on the species-specific feeding ecology (e.g., roe deer are browsers and red deer are intermediate mixed feeders) and the food quality and availability within their habitat (Cederlund 1981). Other endogenous factors have been reported, such as the differences between different sex and age classes (Ellenberg 1978, Turner 1979). The European roe deer do not have a pronounced sexual size dimorphism, but males and females have different demands on their environment, which lead to sex-specific differences in the size of their home range (Mysterud 1998, Kjellander et al. 2004, Ramanzin et al. 2007), habitat use (Cimino & Lovari 2003, Ratikainen et al. 2007), and activity patterns (Ellenberg 1978, Cederlund 1981, Schober et al. 1995, Danilkin & Hewison 1996).

The strongest exogenous factor driving ruminant activity is the changing azimuth of the sun, which divides day and night (Nielsen 1984), causes seasons, and results in circadian activity cycles that change through the seasons. Another exogenous factor is weather, i.e. temperature and precipitation, and especially snow depth (Turner 1979, Cederlund 1981, Nielsen 1984, Danilkin & Hewison 1996). European roe deer are crepuscular, with two pronounced activity peaks at dusk and dawn, and their activity also varies seasonally (Ellenberg 1978, Cederlund 1981, Danilkin & Hewison 1996).

In addition to the endogenous and exogenous factors, European roe deer may show a high level of individuality. Cederlund (1981) and Ellenberg (1978) found evidence that the activity patterns of the individuals are only slightly synchronized.

Earlier studies of European roe deer activity revealed fundamental traits, but the data were constrained to animals kept in enclosures, only a small number of individuals were observed, and observations were discontinuous. The newer methods of tracking animals, e.g. GPS telemetry, allow continuous and autonomous observation of a substantial number of individuals over a longer period. The obtained huge data sets can then be analysed with sophisticated models to provide new insights into animal activity. Also aspects such as the interrelation between weather and activity, and the supposed high individuality of European roe deer can be considered.

The aim of our present study was to achieve a generalization of the annual activity of European roe deer in the Bavarian Forest National Park. We considered the endogenous factors age and sex; the exogenous influences temperature, precipitation, and snow depth; and the individuality of the deer. We used a random-effects model to treat the individual animals as random variations around a population mean, i.e. the mean activity of roe deer. We therefore were able to make inferences about the population from which the individuals were drawn and not about the particular roe deer included in the study.

Material and Methods

Study area

The Bavarian Forest National Park comprises 244 km² and is situated in southeast Germany (49°3′19″ N, 13°12′9″ E) on the border to the Czech Republic and its Šumava National Park. The sub-mountainous area of the Bavarian Forest National Park gently rises from 650 m a.s.l. in the west to 1450 m a.s.l. in the east. The long-term mean annual temperature varies between 3.8 °C and 5.1 °C; the precipitation per year varies between 1200 mm and 1800 mm, depending on the altitude (Bässler et al. 2009), with a pronounced amount as snow. Snow cover lasts for seven to eight months at the higher elevations and for five to six months in the valleys.

Forest covers 98 % of the park area, and is separated into three major forest types: 1) above 1100 m, upper montane spruce forests with Norway spruce (*Picea abies* L.) and some mountain ash (*Sorbus aucuparia* L.) (16 % of the area); 2) between 600 m and 1100 m altitude, mixed montane forests with Norway spruce, white fir (*Abies alba* MILL.), European beech (*Fagus sylvatica* L.), and sycamore maple (*Acer pseudoplatanus* L.) (68 % of the area); and 3) in wet depressions, often associated with cold air pockets in the valley bottoms, spruce forests with Norway spruce, mountain ash, and birches (*Betula pendula* ROTH., *Betula pubescens* EHRH.) (16 % of the area) (Heurich & Neufanger 2005).

Since the late 1990s, a massive proliferation of spruce bark beetles (*Ips typographus*) dramatically changed the forest structure. Virtually all of the mature trees of the high montane Norway spruce forest stands were killed by the bark beetle (end of 2009 ca. 6500 ha, Lausch et al. 2010). European roe deer are the main prey of the Eurasian lynx (*Lynx lynx*) at this site (Mayer et al. 2012); lynx were reintroduced in the 1980s in area now comprising the Šumava National Park (Wölfl et al. 2001). The lynx density estimated by capture-recapture with camera traps was estimated as 0.9 lynx/100 km² (Weingarth et al. 2012); European roe deer density estimated by the game wardens was between 1 and 3 roe deer per 100 hectares; red deer density estimated by snow tracking and counting in winter enclosures was between 1.4 and 1.7 animals per 100 hectares (Heurich et al. 2011).

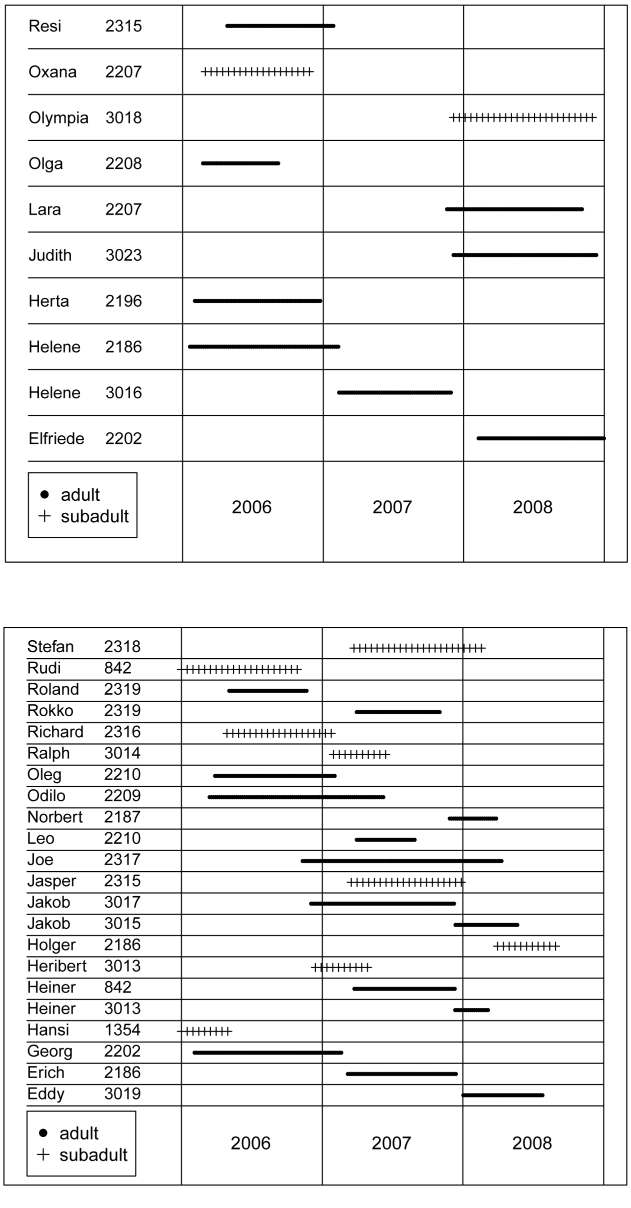

Fig. 1. Observation time of male and female roe deer. The number behind the name of the individual is the serial number of the worn GPS-GMS telemetry collar.

Study animals

For this particular study on roe deer activity, 20 males and 9 females wearing GPS-GSM collars for various times between 2006 and 2008 were analysed (Fig. 1). All individuals were caught within the Rachel-Lusen area (140 km²; Weilnböck et al. 2010), where roe deer management ceased in 2007. The animals lived continuously or most of the time in the national park during the study period. Some of the animals left the national park area for short periods especially during winter for supplementary feeding facilities on private land, where recreational hunting takes place. In general, the human hunting pressure on the roe deer individuals studied can be considered low (Heurich et al. 2011).

Activity data

We used GPS-GSM collars, series 800 to 3000, from VECTRONIC Aerospace. Deer activity was measured by a dual-axis acceleration sensor mounted on the collar; the component horizontal and vertical sensors were oriented perpendicular and parallel to the spine of the animal, respectively. Consequently, left-right and back-forth movements generated x- and y-values, respectively. Data were recorded continuously at 6-8 times per second, and the resulting values were accumulated and averaged in the 5-min time interval between two successive activity fixes. The mean activity values were arranged on a linear numerical scale and ranged from 0 to 255 for both sensors. All values were saved on the collar and could be downloaded after retrieving the collar from the animal. Data in adf (activity data file) format were provided as tables and contained the following information: UTC date, UTC time, LMT date, LMT time, activity X, activity Y, and temperature (UTC, Coordinated Universal Time; LMT, Local Mean Time). A strong correlation between the x- and y-values ($r_{xy} = 0.95$) was found. Since both sensors seemed to provide similar information, we decided to work with the sums of x and y (value range = 0-510) as a measure for activity. The data of the different collar series significantly

Table 1. Variables used for the statistical model.

Minute of the day	m
Day of the year	d
Year	y
Age	a
Collar type	c
Temperature	t
Precipitation	rs
Snow depth	s

Table 2. Model terms of the boosted generalized additive models. Individual is the random effect term.

Bivariate smooth effect of *d* and *m*	*Time*
Linear effect of year	*Year*
Linear effect of age	*Age*
Linear effect of collar type	*Collar*
Smooth effect of temperature	*Temp*
Smooth effect of precipitation	*RS*
Smooth effect of snow depth	*S*
Effect of individuals	*Individual*

and systematically differed, and the collars could be divided into two groups separated by their serial number: collar type 1 comprised serial numbers from 842 to 2319, and collar type 2 comprised serial numbers from 3013 to 3023 (Heurich et al. 2012).

Data analysis

We calculated one model for female roe deer activity and one for male roe deer activity. The variables in the models were time of the day (15-min intervals), date, year, age, temperature, precipitation, snow depth, and collar type (Table 1). Age (subadult and adult) and collar type (1 and 2) were coded binary; all other parameters were metric.

The generalized additive model (GAM) is an extension of the traditional linear model and allows for rather flexible specification of the dependence of the response variable activity on the covariates (e.g., Wood 2006). Both quantitative and qualitative variables are allowed as covariates. Linear and other parametric forms can be mixed with non-linear functions, and this is necessary when categorical variables are present in the model. Linear modelling is adequate for the variables year, age, and collar type. Quantitative variables, e.g. temperature and time, are represented by non-parametric functions. An important feature is that the non-linear terms are not restricted to main effects. Non-linear components may appear in two or more variables. Therefore, we can model the temperature or the amount of precipitation as subject to the day of the year at which they occurred. A random effect term can be added to the model to give an account of the individual variability.

The additive model used in this study contains eight model terms (Table 2) and has the following form:

E (activity/m, d, y, a, c, t, rs, nsh) = Time + Year + Age + Collar + Temp +RS + SH + Individual.

We estimated the additive model for roe deer activity using the mboost function from the R-package mboost (Hothorn et al. 2010) with 600 boosting iterations, a learning rate of nu = 0.2, and squared error loss.

One important aspect of using the boosting approach for the estimation of the smooth functions of the GAM lies in the availability of variable selection (Buehlmann & Hothorn 2007). The variables that have a decisive influence on the response are selected, and their partial contributions can be easily extracted from the boosting fit. After the most relevant variables have been identified, we attempted to interpret the nature of the dependence. For this purpose, we created graphical renderings of the model term Time.

Table 3. Intercepts of female roe deer activity calculated by a boosted generalized additive model, where the individuals were considered as random factors. The roe deer Helene wore in consecutive years collars from different types. These observations were treated like two separate individuals.

Individual	Intercept
Elfriede	–1.423
Herta	3.907
Judith	–12.179
Lara	13.296
Olga	1.072
Olympia	–2.973
Oxana	2.679
Resi	–6.648
Helene collar type 1	8.281
Helene collar type 2	–5.215

Table 4. Intercepts of male roe deer activity calculated by a boosted generalized additive model, where the individuals were considered as random factors. The roe deer Heiner wore in consecutive years collars from different types. These observations were treated like two separate individuals.

Individual	Intercept
Eddy	–7.569
Erich	15.532
Georg	0.105
Hansi	1.594
Heribert	–3.743
Holger	3.295
Jakob	–6.711
Jasper	–1.813
Joe	7.177
Leo	–8.402
Norbert	1.383
Odilo	5.509
Oleg	16.348
Ralph	–3.018
Richard	3.173
Rokko	–7.333
Roland	–5.393
Rudi	–2.068
Stefan	3.322
Heiner collar type 1	–8.146
Heiner collar type 2	–5.837

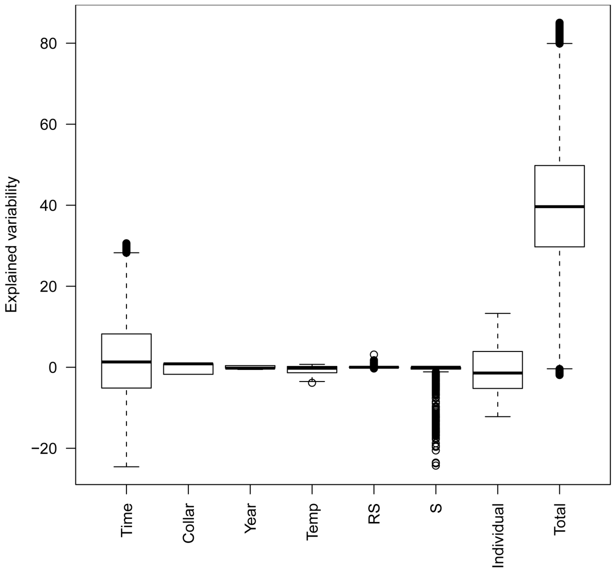

Fig. 2. Model terms of the boosted generalised additive model analysing female roe deer activity in Bavarian Forest National Park. Box-whisker-plots show the explained variability that can be attributed to the variables and the total explained variability. Thick horizontal lines = medians; box = 25- and 75 %- quartiles; dashed lines include 100 % of data, except dots = outliers.

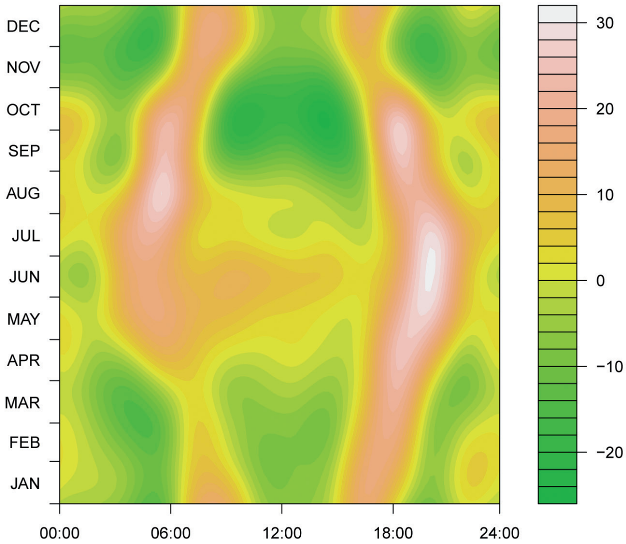

Fig. 3. Annual plot of mean female roe deer activity in Bavarian Forest National Park generated by a Boosted Generalized Additive Model (colour values: from dark green to light red means increasing activity values; x-axis = time of day (hour); y-axis = date).

Results

Owing to the separate models for females and males neither the intercepts (Table 3 and 4) nor the fits of the variable time (Fig. 3 and 4) are comparable among each other.

The relevant variables selected by the boosted GAM for the activity of female roe deer were collar type, year, temperature, precipitation, and snow depth, but their explanatory value was small. Most of the data variability was explained by the variables time (i.e. date and time of day), and individual (Fig. 2). Female roe deer in the Bavarian Forest National Park were crepuscular, and their activity peaks shifted to follow the times of sunset and sunrise throughout the year (Fig. 3). Between the end of October and the beginning of March, the females were most active during dusk and dawn. In January and February a third smaller activity peak was found before midnight. From March until the beginning of June, the overall activity of the females increased. They became more active during the day and at night, but the highest activity remained around sunrise and especially sunset. In mid-May, the pre-noon activity was pronounced; the activity decreased in late afternoon and again increased at dusk. At the beginning of July, the daytime activity decreased and the nighttime activity increased again. The activity around sunset and sunrise remained pronounced, with the activity at dawn higher than at dusk until the beginning of October. The overall female activity began to decrease at the beginning of August. The daytime activity ceased. Between mid-October and the beginning of December, the activity was completely focused on the crepuscular phases. As December progressed, the activity around midnight again increased. The intercept values give the deviation of the random factor from the mean, i.e. in our study the algebraic sign indicate whether an individual was more active than the population mean

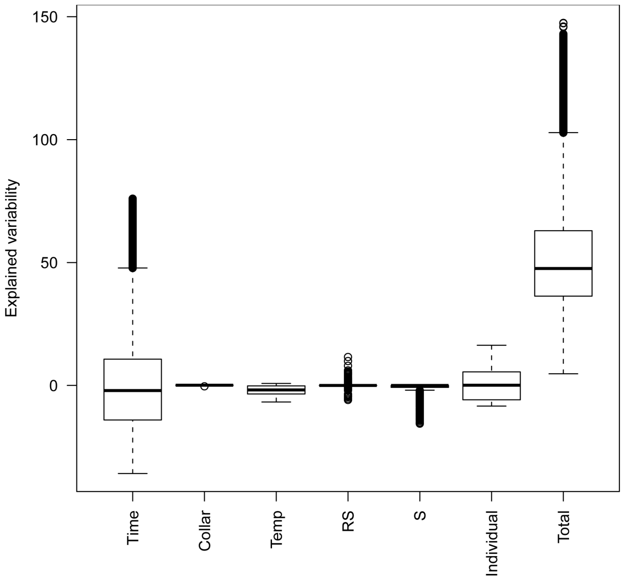

Fig. 4. Model terms of the boosted generalised additive model analysing male roe deer activity in Bavarian Forest National Park. Box-whisker-plots show the explained variability that can be attributed to the variables and the total explained variability. Thick horizontal lines = medians; box = 25- and 75 %- quartiles; dashed lines include 100 % of data, except dots = outliers.

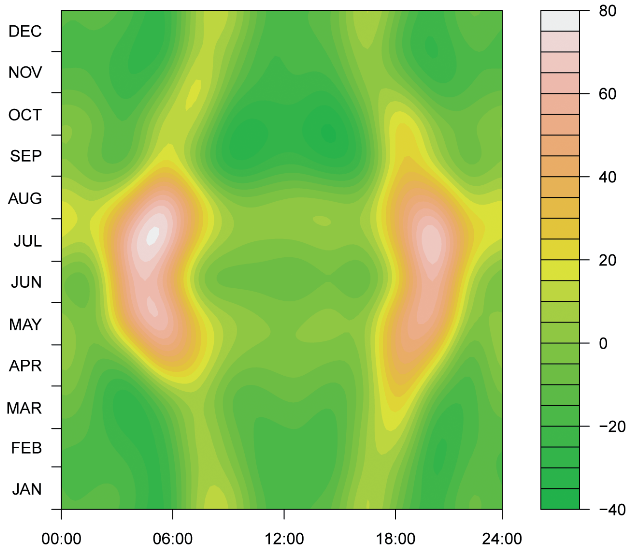

Fig. 5. Annual plot of mean male roe deer activity in Bavarian Forest National Park generated by a Boosted Generalized Additive Model (colour values: from dark green to light red means increasing activity values; x-axis = time of day (hour); y-axis = date).

(positive value) or vice versa an individual was less active than the population mean (negative value). The values are ranked. The female roe deer Lara (13.296) and Judith (–12.179) revealed the highest intercepts and therefore the highest deviation from the mean female roe deer activity (Table 3). Lara was most active and Judith was least active compared to the mean activity of female roe deer.

The relevant variables selected by the boosted GAM for the males were time, individual, collar type, temperature, precipitation, and snow depth. The variables time and individual explained most of the data variability (Fig. 4); the explanatory value of the other variables was negligible. Also the males were crepuscular, with the highest activity around sunset and sunrise (Fig. 5). The male activity pattern was similar to that of the females, but the crepuscular activity of the males was more pronounced. The activity at dusk started to increase in mid-February. From the end of April to mid-June, the deer were active during the day. The activity continued from dawn into the morning, and the activity began in the afternoon and led into dusk. In July, the overall activity was at its high, with daytime and nighttime activity and the highest crepuscular activity. During August, the overall activity was drastically reduced, the nighttime activity ceased, and the crepuscular activity phases were shorter. In October, the male deer were more active at dawn for a short period. The male roe deer Oleg and Leo had the highest intercepts, with Oleg being the most active, and Leo the least active (Table 4).

Discussion

We continuously monitored the activity of a substantial number of female and male European roe deer in the Bavarian Forest National Park over substantial time periods. By remotely collecting the data with GPS-GSM collars, observer disturbances were eliminated. However, neck collars can potentially lead to other problems. First, since the collar is placed around the animal's neck, the acceleration sensor is affected by head movements (Gervasi et al. 2006). Behaviours such as grooming, grazing, or vigilance could lead to high activity values, whereas constant and directed locomotion could lead to lower activity values. We analysed activity patterns without distinction between the different behaviours or even between active and inactive phases. Secondly, tightening of the collar could affect the sensitivity of the acceleration sensors (Adrados et al. 2003, Coulombe et al. 2006, Gervasi et al. 2006, Löttker et al. 2009). Thus, the activity values for the same activity can differ between individuals (Gervasi et al. 2006). Therefore, we considered the individual as a random factor in the models. Thirdly, each collar equipment component could influence the activity values, as shown by our results with older and newer series of the collars. During our study period, VECTRONIC Aerospace updated the acceleration sensors in the collars. The older and newer series of the collars significantly and systematically differed in their measuring activity and could be subdivided into two groups. To accommodate this difference in our analyses, we considered the two groups of collars as variables in the models. Such potential influences of different collar series should be considered in animal monitoring research.

At the same study site, animals of the same species are exposed to the same exogenous conditions (day/night regime, food availability, weather). Therefore, the effects of these factors should be similar for all individuals. However, other factors, e.g. sex and age, also influence activity patterns (Favreau et al. 2009) and could lead to variations in activity.

To accommodate the sex-specific differences, we calculated separate models for females and males. The activity patterns of the two sexes were similar, except that the crepuscular activity of the males was more distinct during spring and summer. The females, in contrast, showed crepuscular activity during these seasons but also were active during the day. This extended activity could be explained by the 50 % higher energy demands of the females in these seasons during gestation and lactation than in winter (Ellenberg 1978). Their higher nutrient requirements lead to an increased feeding activity, despite the simultaneously increasing food availability and quality. The mother-fawn relationship probably generates a more even distribution of female activity throughout the course of a day and not only during crepuscular phases.

We considered age as a variable, but it was shown not to be relevant by the boosted GAM for both female and male roe deer. The intercepts of the two females that were caught as fawns and became yearlings during the observation period were either slightly lower (Olympia = –2.97) or higher (Oxana = 2.68) than the mean activity of all females. The intercepts for the eight male fawns that later became yearlings during the study period ranged from –3.74 to 3.32, which was not the maximum deviation from the mean activity of the males. These results indicate that the age classes had no explanatory relevance for the activity patterns and that there was no distinct trend for more or less activity between subadults and adults. Since we caught the monitored roe deer in the Bavarian Forest National Park between October and March, the youngest individuals were at least six months old. Danilkin & Hewison (1996) mentioned that the activity of adult females and fawns of 2.5-3 months becomes synchronous in space and time. Males reach puberty at the beginning of their second year (Danilkin & Hewison 1996). Especially in their first spring, a higher activity of yearlings is observed due to adult male aggression during their dispersal. Activity also increases one year later as subadults establish their territories (Liberg et al. 1998). Ellenberg (1978) has shown that yearling and adult males were involved equally in territorial fights, and usually the yearlings were unsuccessful. Whereas the activity of both involved individuals should be at the same level. However, since European roe deer are adolescent – in this case defined as the time of autonomous feeding, living in a loose relation with the mother and not being involved in territorial fights – for only a short period, the time period in which differences in activity could be expected is short. We analysed annual activity patterns, which may not detect short-term differences. In addition, the differences between subadults and adults could be suppressed by the individuality of the animals.

The most relevant parameters for the explanation of female and male roe deer activity in the Bavarian Forest National Park were the time (time of day and date) and the animal observed. Although Ellenberg (1978), Cederlund (1981), and Danilkin & Hewison (1996) described roe deer activity patterns at the population level, they also reported a variance among the individuals. The high deviation around the population mean activity pattern could be an evidence of individuals' temperament. Due to the difficulties to quantify and analyse the miscellaneous behavioural expressions of temperament, the ecological relationship between temperament and breeding success, survival, or fitness of free ranging animals is sparsely investigated. But Réale et al. (2007) defined five categories of temperament traits as a basis for measuring behavioural expressions of personality. They mentioned the general level of activity as one of these categories.

Furthermore, activity patterns of solitary species are often synchronized only slightly (Favreau et al. 2009) because of the lack of intraspecific social cues, which leads to high individuality within their activity rhythms.

However, we found a high individuality in our study and therefore strongly recommend that future studies consider the potential influence of the individuality of solitary species.

Despite their individuality, the activity of the roe deer in our study was synchronized because of their crepuscular nature, with the highest levels of activity around sunset and sunrise, as also found previously (Ellenberg 1978, Cederlund 1981, Schober et al. 1995, Danilkin & Hewison 1996). Similar patterns have been observed for several ruminants, such as white-tailed deer (Beier & McCullough 1990), red deer (Georgii & Schröder 1978, Green & Bear 1990), and moose (*Alces alces*) (Cederlund 1989). The change between light and darkness operates as a constant exogenous influence or zeitgeber (Aschoff 1954) and leads to pronounced crepuscular activity peaks. The plasticity of the increased activity always adjusted to the shifted times of sunrise and sunset during the course of the year, which emphasized its influence on roe deer activity. Although there is evidence that especially weather extremes, such as heavy rainfall, high temperatures, high wind speeds (Danilkin & Hewison 1996), and high amounts of snow (Cederlund 1981) could negatively influence roe deer activity, the weather parameters in our study were secondary in explaining the annual activity. Their influence would be difficult to identify in long-term analyses since weather extremes are rare and short-lived, and, therefore, the changes in activity, behaviour, or space use that they cause are probably also very short-lived. On the temporal scale of our study, the changing day length throughout the year was the main factor driving European roe deer activity. This exogenous factor was represented in the model by the term Time and included seasons. Therefore, the prevailing weather conditions, but also food availability and quality, were indirectly represented.

Ellenberg (1978) reported a higher observability of females and males and more direct social interactions between males in October. He assumed that these phenomena either were caused by the shortened day length as a signal to start seasonal migration to the winter ranges or that they were a phylogenetic relic of the ancient natural autumn rut of cervids. We observed an increased activity of male roe deer during October, especially at dawn. Since females did not show an increased activity in October, the activity of the males is most likely not connected to seasonal migrations, which should affect both sexes (Cagnacci et al. 2011). If the increased activity of male roe deer activity is a phylogenetic relic, also other populations of roe deer should show the same activity pattern; such studies need to be conducted. A third possibility is that with the upcoming winter, the European roe deer form small groups and the agonistic behaviour between males increases because of social ranking. Indeed, aggressive interactions at supplementary feeding stations in winter are more common between males than females (Geiger & Krämer 1974). This increased male agonistic behaviour could be emphasized by the manifestation of sexual behaviour among early maturing fawns (Danilkin & Hewison 1996).

Our results are in keeping with the main results of earlier studies that did not use remote-sensing methods; therefore, GPS-GSM collars with one dual-axis acceleration sensor can be used to detect biologically meaningful activity patterns of European roe deer, with the added advantage of allowing long-term, continuous, and remote monitoring. Our analysis approach using generalized additive models revealed the underlying sex-specific activity patterns of the European roe deer population in the Bavarian Forest National Park and can be used as a basis for meta-analysis of different populations.

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