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**Diurnal and seasonal rhythms of red deer (*Cervus
elaphus*) in the Bohemian Switzerland National Park,
Czech Republic**

Master Thesis

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Declaration

This thesis is a presentation of my original research work. Wherever contributions of others are involved, every effort is made to indicate this clearly, with due reference to the literature, and acknowledgement of collaborative research and discussions.

In Prague 27. 4. 2017

.....

Bc. Pavel Zoubek

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Abstract

The aim of this thesis was to determine activity rhythms of red deer (*Cervus elaphus*) in Bohemian Switzerland National Park on diurnal and seasonal basis with special focus on difference between sexes and, in case of male red deer, in age. Moreover, try to connect activity rhythms with red deer life events and human activities, which are known that significantly influence wildlife biorhythms. Purpose of this research was to deepen our knowledge about the largest animal in the park and meet appropriate management steps. Altogether eighteen individuals were monitored, nine males and nine females, with GPS PLUS Collars from Vectronic Aerospace and processed in Activity Pattern software. Acquired data suggest that red deer in the park are affected by human interests. It was also proved that female red deer display higher activity throughout the year and also males show difference in activity according to age.

Key words: telemetry monitoring; biorythms; protected area management; red deer; seasonal behaviour

Abstrakt

Cílem této diplomové práce bylo určit aktivitové rytmy jelenů lesních (*Cervus elaphus*) v národním parku České Švýcarsko na denní a sezónní bázi. Zvláštní důraz byl kladen na pohlavní rozdíly a u samců také na věk. Dále se se práce pokusila spojit aktivitové rytmy s životními událostmi a faktory lidské činnosti, které biorytmy divokých zvířat výrazně ovlivňují. Důvod tohoto výzkumu bylo prohloubení znalostí o největším zvířeti v parku a pokusit se poskytnout informace pro vhodný management chráněného území. Celkem bylo obojkováno osmnáct jedinců, z toho devět samic a devět samců, zařízením GPS PLUS Collar od firmy Vectronic Aerospace a získaná data z obojků byla zpracována v programu Activity Pattern. Výsledky výzkumu naznačují, že jeleni v parku jsou ovlivněni lidskými zájmy. Dalé se potvrdilo, že samice vykazují vyšší aktivitu v průběhu roku a také aktivita samců se liší podle věkové třídy.

Klíčová slova: sledování zvěře, biorytmy, management chráněných území, jelen lesní, sezónní chování

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List of the Abbreviations

BSNP – Bohemian Switzerland National Park

GPS – Global positioning system

SSNP – Saxon Switzerland National Park

RLA – Relative level of activity

VHF – Very high frequency

a.s.l. – Above the sea level

e.g. – For example

etc. – Et cetera

1. Introduction and Literature review

Red deer are the largest animals in the Bohemian Switzerland National Park (BSNP) and form an integral part of a given ecosystem. With absence of large carnivores (wolf, lynx, bear) red deer have long-term tendency to grow their numbers (Forejtek and Červený, 2011) and with their significant impact on local vegetation (Löttker, 2009) it is necessary to continuously control and influence their population by hunting. This is also reason why the BSNP is a hunting ground where is hunted between 100 – 145 individuals every year. However, data from spring censuses from 2003 till 2016 indicate number of red deer between 150 – 250 individuals, nevertheless, exact numbers are hardly estimable. Therefore it is necessary to properly manage red deer population (Berger et al., 2002) in the BSNP.

The area of the park and its use by red deer was the main reason for telemetric monitoring, which nowadays can record next to spatial data also other features, for example degree of activity in case of this research. The research outputs enable to answer crucial information about activity rhythms of red deer in the BSNP – daily and seasonal changes, effects of tourism, hunting season, weather, biological processes (rut, birth of fawns, shedding antlers). With this information it is possible to deepen general knowledge about red deer and also adjust concrete aspects of hunting and management of the park.

1.1 Animal biorhythms

Physiological and behavioural changes generally take place cyclically or rhythmically in all living organisms. Beating of a heart is an example of intrinsic rhythm that have short period. On the other hand, there are also endogenous rhythms with a periodicity of about a year in a number of long-lived plant and animal species. (Cloudsley-Thompson, 1978). Rhythms of ecological significance in animals can be generally divided into at least three levels: ultradian rhythms – period usually shorter than 24 h often affected by feeding physiology; circadian rhythms – period synchronising organisms to the solar cycle, which means 24 h; and seasonal or annual rhythms related to changes in climate, vegetation and reproduction (Scheibe et al., 2001). According to Dunlap et al. (2004) circadian and seasonal rhythms are genetically determined and connected to physiological parameters whereas ultradian rhythms have strong extrinsic motivation (Aschoff and Gerkema 1985).

All physiological and behavioural rhythms of a healthy animal are synchronised in a meaningful way to both the time structure of the environment as well as to each other. Many functions are included in complex functions, such as activity and feeding, which are thus modulated by distinct biological time patterns, for example reproduction or digestion (Aschoff, 1958). One of the most prominent environmental rhythm is the light – dark cycle, by other words solar cycle, which also includes certain periodic changes in light intensity, temperature and UV radiation. The solar cycle affects all organisms that are exposed to it and therefore leads to changes in many body parameters. Animals are usually divided into diurnal, nocturnal and in some cases are classified as a crepuscular, which means active during dawn and dusk. However, many species show regular activity through the 24 h cycle and some of them seem to have random activity patterns. Classification of those animals might appear to be inaccurate (Krop-Benesch et al., 2011). There is also a hypothesis that burrowing animals have a strong need for an internal representation of the daily cycle in the form of a circadian clock, while non-burrowing animals like the ungulates may have lost the need for a circadian clock to regulate their activity patterns. This alternative hypothesis would predict that ungulates in temperate zones would also have weak circadian influence on their activity patterns, which should lead to relatively fixed phase angles between activity peaks and light intensity changes around twilight (Ensing et al., 2014).

Crucial aspect for the survival and reproduction of animals is the timing of activity. Species specific activity patterns were evolved in response to the environment where they live including food availability, predator avoidance, abiotic factors and others (Enricht, 1970; Ashby, 1972; Daan and Aschoff, 1975). Being active during a period which is not favourable (e.g. temperature, food availability) might result in loss of energy (Krop-Benesch et al., 2011).

Intraspecific coordination of activity plays a crucial role among social animals. This feature is beneficial for many aspects of their life including safety in numbers from predators, protection of territory, acquisition of mates and prey etc. Interspecific coordination of activity is also important and predators, for example, increase their success by orientating their activity to that of prey. However, some species evolved different time activity in order to use the same resources but avoid direct competition with other species (Krop-Benesch et al., 2011). Moreover, in some cases, individual differences in movement patterns have been shown to lead to within-species segregation, such as sexual segregation in the case of ungulates (Ruckstuhl, 1998; Ruckstuhl and Neuhaus, 2002).

Since activity patterns are the basic characteristic of each species, it is crucial to study them and their seasonal changes for a better understanding of habitat use and other aspects of the ecology of a species. With growing anthropogenic pressure on wildlife habitats from recreation, tourism and other purposes (Arlettaz et al., 2007), this can improve the insight into the forces shaping activity in free-ranging wildlife and the limits of their flexibility to successfully cope with altered conditions (Berger et al., 2002; Löttker et al., 2009).

High selection pressure might result in change of the activity pattern of a species, and nutritional chains may depend on activity rhythms (Remmert, 1969). Biological rhythms express adaptation to the annual change of the photoperiod and also provide information on physical parameters, such as the nutritional state, social status or stress. Hence, they are tools to describe the situation of individuals and groups of animals (Tester and Figala, 1990).

Because of increasing interference of humans in natural habitats, wild-living animals are put under growing pressure by man with regard to their space and time requirements (Berger et al., 2002; Gervasi et al., 2006). Investigation of the spatiotemporal behaviour of wild animals is important for the management of potentially disturbing anthropogenic activities and for conservation of endangered species. Information about animal activity deepens our knowledge about their foraging behaviour and may help to wildlife managers and land use planners to create predictive models which can be integrated into plant-herbivore relationships into forest and wildlife management (Coulombe et al. 2006). The conflict between wildlife management and conservation on the one hand and requirements of human recreation and tourism on the other hand is especially pronounced in national parks, which by definition have to fulfil both functions (Löttker, 2009).

1.2 Telemetry monitoring

Continuous, long-term records of free-ranging individuals are required to analyse animal activity (Scheibe et al. 1999). Formerly, direct observation was the only way to study animal activity. These studies were dependent on light, habitat, visibility of the animals and oftenly restricted to the daytime. Thus this method is usually limited to artificial enclosures (Schober et al., 1995; Borkowski, 2000).

One of the first indirect methods is VHF (Very high frequency) or GPS (Global positioning system) telemetry which was originally developed for position determination, but technological progress allows to study animal activity with little disturbance due to observer's presence as well. Based on the assumption that animal movement can influence the transmission of radio signals, early studies interpreted signal changes in tone or strength during a fixed time interval as active behaviour (Gervasi et al. 2006). Carranza et al. (1991) used this system to document red deer activity (*Cervus elaphus*) among first. However, this system was considered to be subjective in a certain degree. Later radio-collars contained motion-sensitive devices which are activated by animal movement, which leads to a change in the signal mode, usually in the pulse rate. This methodology allows to distinguish not only active and inactive behaviour and its categories, but also discriminate between feeding and slow

locomotion, and between rumination and sleeping in red deer (*Cervus elaphus*) (Georgii and Schröder, 1978; Georgii, 1981; Green and Bear, 1990) and white-tailed deer (*Odocoileus virginianus*) (Beier and McCullough, 1990).

All methods mentioned above are time consuming, labour intensive and expensive, which makes them not fully suitable for longer continuous activity data acquisition and for larger number of individuals. These problems were solved with automatic telemetry system ETHOSYS, which was incorporated into collars. Collars with this system has one sensor for acceleration and one for tracking the position of the animal's head in order to distinguish between general activity and feeding. (Scheibe et al. 1998; Berger et al. 2002; Berger et al. 2003; Pépin et al. 2006). Some GPS collars are combined with dual-axis motion sensors to record data on animal activity (GPS collars from Lotek Engineering: e.g. Adrados et al. 2003; Coulombe et al. 2006; Ungar et al. 2005; from VECTRONICS Aerospace: e.g. Gervasi et al. 2006, Gremse, 2004; Löttker et al. 2009, Krop-Benesch et al. 2013). These collars allow insights into animal activity by continuous distribution of x and y values on a unitless scale from 0 to 255. However, studies using these collars reported that the sensor-measured values provided information on the degree of activity only at a broader scale (active vs. passive), whereas distinction of the different active behaviours failed (Adrados et al. 2003, Gremse 2004, Coulombe et al. 2006, Gervasi et al. 2006).

Modern wildlife collars are normally used to obtain GPS locations which give information about home range size, migration paths, etc. Unfortunately, recording GPS fixes requires a considerable amount of energy, therefore many studies rely only on few GPS fixes per day. This results in a low number and frequency of data. As it was mentioned before some GPS collars are equipped with acceleration sensors constantly measuring the activity of the collared animal independent from the GPS location, which have little energy demands. This enables to record the activity of animals over long periods of time (Löttker et al., 2009) and also provide with information on stationary behaviour, e.g. feeding (Löttker et al. 2009; Gottardi et al. 2010; Heurich et al. 2011).

1.3 Activity rhythms of red deer

Red deer, in its original habitat, present an intergral part of the evolutionary and complex network of space and time requirements of all species (Tembrock, 1976). However, wild-living red deer, and other animals, are nowadays facing serious pressure by anthropogenic interferences that might lead to significant changes in wildlife behaviour. This may present reduced rumination and food intake, increased vigilance and higher tendency to avoid or flee from sources of disturbance (Cederna and Lovari, 1985; Skogland and Grovan, 1988; Humphries et al., 1989; Schnidrig et al., 1991). All mentioned changes in behaviour present potential source of stress and might lead to deterioration of general health, physical condition and affect reproduction (Squibb et al., 1986; Hofer and East, 1998). One of the possible reason is increasing forest and field damage that is in many cases attributed to red and roe deer and thus leads to conflict between wildlife and human interests (Guthörl, 1994; Schütz, 1994). Neglecting wildlife demands on the environment has been identified as one cause of animal suffering (Scheibe, 1997). In addition, according to Berger et al. (2002), wild animals do not display their suffering but conceal it as far as possible, in order not to attract predators or to lose protection by their social group. Nevertheless, long-term effects may become manifest in the frequency and time structure of behavior. Since simple behavioral parameters, such as activity, can be conveniently recorded by telemetry, it should be possible to investigate such stressors by following biological rhythms. Therefore, it is necessary to study environmental needs and activity patterns of species to detect possible disturbances and take reasonable steps in forest and wildlife management (Berger et al., 2002).

It was proved that in areas where there is disturbance, red deer activity becomes restricted to brief periods around dawn and dusk or they may increase their nocturnal activity (Georgii and Schröder, 1978; Georgii, 1981; Punga, 1990; Hester et al., 1996). Conversely, in areas free from hunting disturbance, red deer display the highest activity in daytime throughout the year (Bubenik and Bubenikova, 1967; Hofmann and Nievergelt, 1972; Clutton-Brock et al., 1982). However, activity patterns of members of the family Cervidae are widely discussed (i.e., Craighead et al., 1973; Georgii, 1981; Risenhoover, 1986; Beier and McCullough, 1990; Green and Bear, 1990) and general consensus is that the time patterns of red deer are highly variable and depend on a wide

range of different factors (Berger et al., 2002). For ungulates in temperate zone in general, a regular daily pattern of alternating feeding and resting bouts is typical (Scheibe et al. 2001). Red deer (*Cervus elaphus*) show this pattern with distinct activity peaks at twilight (Georgii, 1981; Georgii and Schröder, 1983). Among Cervids, roe deer (*Capreolus capreolus*) (Cederlund 1981; 1989; Jeppesen, 1989), rocky mountain elk (*Cervus canadensis nelsoni*) (Green and Bear, 1990), white-tailed deer (*Odocoileus virginianus*) (Kammermayer and Marchinton, 1977; Beier and McCullough, 1990; Coulombe et al., 2006). The duration of one digestive cycle, i.e. feeding and digestion, depends on the species-specific feeding ecology (red deer are intermediate mixed feeders) and the food quality and availability within their habitat (Cederlund, 1981). According to Pagon (2010), other factors that significantly influence deer activity are sex, season, time of the day and hunting season.

Because access to high-quality resources is often linked to higher predation risk (Benhaiem et al., 2008), changes in the level and the type of predation risk or in resource availability often result in behavioral adjustments among prey (Sih, 1980; Fraser and Huntingford, 1986; Lima, 1998). One common way for prey to trade off acquisition of high-quality resources with the avoidance of predation risk or disturbance is through alteration of habitat selection and activity rhythms (Lima and Dill, 1990; Kronfeld-Schor and Dayan, 2003; Caro, 2005). Although activity rhythms can be constrained by endogenous traits, many studies suggest that patterns of habitat selection and activity are highly flexible behaviors that can be adjusted to variations in resource availability and predation risk. Nevertheless, on the other hand, Ozoga & Verme (1970) found that although environmental conditions can either partially suppress or emphasise activity patterns, they are not capable of generating new structures. Anyway, prey often minimize their exposure to predation risk by resting in safer habitats during riskier periods and by concentrating their foraging activities in risky forage-rich habitats when risk is lower (Lima and Bednekoff, 1999; Fortin et al., 2015). For example, many hunted ungulate populations are more active and prefer forage-rich habitats during nighttime when risk and disturbance linked to human activity are lower (e.g., Godvik et al., 2009; Lone et al., 2014; Bonnot et al., 2015). Moreover, the circadian activity peaks at sunrise and sunset of many wild ungulates are often considered to be an antipredator response to temporal variation in predation risk (Caro, 2005; Kamler et al., 2007; Loe et

al., 2007; Long et al., 2013). Also aspects such as the interrelation between weather and activity, and the supposed high individuality of European roe deer can be considered (Stache et al., 2012).

1.4 Life events of red deer

In the BSNP (Czech Republic), the rutting season begins in the second half of September till the beginning of October. Both sexes group and males tempt either ritual or real fights for females. Rutting groups fall apart during autumn or at the beginning of winter. During the rutting season, males also extend their territory. Gestation period of females is approximately 240–262 days and have usually one fawn, rarely two. Fawns are concealed on the forest edge and after 7–10 days they join with its mother to their herd. Lactation period lasts about five to seven months, however, fawns start to feed themselves after the second month of life. Red deer reach maturity around second or third year of life, nevertheless, males start to participate on reproduction process approximately at age of four. Males shed antlers from February till April. Life expectancy is around twenty years (Dungel and Gaisler, 2002). Hunting season in the BSNP starts from the 1 of August till the 15 of January of the next year. The main touristic season begins in May and lasts till October, but it is very variable according to weather conditions.



Figure 1: A collared male red deer shortly after remobilisation (*source: M. Klitsch*).

2 Aims of the Thesis

The general aim of the thesis was evaluation of diurnal and seasonal activities of red deer, both males and females, in the Bohemian Switzerland National Park.

Specific aims were:

- To evaluate principal activity rhythms of male and female red deer on diurnal basis.
- To evaluate seasonal activities of male and female red deer and to determine time periods which have significant effect on them.

H1: We hypothesize that activity rhythms of male and female red deer will differ according to their behaviour and sociality. And, that activity rhythms of male red deer among the age classes will differ with respect to their life experience and vitality.

H2: We hypothesise that life events of both sexes together with anthropogenic aspects will affect seasonal rhythms of red deer in the Bohemian Switzerland National Park.

3 Study area

The Bohemian Switzerland National Park (BSNP), with geographic coordinates 50° 51' N, 14° 23' E, is situated in the northern part of the Czech Republic along borders with Germany where it is directly connected to the Saxon Switzerland National Park (SSNP). The BSNP was established in 1. 1. 2000 on an area that covers approximately 80 km². The park's mission is to preserve and conserve local environment with all its wildlife and geomorphological formations (Bohemian Switzerland National Park, 2017).

3.1 Environmental conditions

The area of the BSNP is a part of Bohemian Cretaceous basin with sedimentary rocks – quartz sandstone. The altitude of the area fluctuate between 115 m a.s.l. (the level of river Labe in Hřensko) and 619 m a.s.l. (the peak of Růžový vrch). The area is characteristic by its immense forest cover (97 %) – Norway spruce monoculture (*Pinus strobus*) with fragments of indigenous beeches (*Fagus sylvatica*) dominate. The park has a highly rugged georelief (“sandstone cities”) where most hills have their peaks between 450 – 480 m a.s.l. (Bohemian Switzerland National Park, 2017).

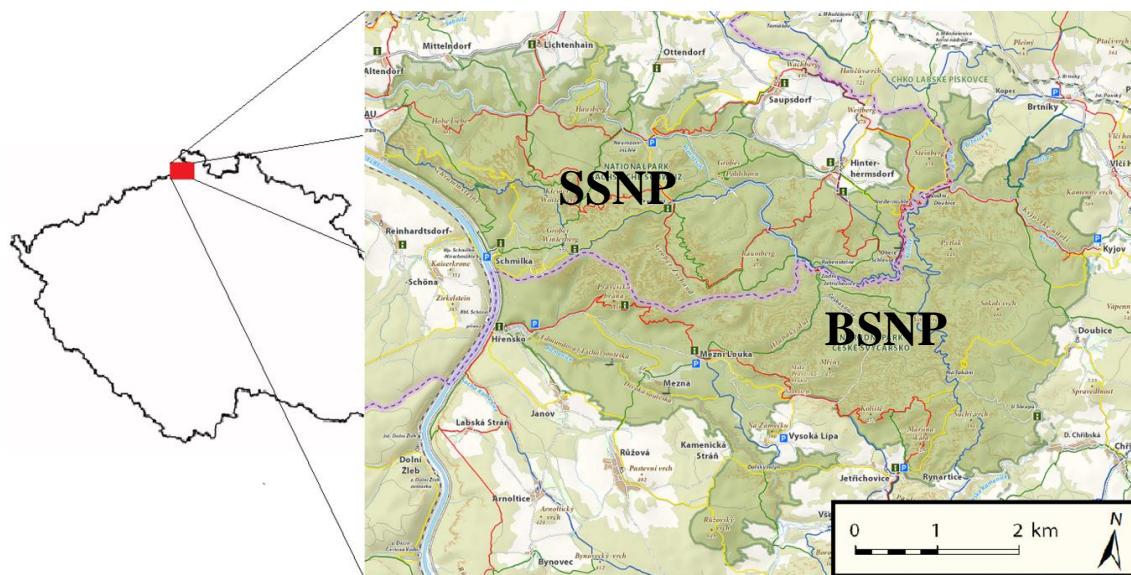


Figure 2: Position of the Bohemian Switzerland National Park in the Czech Republic and its area together with the Saxon Switzerland National Park. (source: © Administration office of the BSNP, basemap ME CR).

3.3 Climatic conditions

According to map of climatic regions of the Czech Republic (Tolasz, 2007; Quitt, 1971) the BSNP belongs to six climatic units: T2 (warm), MT2, MT4 MT7, MT9 (mild) and CH2 (cold). Balanced ratio of precipitation in vegetation (April to September) and non-vegetation period (October to March) indicates tendency to oceanicity. Within the area there are significant temperature and total precipitation differences. Diversity of the climate in the park is a subject of rugged terrain which certainly predetermine microclimatic conditions. In the BSNP also occurs phenomenon of climatic inversion. The average annual temperature fluctuates around 7 °C and total precipitation per year is 800 mm. Temperature curves for chosen years (2009, 2010, 2011) were based on the data from weather station “Tokáň” in the BSNP during monitoring of red deer are shown on Figures 3–5.



Figure 3: Temperature curve in the BSNP from 23. 10. 2009 to 31. 12. 2009. (*source: Weather station “Tokáň”*)

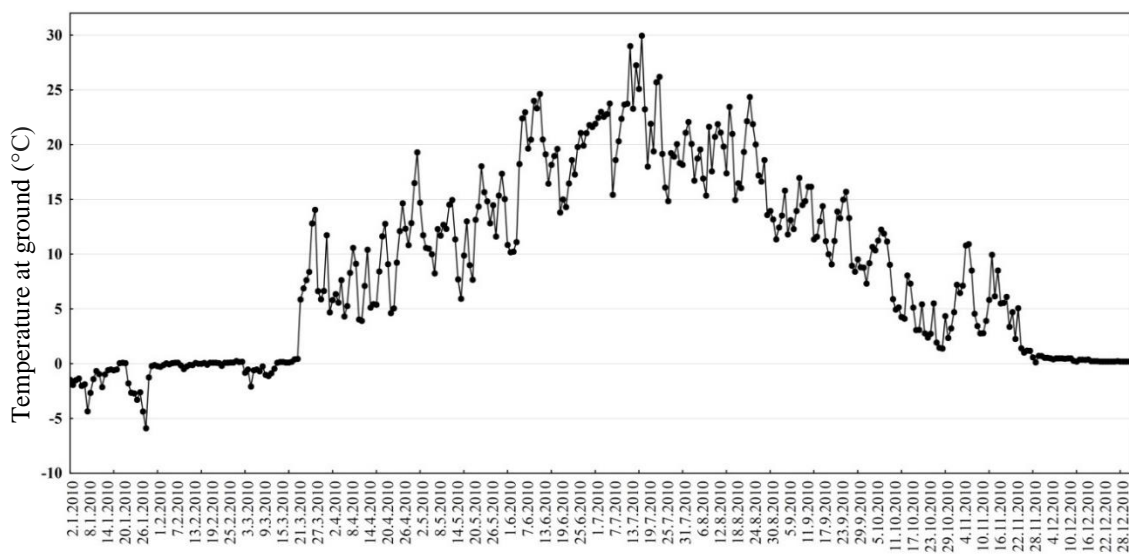


Figure 4: Temperature curve in the BSNP from 1. 1. 2010 to 31. 12. 2010. (source: Weather station “Tokáň”)

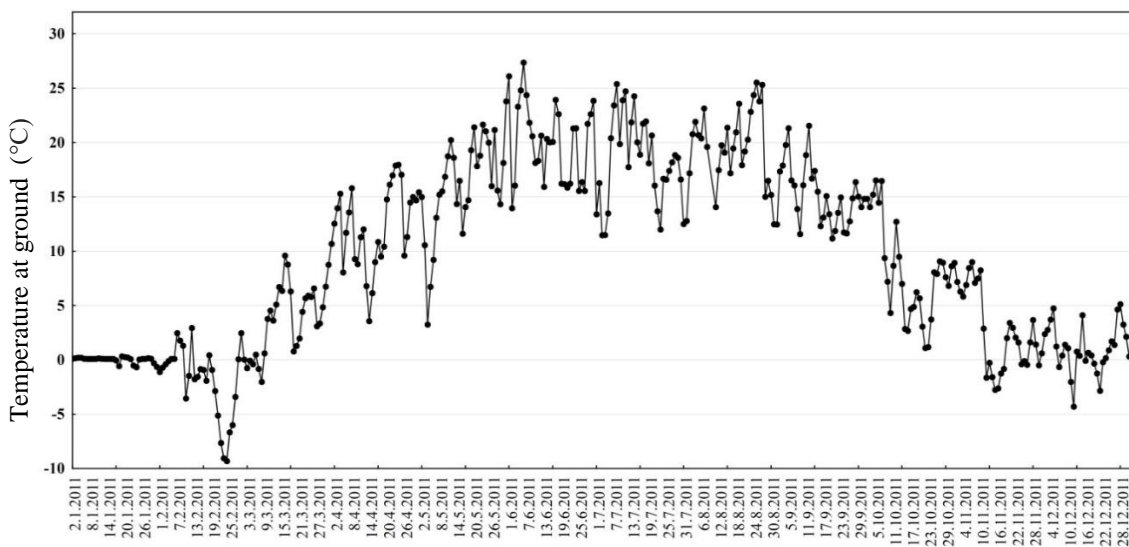


Figure 5: Temperature curve in the BSNP from 2. 1. 2011 to 28. 12. 2011. (source: Weather station “Tokáň”)

4 Materials and Methods

4.1 Monitored animals

Altogether 18 individuals were collared from which there were 9 males and 9 females (Table 1). From mentioned 18 individuals 3 were collared twice. Concretely it was a male red deer with collar No. 02152_100331125633 and 06757_101012152041; a female red deer with collar No. 06761_140922113916 and 06763_120413142921; and a female red deer with collar No. 06762_170327112104 and 06767_120412140212.

Table 1: List of collared red deer. Symbol * and its number expresses individuals that were collared twice in different time period with different collar. Age class of male red deer corresponds with age estimation: I = 2 – 3 years, II = 5 – 8 years, III = 9 and more years.

Number of collar	Sex	Age estimation when captured (years)	Age class	Place of capture	Start	End	Number of monitoring days
02152_100331125633*	Male	8	II	Rynartice	7. 8. 2007	8. 5. 2009	641
06757_101012152041 *	Male	9	III	Rynartice	11. 8. 2009	5. 9. 2009	26
06752_110216135734	Male	2	I	Černý grunt	18. 2. 2010	25. 8. 2010	190
06752_140306122515	Male	-	III	Studeňák	18. 2. 2012	19. 9. 2013	580
06753_110207083642	Male	3	I	Z. Jetřichovice	9. 2. 2010	21. 7. 2010	163
06754_110216124921	Male	3	I	Doubice	4. 3. 2009	12. 9. 2010	559
06754_140211184502	Male	-	II	Černý grunt	14. 12. 2012	22. 1. 2014	405
06756_110207082911	Male	9	III	Jetřichovice	27. 2. 2009	3. 10. 2009	219
06756_140409095741	Male	-	I	Mezná	24. 3. 2013	10. 12. 2013	262
06759_110721102647	Male	8	II	Doubice	1. 2. 2010	30. 11. 2010	309
06760_101015103428	Female	3	-	Z. Jetřichovice	19. 2. 2009	22. 9. 2010	581
06761_110207090101	Female	6	-	Vysoká Lípa	30. 10. 2009	23. 12. 2010	420
06761_140922113916**	Female	9	-	Mezní Louka	5. 3. 2012	11. 3. 2014	737
06763_120413142921**	Female	7	-	Mezní Louka	25. 2. 2010	22. 2. 2011	363
06762_110207084445	Female	5	-	Mezná	12. 2. 2009	18. 12. 2009	310
06764_110216125953	Female	4	-	Mezní louka	5. 3. 2009	27. 8. 2010	488
06765_110216140857	Female	8	-	Černý grunt	14. 2. 2009	20. 4. 2010	431
06766_110721102514	Female	3	-	Doubice	25. 2. 2009	27. 6. 2010	488
06762_170327112104***	Female	8	-	Chřibská	17. 2. 2012	19. 11. 2012	277
06767_120412140212***	Female	6	-	Chřibská	17. 2. 2010	17. 2. 2012	731
06769_120413135629	Female	7	-	Mlýnská rokle	8. 3. 2010	24. 1. 2012	688

4.2 Capturing red deer

All captured individuals were immobilised in the BSNP with dart rifle on distance 20 – 40 m. As an immobilisation substance was used a mixture of xylazine and ketamine. Most of the animals were immobilised during winter periods near the feeding stations. Age of all individuals were estimated by teeth wear and general physique.



Figure 6: A male red deer darted into the left rump. (*source: M. Klitsch*).



Figure 7: Collaring of an immobilised male red deer. (*source: M. Klitsch*)

4.3 Acquiring data from collars

For acquiring activity data GPS PLUS Collars from Vectronic Aerospace were used. These collars had an acceleration sensor for measuring the activity. The measure of movement was based on acceleration in given directions (parameter x : forward – backward, parameter y : left – right, Figure 8). The acceleration sensor stored activity data in defined intervals. One interval had 288 seconds and the data were stored into the collar's memory. All data were downloaded via Link Manager package just after the removing of the collar from the animal.



Figure 8: A collared male red deer. The green arrow indicates forward – backward direction (parameter x) and red arrow indicates left - right direction (parameter y).
(source: M. Klitsch).

4.4 Analyses of activity data

Activity data from GPS PLUS collars were processed with Activity Pattern software, which was developed by Vectronic Aerospace company especially for data treatment from acceleration sensors built in the collars.

The principal parameter, which was measured by the acceleration sensor (line x), was the relative quantity of motion – acceleration in chosen direction (forward – backward) during measuring interval (288 seconds). It was not primarily an information about concrete behaviour of an animal, however, based on the pilot observations, it is possible to deduce movements of an animal, more precisely an activity and its length and to connect these information with time and space (Löttker et al. 2009). This parameter has been labelled by term "relative level of activity". Its values are arranged on a linear unitless scale from 0 to 255 (Krop-Benesch et al., 2011).

Circadian and diurnal rhythms of red deer were set by relative level of activity and relative level of inactivity during 24 h and during day and night. Day and night were set by sunrise and sunset in the BSNP (N 50°, E 14°). Seasonal changes of sunrise and sunset were managed in Activity Pattern software by inserting geographic coordinates. Time zone in the BSNP corresponds with UTC+1. Time of activity and inactivity (or relaxation) was calculated as a mean for all monitored males and for all monitored females separately in order to test the difference between sexes. Further, all parameters of each animal were calculated to prove differences among individuals. By analysis of circadian and diurnal rhythms was set number and length of active and inactive periods during 24 h (day and night).

The diurnality index was also calculated to specify the ratio of activity during day (between sunrise and sunset) and night (between sunset and sunrise). The calculation in Activity Pattern software is based on equation according to Hoogenboom *et al.* (1984):

$$DiurnalityIndex = \frac{\frac{c_d}{t_d} \cdot \frac{c_n}{t_n}}{\frac{c_d}{t_d} + \frac{c_n}{t_n}}$$

Where c_d , respectively c_n is sum of activity values during day, respectively during night, t_d is number of records during day, respectively during night t_n . Values of diurnality

index range from -1 to $+1$, where $+1$ means that the animal is active only during the day, 0 means that the animal is equally active during the day and the night and -1 means that the animal is active only during the night (Krop-Benesch et al., 2011).

The number of activity peaks and the peak threshold is the mean activity value stored by the collar for one interval. The longer the sampling interval, the higher the probability that short peaks are not accounted. The program checks the time series for intervals in which the activity level is 10 or higher. Afterwards it counts the number of successive intervals in which this condition is fulfilled. If the intervals cover 10 minutes or longer, one peak is counted and its duration exceeding the threshold is noted (Krop-Benesch et al., 2011).

Seasonal and daily levels of activity rhythms during the year for both males and females were determined and displayed in graphs. Differences in activity rhythms during the year between sexes and among age classes were tested in programme Statistica 12 (StatSoft, Tulsa) by t-tests and one way or two way analysis of variance and followed by post hoc Tukey tests.

Seasonal activity of each individual were also presented by actograms, which represent graphical demonstration of results in time lines. Axis x represents interval of 48 h (2 days from 00:00 h of the first day to 23:59 h of the second day, so called double plot), in order to highlight continuity of activity of an animal during the night. On axis y are dates of records where each line represents 2 days. In an actogram it is also displayed 00:00 (midnight) and 12:00 (noon) and also sunrise, sunset and nautical dawn and dusk. Nautical dawn and dusk is defined by a point where the centre of a solar disk is between 6° to 12° below the horizon. Nautical dawn and dusk enables to people perceive shapes of objects whereas animals probably can see objects clearly. Level of activity is expressed by colour intensity according to scale 0 – 255. Lighter colours indicate lower level of activity and darker colours higher level of intensity (Krop-Benesch et al., 2011).

5 Results

5.1 Circadian and diurnal rhythms of red deer

The total duration of active time of all red deer during the day (24 h) was 9.85 h (\pm 3.22 h SD). However, female red deer were more active with 10.02 h (\pm 3.18 h SD), whilst males were active 9.55 h (\pm 3.27 h SD), ($t = -5.99$, $p < 0.001$). Detailed information about active and resting time period of each monitored individual during the day cycle (24 h) are shown in Table 2. Red deer generally showed higher activity during the night 6.41 h (\pm 2.59 h SD). Activity during the day were significantly lower 3.44 h (\pm 1.51 h SD), ($t = -90.25$, $p < 0.05$). Both sexes display the same activity period during the night – 6.42 h (\pm 2.54 h SD) for females and 6.41 h (\pm 2.69 h SD) for males ($t = -0.24$, $p > 0.05$), nevertheless, females are more active during the day 3.61 h (\pm 1.51 h SD) while males only 3.16 h (\pm 1.49 h SD), ($t = -12.25$, $p < 0.05$). Complete information about active and resting time during the day and the night are in Table 3.

The index of diurnality indicated that all red deer were predominantly more active during the night. The average index of diurnality for male red deer was -0.27 (\pm 0.29 SD) and for female red deer -0.23 (\pm 0.28 SD), ($t = -5.60$, $p < 0.001$). Comparison of the diurnality index between males and females is shown in Figure 9.

The relative level of activity of all red deer during the day (24 h) was 37.38 (\pm 18.76). The average level of activity of male red deer was 34.1 (\pm 19.21 SD), which was lower than female red deer – 41.0 (\pm 17.75 SD), ($t = -4.18$, $p < 0.001$). Comparison of the relative level of activity between males and females is shown in Figure 10.

The number of activity peaks during the day (24 h) was 14.37 (\pm 5.7 SD) for male red deer and 12.9 (\pm 5.0 SD) for female red deer ($t = 11.43$, $p < 0.001$). Comparison of the number of activity peaks during the day (24 h) between males and females is shown in Figure 11.

Table 2: The overview of active and resting time of all monitored individuals during 24 h cycle. SD indicates standard deviation. Age class of males correspond with age estimation: I = 2 – 3 years, II = 5 – 8 years, III = 9 and more years. Symbol * and its number expresses individuals that were collared twice in different time period with different collar.

Sex/Number of collar	Age class/Age	Mean act. time 24h [h]	Mean act. time 24h [%]	Mean rest time 24h [h]	Mean rest time 24h [%]
	(years)	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Males					
06752_110216135734	I	10.0 ± 2.7	41.8 ± 11.1	13.8 ± 2.6	57.6 ± 10.8
06753_110207083642	I	9.9 ± 3.8	41.5 ± 16.0	13.8 ± 3.8	57.5 ± 15.7
06754_110216124921	I	10.5 ± 2.5	43.6 ± 10.5	13.5 ± 2.5	56.3 ± 10.3
06756_140409095741	I	10.8 ± 2.3	44.6 ± 9.4	13.2 ± 2.1	55.1 ± 8.8
06754_140211184502	II	9.4 ± 3.9	40.0 ± 16.0	14.7 ± 3.8	61.3 ± 16.0
06759_110721102647	II	9.9 ± 2.8	41.2 ± 11.9	14.0 ± 2.9	58.5 ± 11.9
02152_100331125633*	II	8.4 ± 3.4	35.1 ± 14.4	15.6 ± 3.4	64.9 ± 14.4
06757_101012152041*	III	7.9 ± 3.1	32.8 ± 12.8	15.4 ± 3.6	64.2 ± 14.9
06752_140306122515	III	9.8 ± 3.2	40.8 ± 13.2	14.2 ± 3.2	59.3 ± 13.3
06756_110207082911	III	10.2 ± 2.0	42.4 ± 8.5	13.8 ± 1.9	57.5 ± 7.9
Females					
06760_101015103428	3	10.4 ± 2.7	43.5 ± 11.4	13.6 ± 2.7	56.7 ± 11.5
06761_110207090101	6	9.4 ± 2.7	39.3 ± 11.2	14.5 ± 2.6	60.6 ± 11.1
06761_140922113916**	9	10.7 ± 3.6	44.8 ± 15.1	13.2 ± 3.6	55.1 ± 14.9
06762_110207084445	5	10.4 ± 2.7	43.3 ± 11.3	13.6 ± 2.7	56.6 ± 11.2
06763_120413142921**	7	10.3 ± 4.1	42.9 ± 17.0	13.7 ± 4.0	57.2 ± 16.9
06764_110216125953	4	10.3 ± 3.7	42.9 ± 15.4	13.7 ± 3.7	56.9 ± 15.3
06765_110216140857	8	9.8 ± 4.1	40.9 ± 17.0	14.2 ± 4.0	59.2 ± 16.9
06766_110721102514	3	10.5 ± 3.5	43.7 ± 14.5	13.5 ± 3.4	56.2 ± 14.3
06762_170327112104***	6	8.8 ± 1.7	36.7 ± 7.0	15.1 ± 1.6	63.1 ± 6.8
06767_120412140212***	8	9.8 ± 2.3	40.9 ± 9.7	14.6 ± 2.4	59.4 ± 9.9
06769_120413135629	7	9.5 ± 2.9	39.6 ± 12.0	14.5 ± 2.9	60.5 ± 12.0

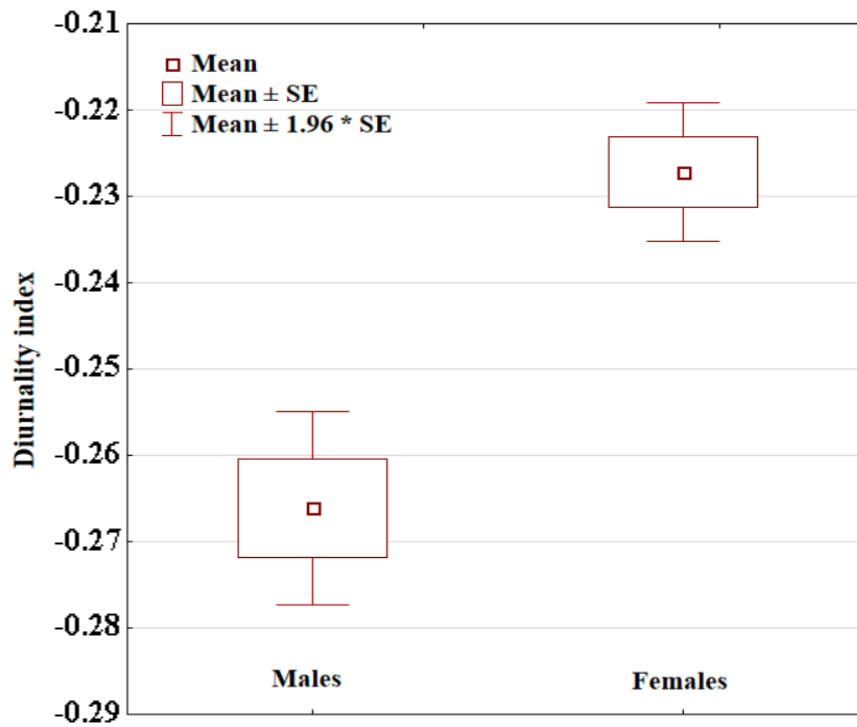


Figure 9: Comparison of the diurnality index between male and female red deer.

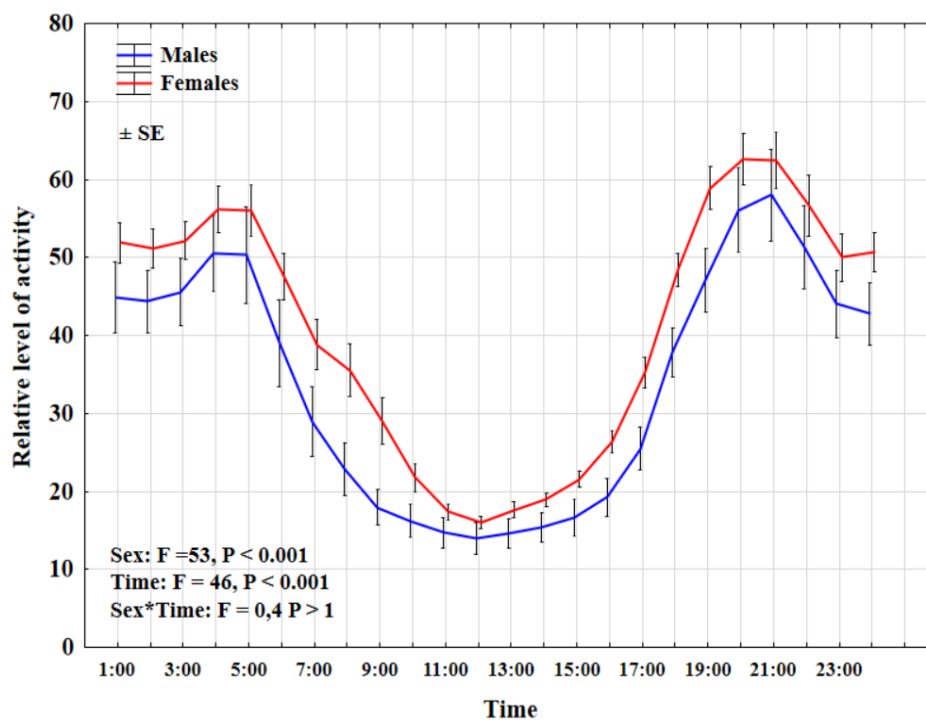


Figure 10: The relative level of activity during the day (24 h) separately for all male and female red deer. Vertical bars indicate \pm SE.

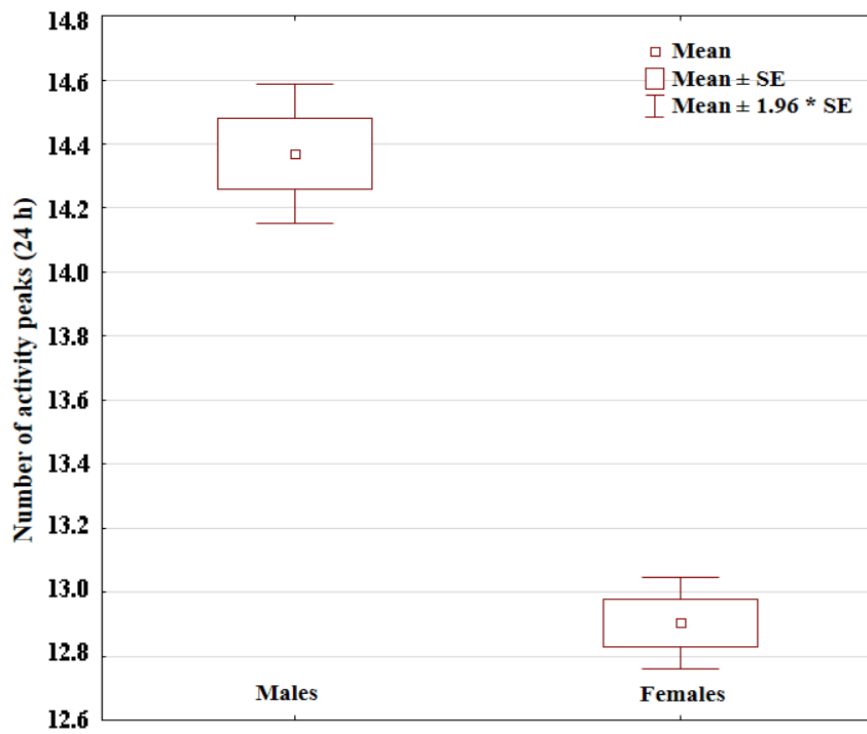


Figure 11: Comparison of the number of activity peaks during the day (24 h) between male and female red deer.

Table 3: The overview of active and resting time of all monitored individuals during the day and the night. SD indicates standard deviation. Age class of male red deer correspond with age estimation: I = 2 – 3 years, II = 5 – 8 years, III = 9 and more years. Symbol * and its number expresses individuals that were collared twice in different time period with different collar.

Sex/Number of collar	Age class/Age (years)	Mean act. time Day [h] <i>Mean ± SD</i>	Mean act. time Day [%] <i>Mean ± SD</i>	Mean rest time Day [h] <i>Mean ± SD</i>	Mean rest time Day [%] <i>Mean ± SD</i>	Mean act. time Night [h] <i>Mean ± SD</i>	Mean act. time Night [%] <i>Mean ± SD</i>	Mean rest time Night [h] <i>Mean ± SD</i>	Mean rest time Night [%] <i>Mean ± SD</i>
Males									
06752_110216135734	I	4.4 ± 1.8	18.2 ± 7.5	10.1 ± 1.8	42.1 ± 7.3	5.7 ± 1.8	23.7 ± 7.3	3.8 ± 2.9	15.7 ± 12.0
06753_110207083642	I	4.2 ± 1.9	17.4 ± 8.0	9.9 ± 1.6	41.4 ± 6.8	5.8 ± 2.5	24.2 ± 10.3	3.9 ± 4.2	16.5 ± 17.5
06754_110216124921	I	3.9 ± 2.3	16.1 ± 9.6	9.2 ± 1.7	38.5 ± 7.0	6.6 ± 2.0	27.5 ± 8.4	4.3 ± 2.5	17.9 ± 10.6
06756_140409095741	I	3.6 ± 1.8	15.1 ± 7.4	9.8 ± 2.1	40.9 ± 8.6	7.2 ± 2.3	30.0 ± 9.4	3.4 ± 2.6	14.3 ± 11.0
06754_140211184502	II	3.0 ± 1.9	12.6 ± 7.8	8.9 ± 2.4	37.1 ± 10.0	6.3 ± 3.0	26.3 ± 12.5	5.8 ± 4.1	24.2 ± 17.0
06759_110721102647	II	3.3 ± 2.2	13.6 ± 9.1	9.8 ± 1.6	41.0 ± 6.8	6.6 ± 2.3	27.6 ± 9.6	4.2 ± 3.1	17.6 ± 12.9
02152_100331125633*	II	2.9 ± 1.5	12.0 ± 6.4	9.2 ± 1.5	38.4 ± 6.4	5.5 ± 2.6	23.1 ± 10.8	6.3 ± 2.6	26.4 ± 10.9
06757_101012152041*	III	1.7 ± 0.9	7.2 ± 3.9	12.0 ± 1.9	50.0 ± 7.9	6.1 ± 2.6	25.6 ± 10.8	3.4 ± 2.3	14.2 ± 9.5
06752_140306122515	III	4.1 ± 2.4	16.9 ± 10.0	9.0 ± 1.9	37.4 ± 8.1	5.7 ± 2.2	23.8 ± 9.0	5.3 ± 3.8	21.9 ± 15.7
06756_110207082911	III	3.9 ± 1.6	16.4 ± 6.6	10.5 ± 1.1	43.6 ± 4.4	6.3 ± 1.6	26.0 ± 6.7	3.4 ± 2.0	14.1 ± 8.4
Females									
06760_101015103428	3	4.0 ± 2.2	16.6 ± 9.0	9.0 ± 1.8	38.0 ± 7.4	6.5 ± 2.1	27.0 ± 8.8	4.5 ± 3.3	18.8 ± 13.7
06761_110207090101	6	2.8 ± 2.2	11.5 ± 9.1	9.0 ± 1.6	37.7 ± 6.7	6.7 ± 1.8	27.8 ± 7.5	5.5 ± 3.3	22.9 ± 13.7
06761_140922113916**	9	3.8 ± 2.1	15.9 ± 8.9	8.4 ± 2.1	35.2 ± 8.7	6.9 ± 2.7	28.9 ± 11.4	4.8 ± 4.1	19.9 ± 16.9
06762_110207084445	5	3.8 ± 2.2	15.7 ± 9.2	9.2 ± 1.7	38.2 ± 6.9	6.6 ± 2.2	27.6 ± 9.0	4.4 ± 2.9	18.4 ± 12.3
06763_120413142921**	7	4.1 ± 2.1	16.9 ± 8.8	8.3 ± 2.0	34.5 ± 8.2	6.3 ± 2.7	26.0 ± 11.5	5.5 ± 4.6	22.8 ± 19.3
06764_110216125953	4	3.8 ± 2.2	15.9 ± 9.1	9.2 ± 1.9	38.5 ± 8.1	6.5 ± 2.5	27.1 ± 10.6	4.4 ± 4.0	18.4 ± 16.8
06765_110216140857	8	3.8 ± 2.4	15.7 ± 10.0	8.5 ± 1.5	35.3 ± 6.3	6.0 ± 2.8	25.2 ± 11.8	5.7 ± 4.2	23.9 ± 17.6
06766_110721102514	3	4.2 ± 2.2	17.6 ± 9.0	8.6 ± 1.7	35.6 ± 7.3	6.3 ± 2.5	26.1 ± 10.2	5.0 ± 3.8	20.7 ± 15.8
06762_170327112104***	6	2.8 ± 1.7	11.6 ± 7.1	10.7 ± 1.8	44.5 ± 7.4	6.0 ± 1.7	25.1 ± 7.1	4.5 ± 2.0	18.7 ± 8.4
06767_120412140212***	8	3.4 ± 2.0	14.2 ± 8.43	8.9 ± 2.4	37.2 ± 10.0	6.4 ± 2.0	26.8 ± 8.2	5.3 ± 2.6	22.2 ± 10.7
06769_120413135629	7	4.0 ± 2.1	16.5 ± 8.6	8.5 ± 2.2	35.3 ± 9.3	5.5 ± 2.2	23.1 ± 9.0	6.1 ± 3.1	25.3 ± 13.0

5.2 Seasonal activity dynamics of red deer

5.2.1 Activity of red deer during the year

The relative level of activity (RLA) of red deer throughout the year significantly varied (Figure 12). The RLA was generally lower in winter with the lowest point in February. From March the RLA continuously rised with the highest peak in June. Male red deer showed a little step up from descending tendency in September, but afterwards the tendency continues to fall.

Even though all male red deer copied the same tendency of activity rhythms throughout the year, there were differences among age classes in the RLA values (Figure 13) – class I: 43.9 (± 0.38 SE); class II: 19.5 (± 0.35 SE); class III: 33.5 (± 0.41 SE), ($F = 1761$, $p < 0.001$).

The average time of activity throughout the year also varied (Figure 14) with generally lower level in winter and lowest point in February. From March the tendency was increasing with highest peak in May. Then the tendency was decreasing, however, in August, the tendency started to grow again, but in October continued to decrease again.

The number of activity peaks during the year varied throughout the year (Figure 15). In January and February the number was higher, but then it starts to decrease till April. Number of activity peaks started to slowly grow for males, however, females have noticeably jumped up in May and after the tendency was decreasing till the lowest point in August. Then the number of activity peaks started to grow. Males after slight increase had significant jump up with the highest peak in September. Afterwards the tendency had decreasing character.

The diurnality index developed during the year as well (Figure 16). The highest peak above “zero level” was in February. The the tendency went sharply down with the lowest point for both sexes in April, nevertheless, males, after short increase till May, jumped down with the lowest point in August, then the tendency was growing. Females after April had increasing tendency till June, afterwards there was a slight tendency to fall till September from which the diurnality index started to grow again.

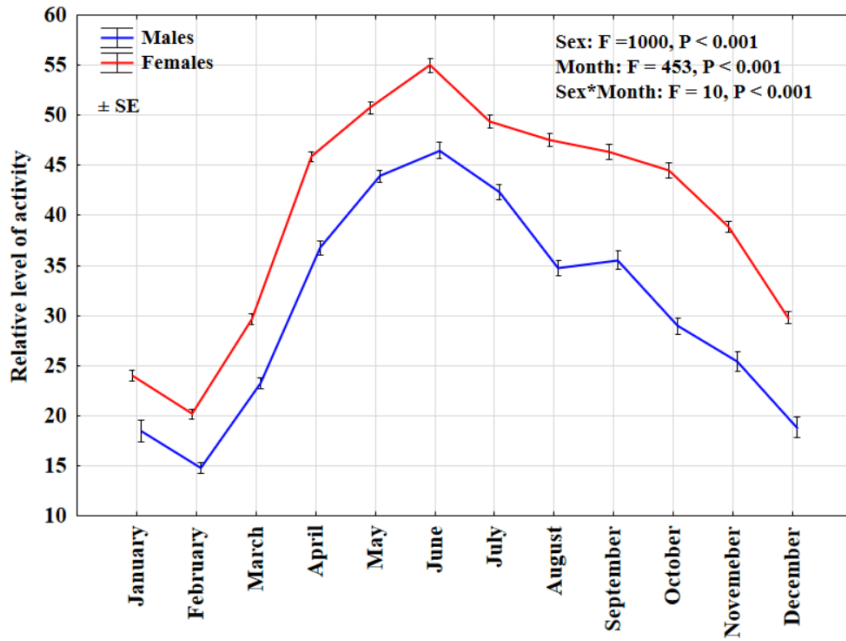


Figure 12: The average relative level of activity for separately all male and female red deer during different seasons. Vertical bars indicate \pm SE.

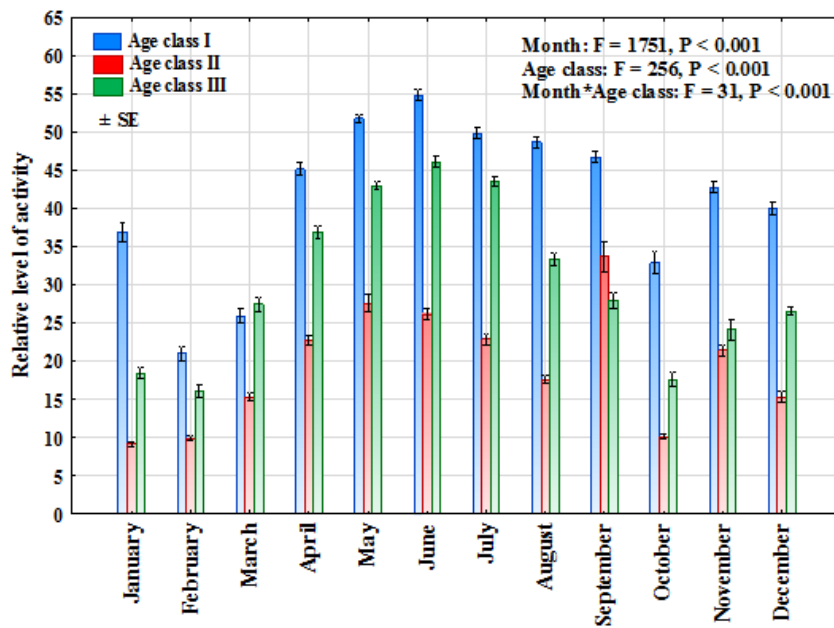


Figure 13: The average relative level of activity for all male of red deer in different age class. Age class of males correspond with age estimation: I = 2 – 3 years, II = 5 – 8 years, III = 9 and more years. Vertical bars indicate \pm SE.

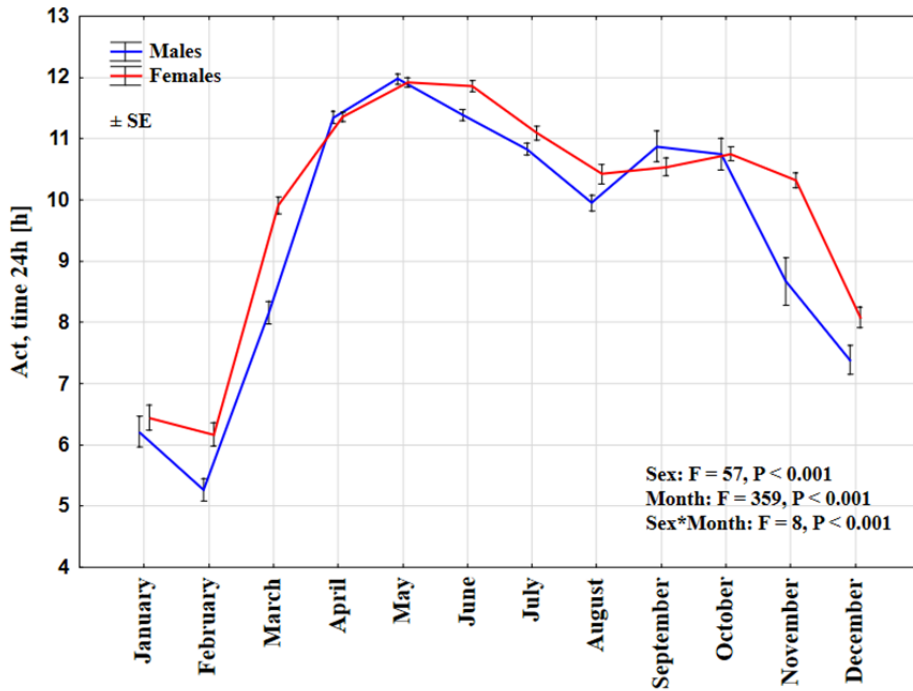


Figure 14: The average time of activity during 24 h cycle separately for all male and female red deer during different seasons. Vertical bars indicate \pm SE.

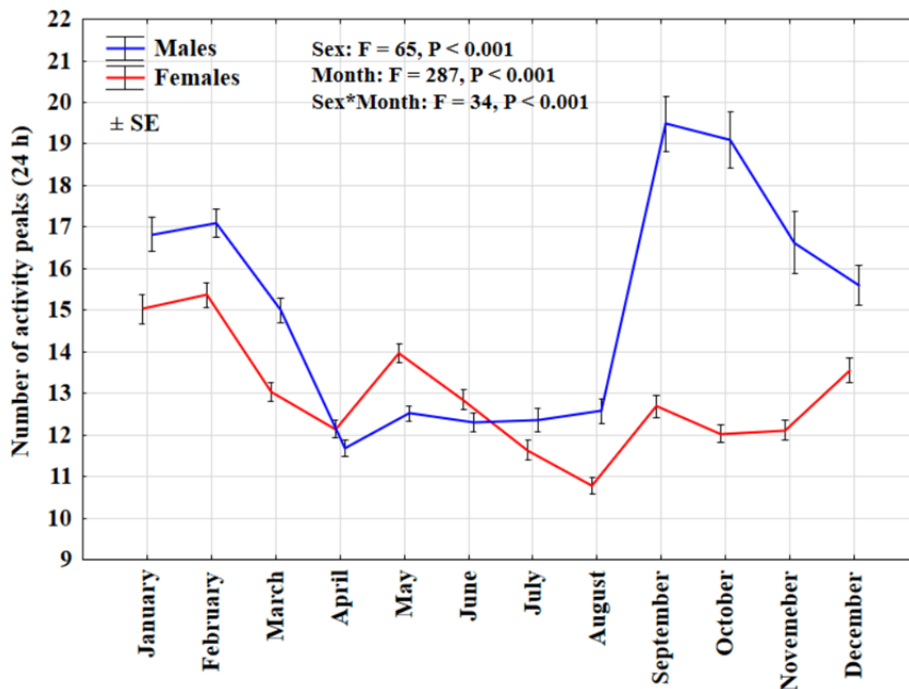


Figure 15: The average number of activity peaks during 24 h cycle separately for all male and female red deer during different seasons.

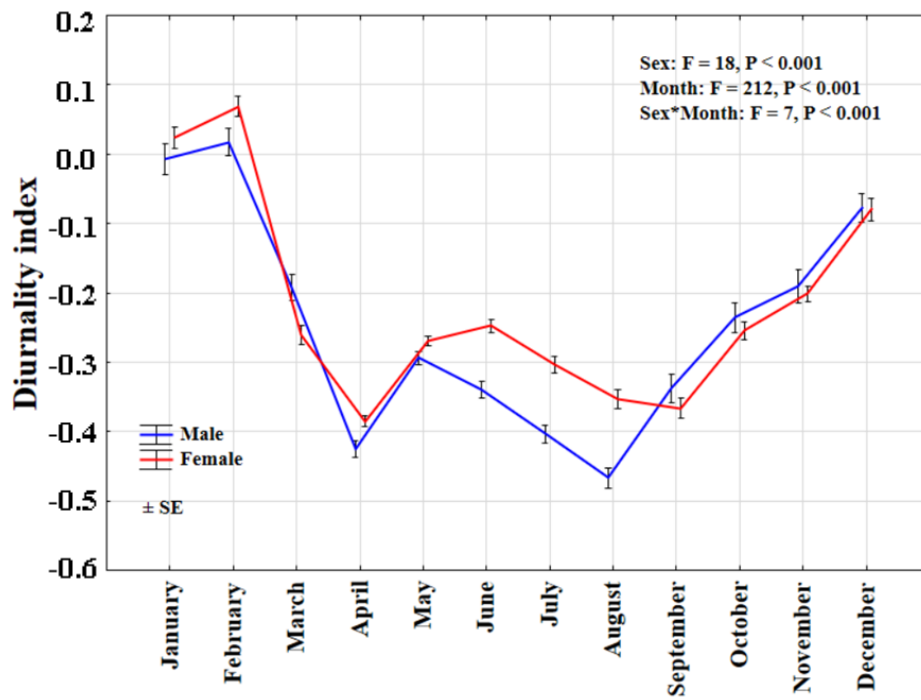


Figure 16: The average index of diurnality separately for all male and female red deer during different seasons. Vertical bars indicate \pm SE.

5.3 Activity of individual red deer

Displayed actograms clearly shows that red deer in the BSNP are active mostly in the night with main activity peaks around sunrise and sunset. The first vertical line from the left in the figures represents nautical dawn and around this line (moment) it is visible that activity of red deer was higher and continued to grow with the highest peak around or just after the sunrise (the second vertical line in the figures). Afterwards red deer started to sharply reduce their activity. This was also valid conversely – when sunset was about to start (the fourth line in the figures) the activity started to sharply grow and reach the highest values (Figures 18, 23, 26, 27, 28, 29, 31, 32 and 33). However, in case of sunset the relative level of activity tended to stay at higher values throughout the night.

From Figures 18, 21, 24, 26, 28/2, 30, 32, 33/1 and 34 is apparent, thanks to longer monitoring period, how red deer changed their activity patterns according to the length of light availability.

Figures 23, 24, 26, 28, 30, 31 and 32 show similar pattern of decreased activity from the 1 of January. In some Figures (24, 28) the pattern was detectable from the 1 of December. This period of decreased activity usually lasted till the beginning of March.

Figure 21/1 (male, age class II), as the only individual, showed noticeably increased activity during September 2007 and 2008. On the other hand, a male red deer (age class III) showed very low activity during September 2012 (Figure 24).

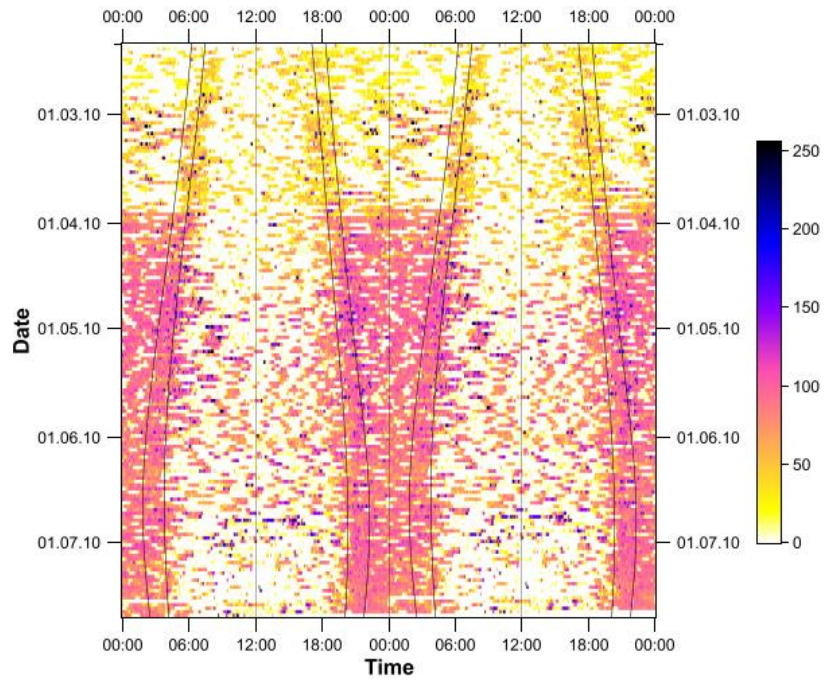


Figure 17: The actogram of a male red deer (age class i) with collar number 06753_110207083642 during period 9. 2. 2010 – 21. 7. 2010.

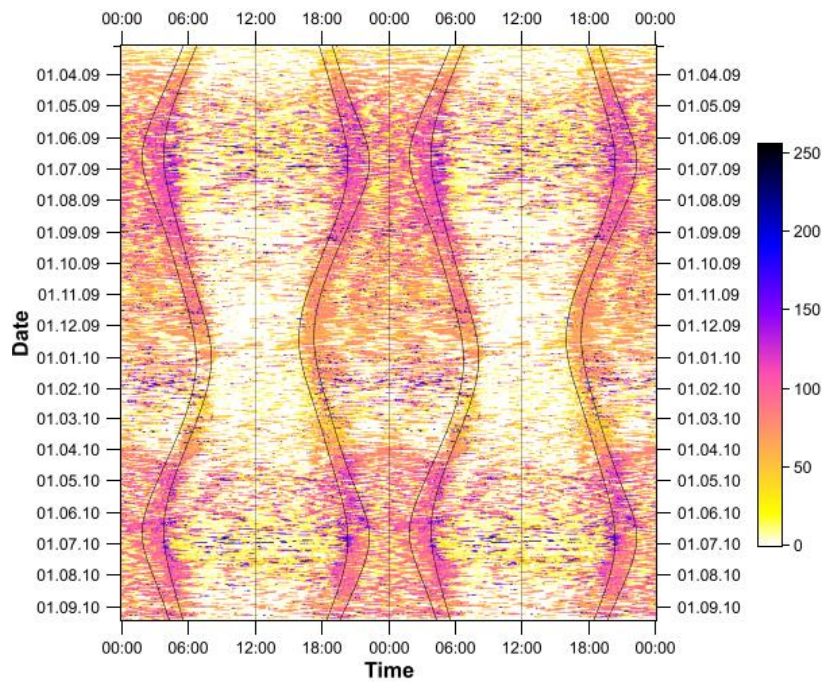


Figure 18: The actogram of a male red deer (age class I) with collar number 06754_110216124921 during period 4. 3. 2009 – 12. 9. 2010.

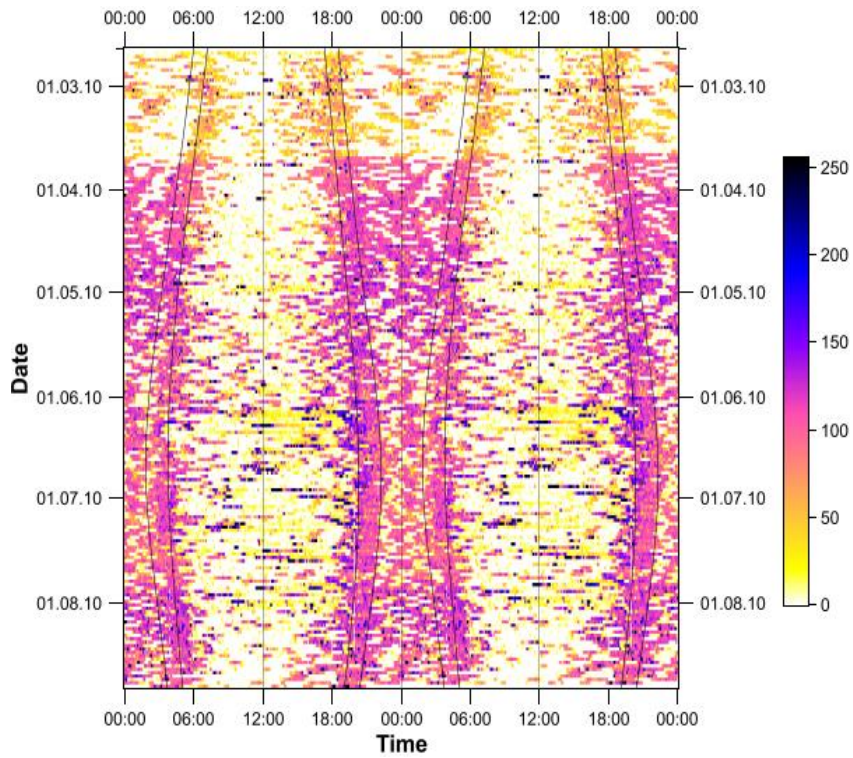


Figure 19: The actogram of a male red deer (age class I) with collar number 06752_110216135734 during period 18. 2. 2010 – 25. 8. 2010.

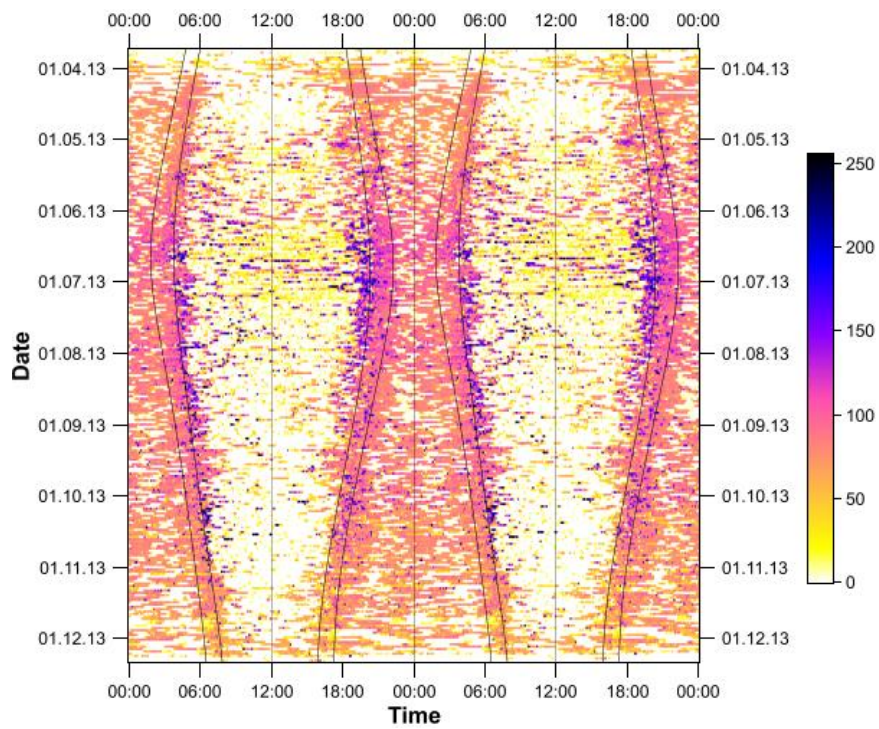


Figure 20: The actogram of a male red deer (age class I) with collar number 06756_140409095741 during period 24. 3. 2013 – 10. 12. 2013.

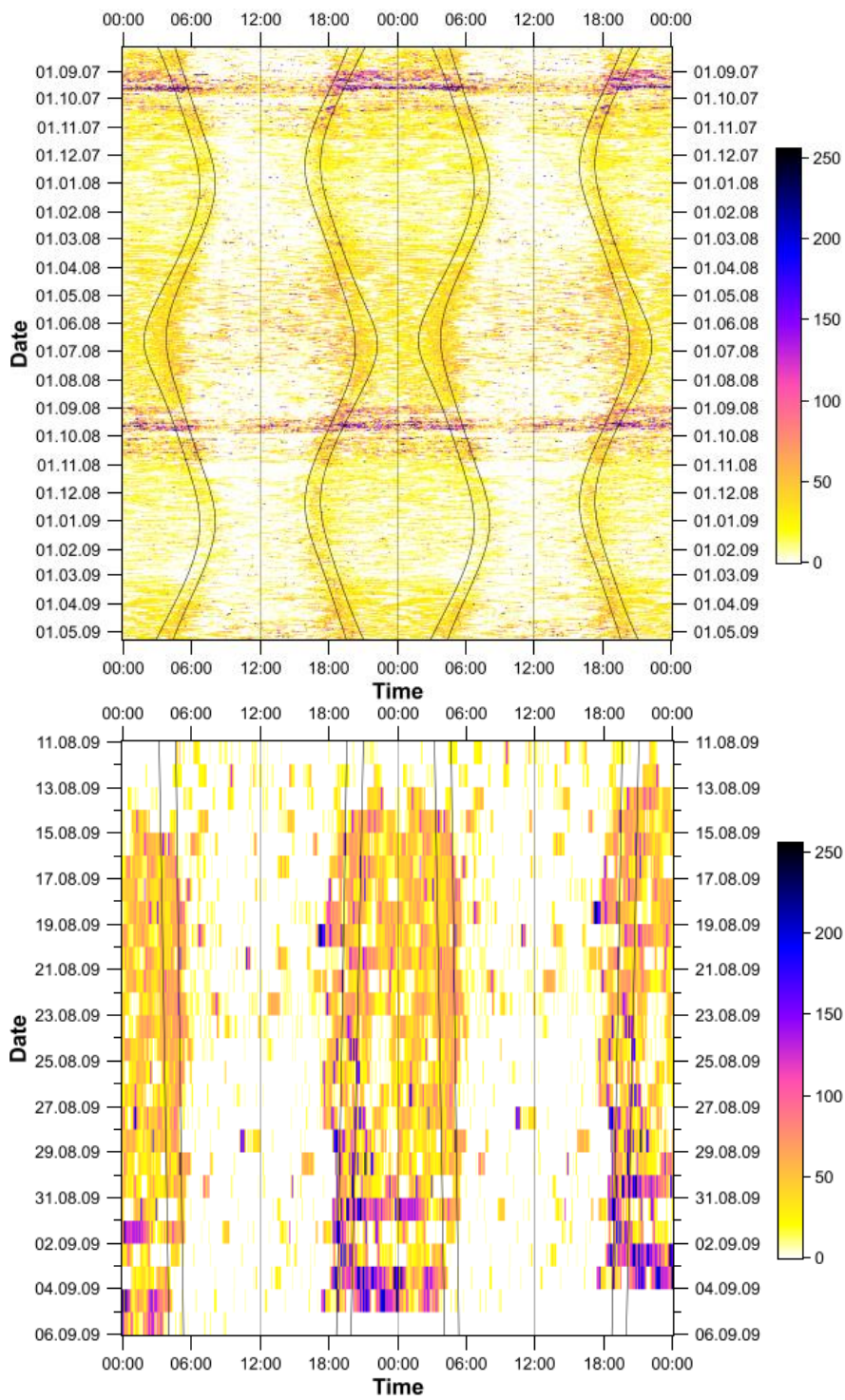


Figure 21: Two actograms of a male red deer (age class II) with collar number 02152_100331125633 during period 7. 8. 2007 – 8. 5. 2009 and collar number 06757_101012152041 during period 11. 8. 2009 – 5. 9. 2009.

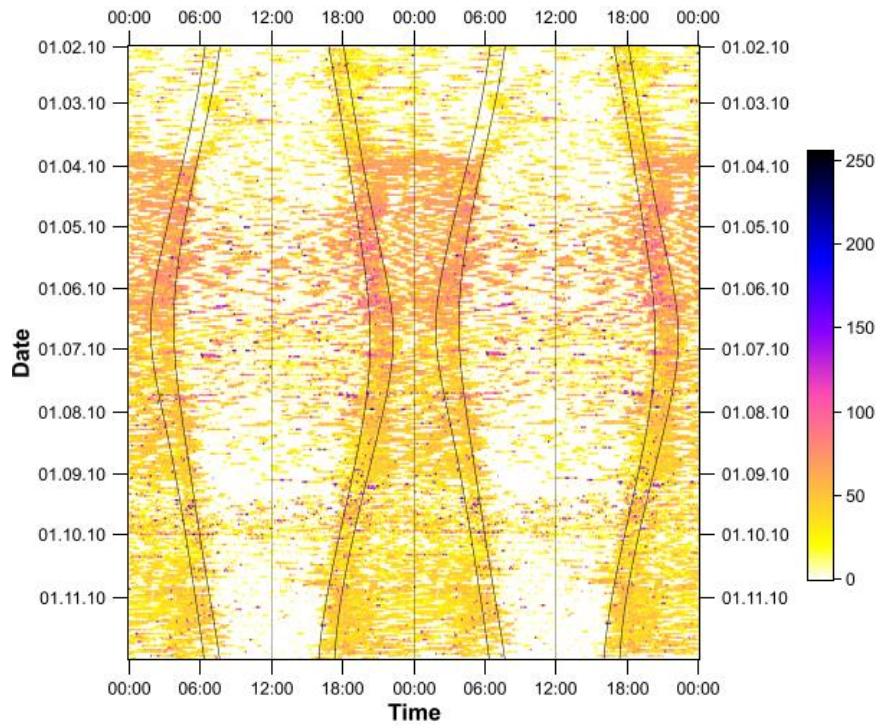


Figure 22: The actogram of a male red deer (age class II) with collar number 06759_110721102647 during period 1. 2. 2010 – 30. 11. 2010.

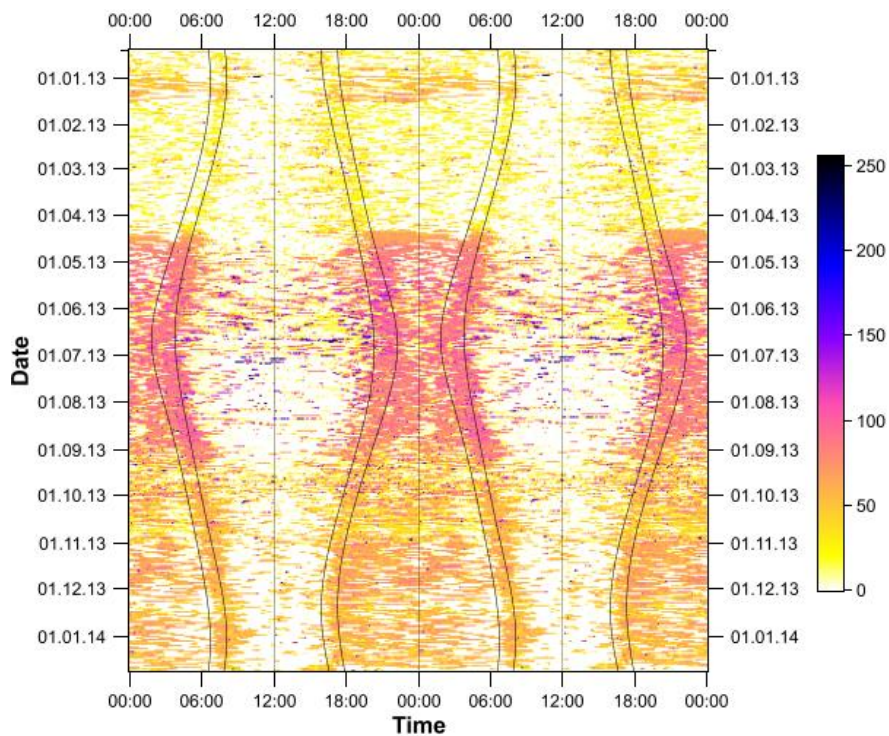


Figure 23: The actogram of a male red deer (age class II) with collar number 06754_140211184502 during period 14. 12. 2012 – 22. 1. 2014.

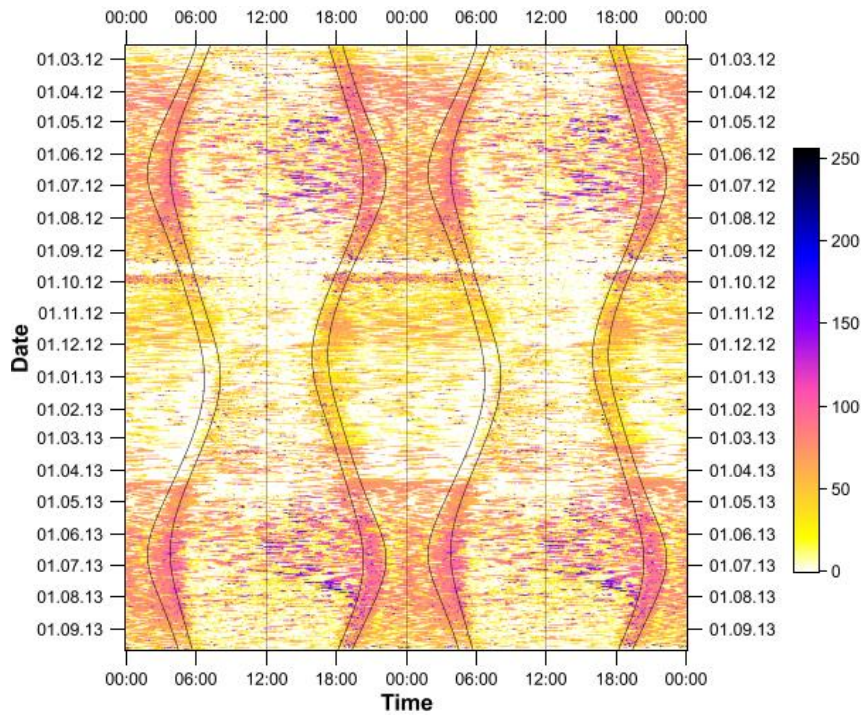


Figure 24: The actogram of a male red deer (age class III) with collar number 06752_140306122515 during period 18. 2. 2012 – 19. 9. 2013.

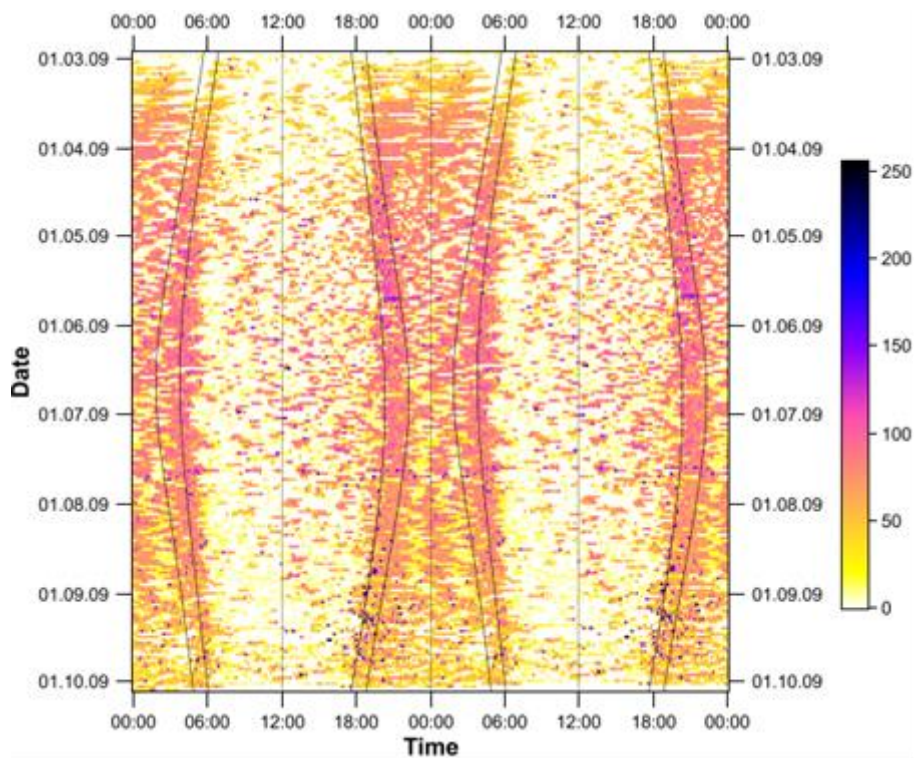


Figure 25: The actogram of a male red deer (age class III) with collar number 06756_110207082911 during period 27. 2. 2009 – 3. 10. 2009.

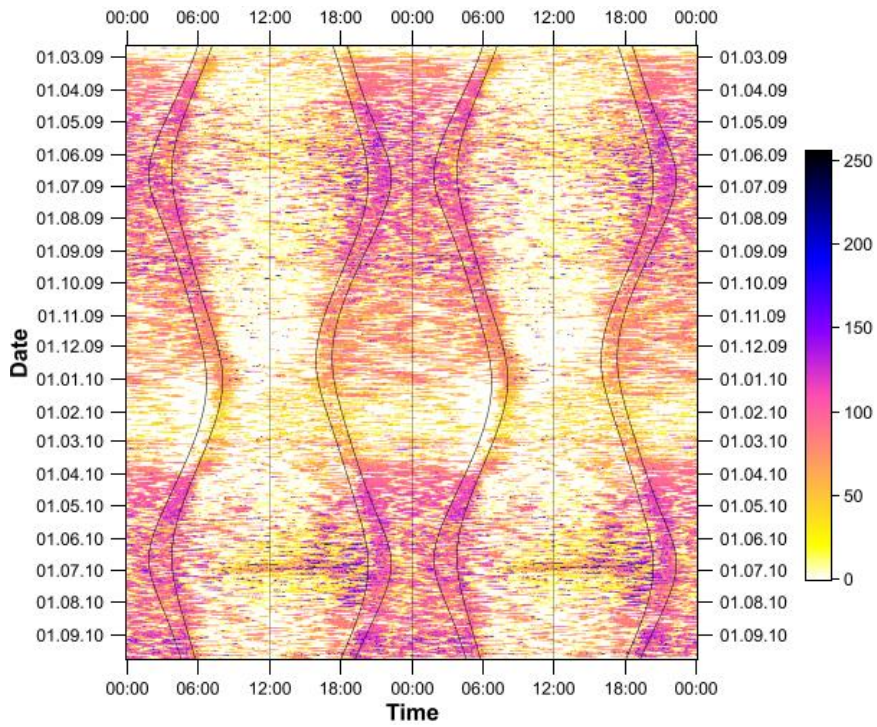


Figure 26: The actogram of a female red deer (age 3 years) with collar number 06760_101015103428 during period 19. 2. 2009 – 22. 9. 2010.

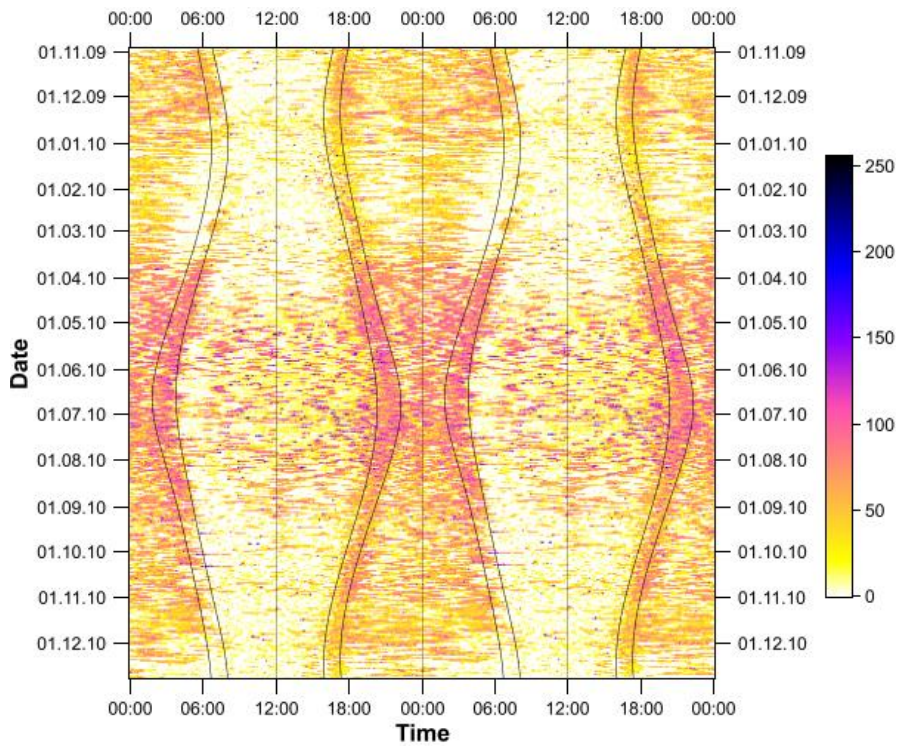


Figure 27: The actogram of a female red deer (age 6 years) with collar number 06761_110207090101 during period 30. 10. 2009 – 23. 12. 2010.

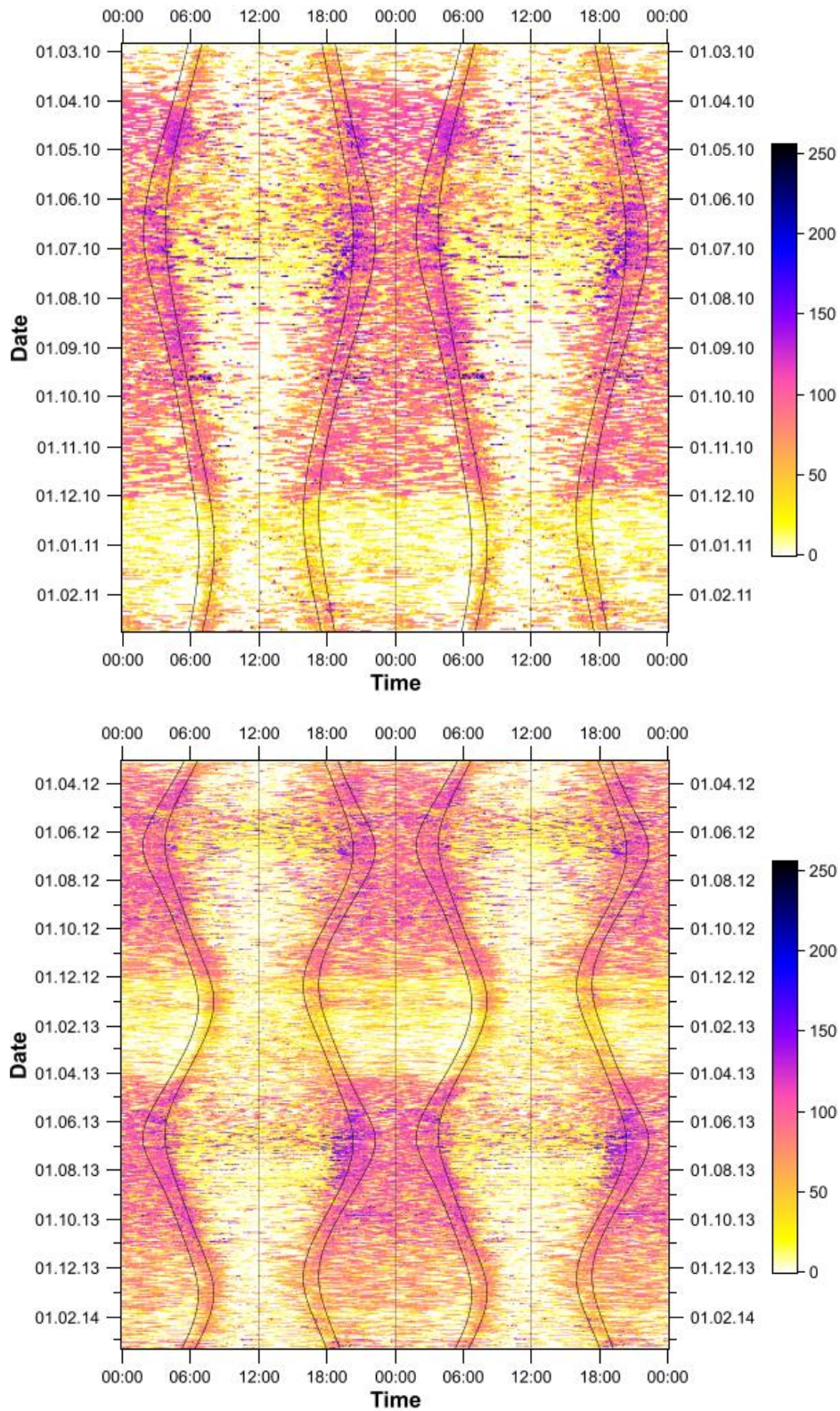


Figure 28: Two actograms of a female red deer (age 7 years) with collar number 06763_120413142921 during period 25. 2. 2010 – 22. 2. 2011 and collar number 06761_140922113916 during period 5. 3. 2012 – 11. 3. 2014.

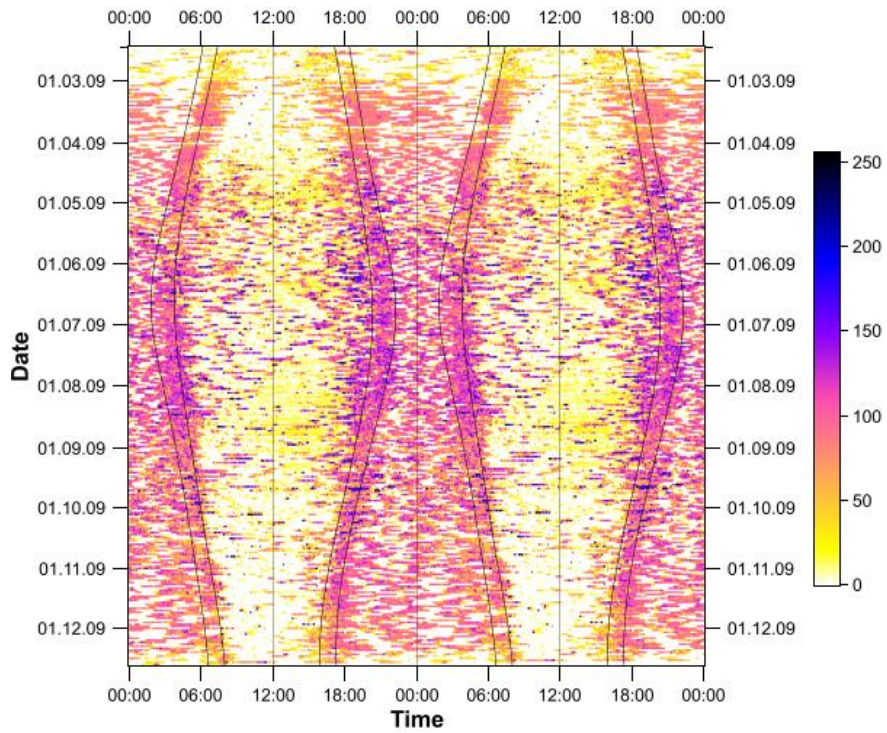


Figure 29: The actogram of a female red deer (age 5 years) with collar number 06762_110207084445 during period 12. 2. 2009 – 18. 12. 2009.

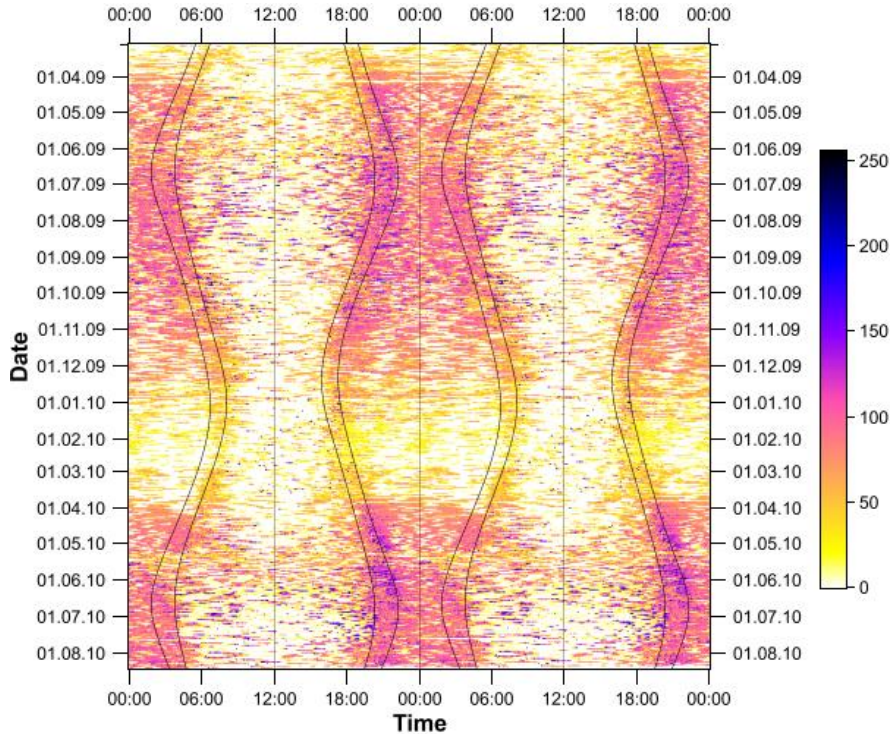


Figure 30: The actogram of a female red deer (age 4 years) with collar number 06764_110216125953 during period 5. 3. 2009 – 27. 8. 2010.

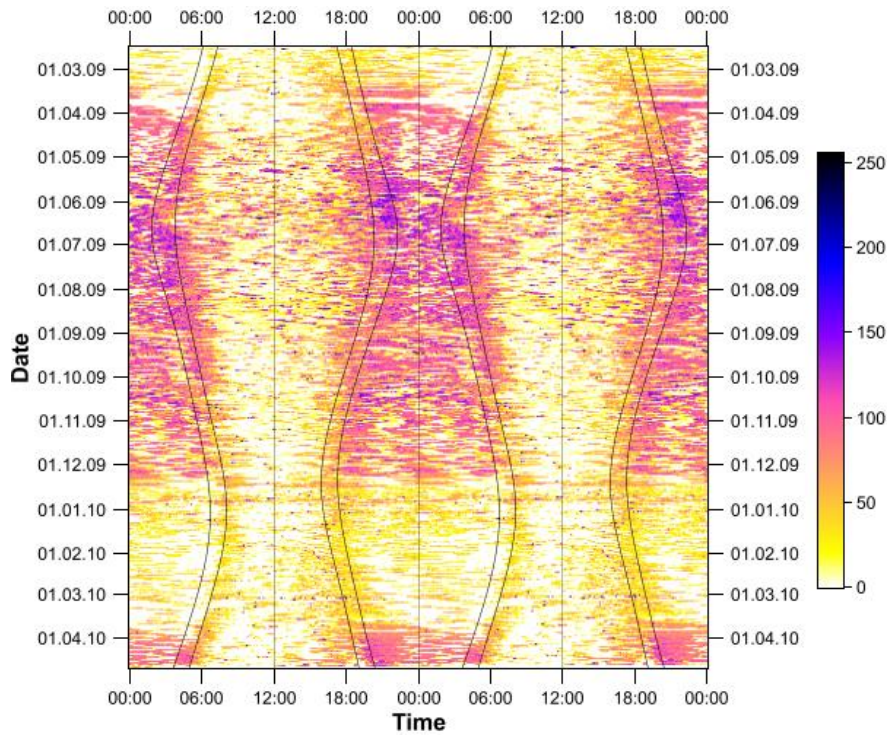


Figure 31: The actogram of a female red deer (age 8 years) with collar number 06765_110216140857 during period 14. 2. 2009 – 20. 4. 2010.

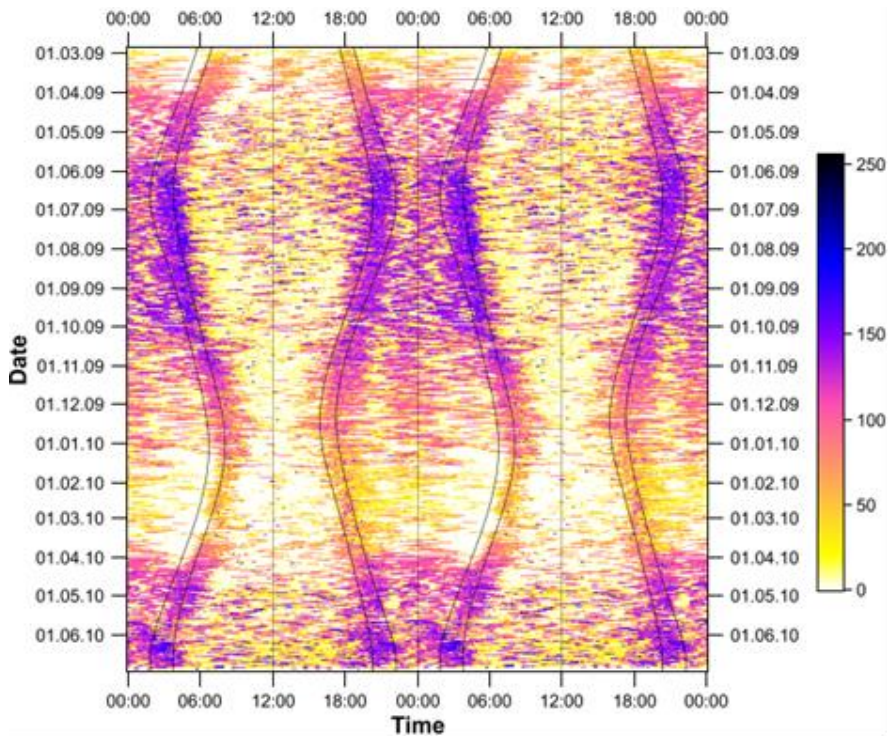


Figure 32: The actogram of a female red deer (age 3 years) with collar number 06766_110721102514 during period 25. 2. 2009 – 27. 6. 2010.

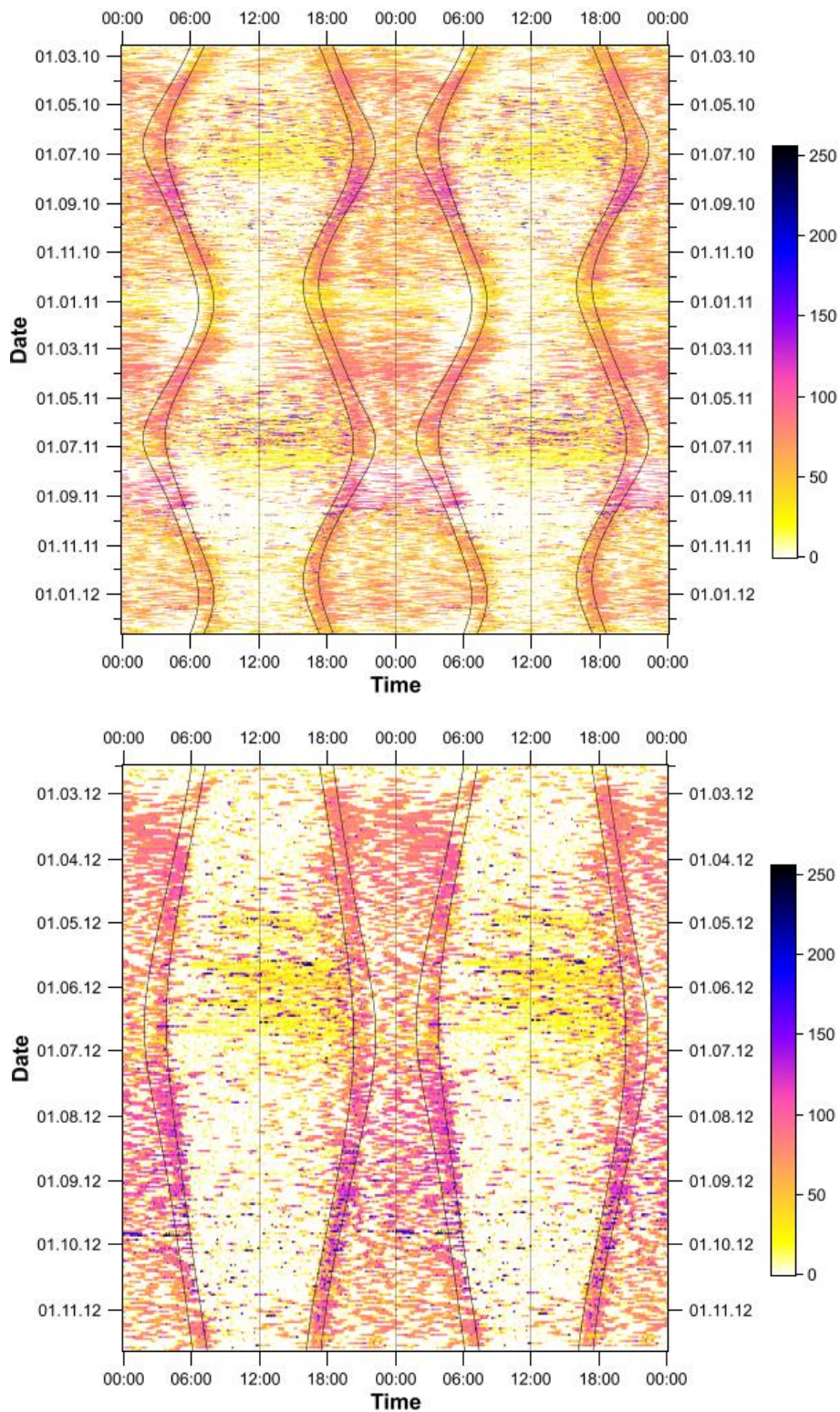


Figure 33: Two actograms of a female red deer (age 6 years) with collar number 06767_120412140212 during period 17. 2. 2010 – 17. 2. 2012 and collar number 06762_170327112104 during period 17. 2. 2012 – 19. 11. 2012.

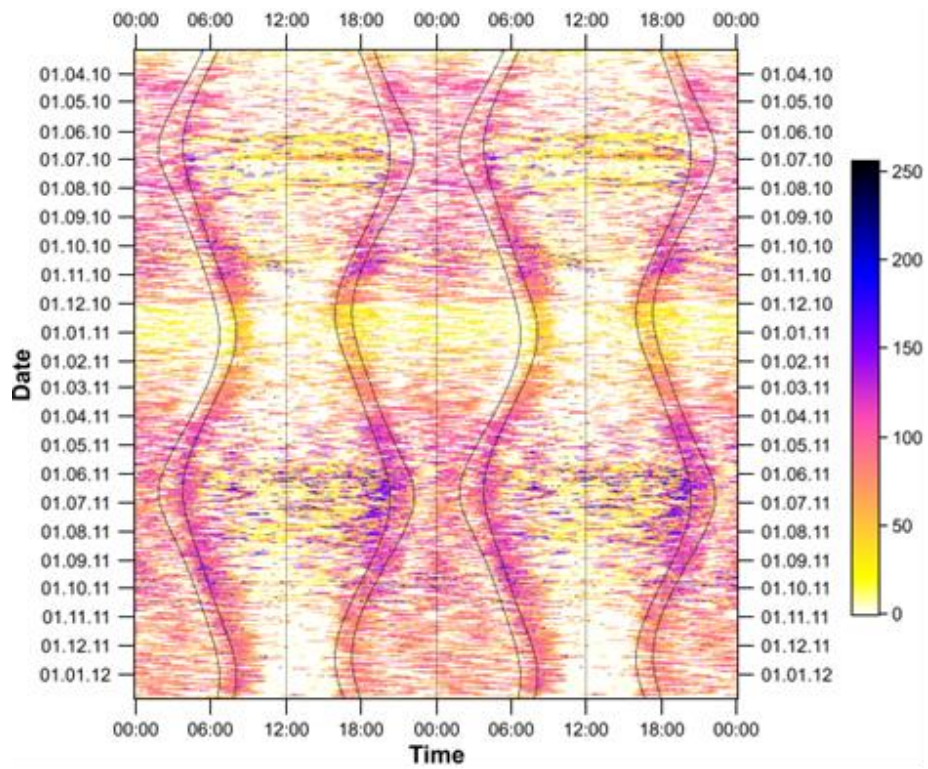


Figure 34: The actogram of a female red deer (age 7 years) with collar number 06769_120413135629 during period 8. 3. 2010 – 24. 1. 2012.

6 Discussion

Capturing of red deer, as an extremely stressful situation for the animal, could have led to post-release shock, trauma or injury which could possibly alternate general behaviour of the animal and therefore affected whole data collection (Morellet, 2009). Nonetheless, any of all monitored animals in Bohemian Switzerland National Park according to acquired data showed strange behaviour which would indicate a problem after releasing the animal.

6.1 Circadian and diurnal rhythms of red deer

Red deer of Bohemian Switzerland National Park were generally more active during the nighttime, which was confirmed by the length of activity during the night and by the index of diurnality. These results correspond with findings that red deer restricted their activity around dawn and dusk and increase their nocturnal activity where continuous disturbance is present (Georgii and Schröder, 1978; Georgii, 1981; Punga, 1990; Hester et al., 1996). With absence of large carnivores the only source of disturbance of red deer were anthropogenic activities. For instance, Figure 16 indicates that there was a possible connection between nocturnality of red deer and beginning of tourist season (approximately from March till October) in the BSNP. This might suggest that tourism in the BSNP reach levels that force red deer to be predominantly crepuscular. And even though hunting season (from the 1 of August till the 15 of January) as another human interest in the park is not clearly detectable from the length of activity throughout the day (24 h) and by the index of diurnality, there is probably some kind of effect on red deer activity rhythms, which has to be yet detected with respect to reactions of red deer to hunting. Whether it leads to increased activity as they flee from the hunters; decreased activity as a hiding strategy; combination of both or none.

However, both sexes show activity during the daytime as well and females are even more active than males when light dominates. It is not sure why there is this difference, but it might be caused by female's sociality as a form of antipredator strategy (Krop-

Benesch et al., 2011) which could have led to mitigation of stress from sources of disturbance during the light period.

From actograms (Figures 17–34) is also apparent that red deer were mostly nocturnal with main peaks around dawn and dusk. Moreover, these actograms clearly show seasonal changes of light availability, which is according to Nielsen (1984) the main exogenous driver of activity in wild ruminants.

6.2 Seasonal activity dynamics of red deer

Differences between male and female red deer in the relative level of activity during the day (24 h) (Figure 10) where females show higher values was valid throughout the whole season (year) (Figure 12). This could have been caused again by social interactions in more numerous herds or by lactation period which might last five to seven months (Dungel and Gaisler, 2002).

The low relative level of activity (Figure 12) during the winter period was probably caused by energy saving and low food availability, however, from March, the RLA simultaneously increased with feed offer (Berger et al., 2002). The RLA peak was for both sexes in June which is for females a period shortly after the calving or around. The RLA from June slowly descended till winter which correlates with decrease of biomass production. Nevertheless, males during the rutting period in September showed a slight increase of RLA probably thanks to extending of their territory and competition among rivals (Dungel and Gaisler, 2002).

The same tendency has graph with the average time of activity during 24 h cycle throughout the year (Figure 14), but with more distinct deflection up from the decreasing tendency with beginning in August. This could have been possibly a minor reflection of the beginning of the hunting season in the BSNP. However, the mid September is also rutting period, which was also a reason why there was a growing tendency. The tendency finally stops in October and started simultaneously decrease with the reduction of biomass.

The highest RLA in age class I was probably caused by searching of territory and gaining experience. This correspond with the age class II that showed the lowest RLA,

because they were already more experienced and powerful enough to protect their territory and had opportunities to mate. However, during the rutting period in September, the age class II was more active than the class III, which was otherwise more active throughout the year. Class III also contained old individuals that were usually challenged by young ones from class I and therefore had to protect their territory more often which led to higher RLA (Figure 13).

The index of diurnality of red deer indicates predominantly nocturnal (crepuscular) life style, nonetheless, in January and February the index of diurnality show positive values, which means that red deer were slightly more diurnal these months. This could have been somehow connected again with food availability, energy saving and probably with weather conditions. Afterwards the tendency sharply fall probably with increasing movement of people (Ensing et al., 2014) in the park and in case of males with shedding of antlers, which was possibly more sensitive period and males therefore tried to avoid any direct interaction with other males. From April till May, in case of males, and till June, in case of females, the tendency was growing. In case of females it could have been caused by giving birth and males might have been ready to use again their antlers as a “territory tool”. Then the tendency fell, which can be associated with the peak of tourist season and from August, in case of males, and in September, in case of females, the diurnality index approaching values around the zero level probably thanks to decreasing number of tourists.

The number of activity peaks and its results are similar with the results of the diurnality index. Based on that, we can hypothesise, that number of activity peaks correspond with the diurnality index, concretely the more red deer are around the zero level in the diurnality index the more are active during the daytime and therefore more prone to anthropogenic disturbances which might lead to higher number of stressful situation that is often solved by flight, which is reflected as a activity. However, from this hypothesis deviate a fact that the number of activity peaks clearly reflected the start of the rutting season (possibly hunting season) and results from the diurnality index to a certain point not (Figure 15 and 16).

In Figure 15 (number of activity peaks) is also apparent the huge jump up in August which could have been a response to the beginning of the hunting season in the BSNP and red deer were more often exposed to a danger situation represented by hunters. However, only males showed this significant jump, probably because they represent much more wanted trophy.

6.3 Activity of individual red deer

All actograms of monitored red deer in the Bohemian Switzerland National Park reflect general nocturnality of red deer with two distinct peaks around sunrise and sunset, which might be also called as crepuscularity. From actograms it is possible to define certain life events which resulted in different representation of activity. For example the actogram (Figure 21/1) of a male red deer (age class II) showed increased activity in September 2007 and 2008 which might be connected with rut. However, this was the only individual that showed this pattern. Another male red deer (age class III) in the actogram (Figure 24) showed hardly any detectable activity in September 2012. This could have been caused by injury or temporal disorder of the acceleration sensor.

The similar pattern of decreased activity (Figures 23, 24, 26, 28, 30, 31 and 32) could have had relation with weather conditions, which means low temperatures, or with increased activity of people connected with celebration of the New Year's Eve, which means fireworks.

It is apparent that colours of each actograms differ. It was caused by several factors and its complexity. The GPS Plus Collars do not discriminate between active and inactive state, but gives a quantitative measure on the intensity of activity, therefore it is necessary to define a meaningful activity threshold. The activity threshold might differ due to the characteristics of the collar, difference between animals and individuals and also by variable body conditions such as diameter of a neck, thickness of fur or position on the body (Krop-Benesch et al., 2011).

7 Conclusion

Telemetry monitoring of red deer in the Bohemian Switzerland National Park confirmed that they were mainly active throughout the nighttime with two main activity peaks around the sunrise and sunset. Thanks to graphical representation of activity (actograms) it was possible to observe changing activity patterns according to light. The relative level of activity and also average time of activity during 24 h throughout the year showed connection between environmental conditions such as weather and feed availability; and also between life events where the most apparent event was rutting period. The index of diurnality suggests that nocturnal and crepuscular life style is related to human interest such as tourism. Surprisingly, hunting period was not clearly detectable from the results except from the number of activity peaks and only in case of male red deer. However, this connection could have been influenced by rutting period as well. It was also confirmed that distinction between males and females in behaviour were reflected in activity rhythms and that age classes of male red deer indicated difference in activity rhythms as well. Red deer as the largest animals in the BSNP are directly or indirectly influenced by anthropogenic activities, therefore this research helped to deepen our knowledge about their behaviour and activity patterns which can generally contribute to the proper management of the park.

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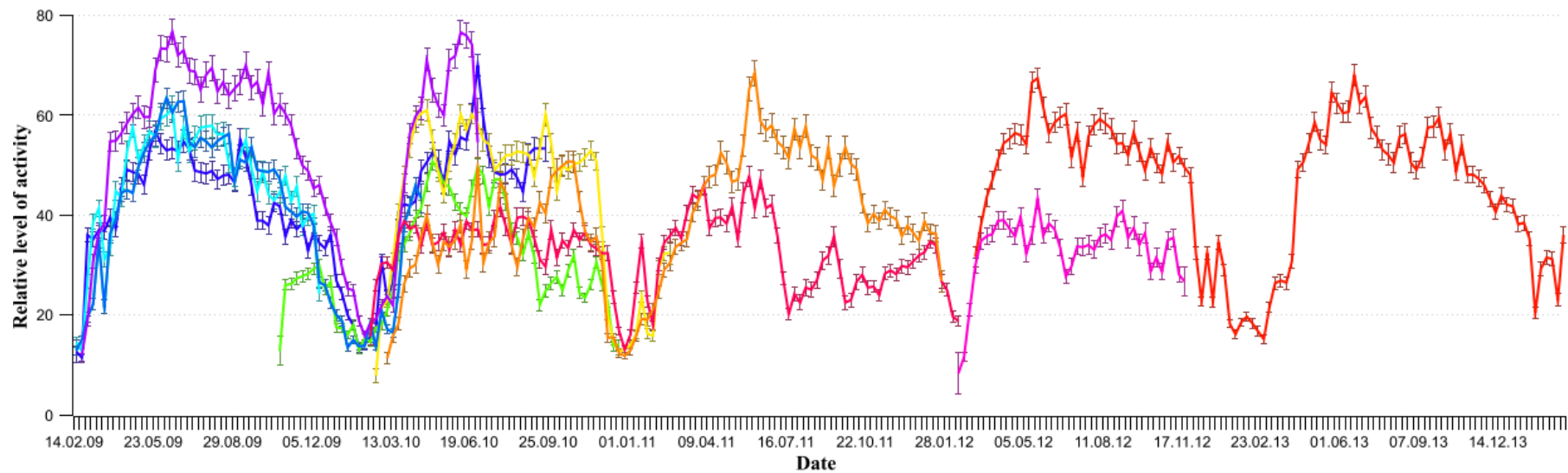
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List of the Appendices

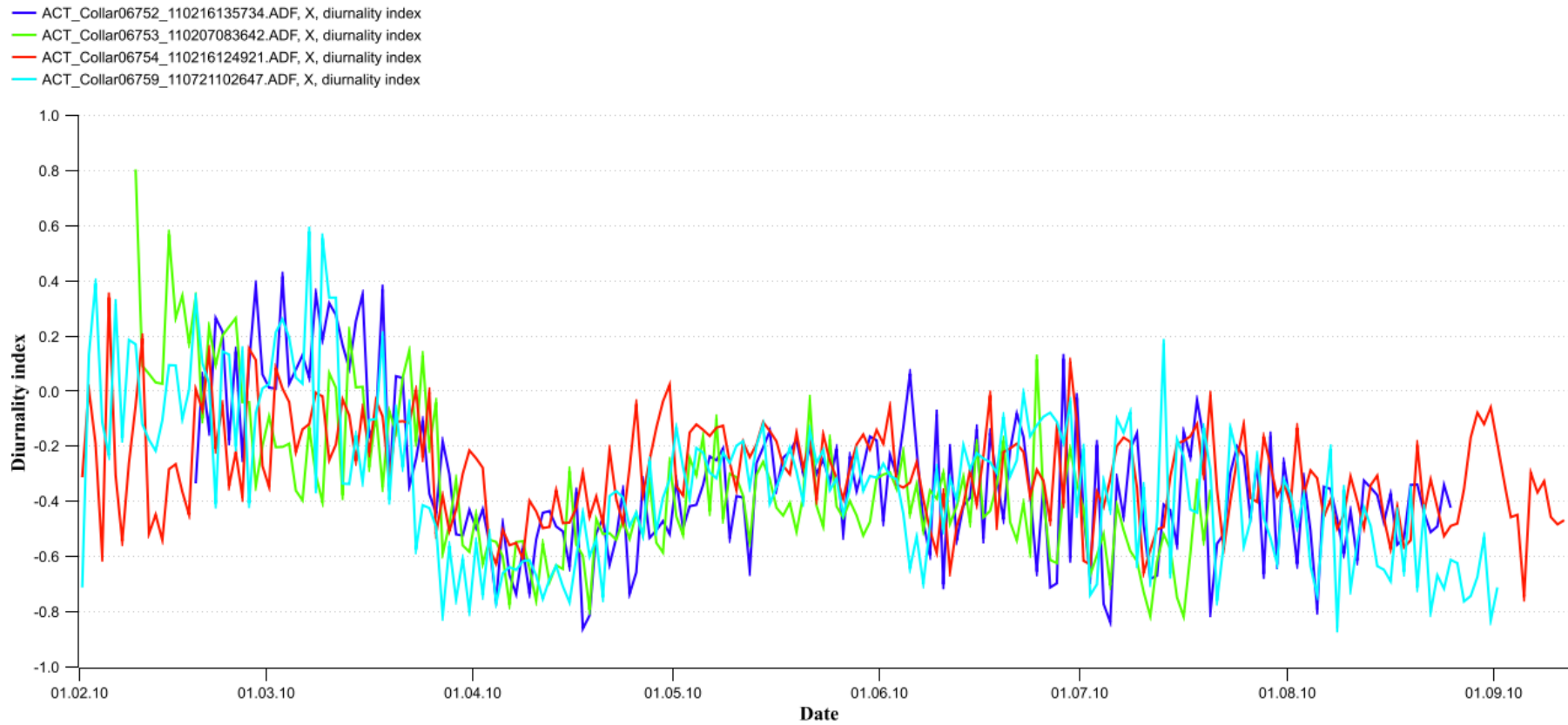
Appendix 1: Activity of all female red deer.....II

Appendix 2: The index of diurnality for selected male red deer..... III

- ACT_Collar06760_101015103428.ADF, X, mean \pm alpha 0.05
- ACT_Collar06761_110207090101.ADF, X, mean \pm alpha 0.05
- ACT_Collar06761_140922113916.ADF, X, mean \pm alpha 0.05
- ACT_Collar06762_110207084445.ADF, X, mean \pm alpha 0.05
- ACT_Collar06762_170327112104.ADF, X, mean \pm alpha 0.05
- ACT_Collar06763_120413142921.ADF, X, mean \pm alpha 0.05
- ACT_Collar06765_110216140857.ADF, X, mean \pm alpha 0.05
- ACT_Collar06765_110216140857.ADF, X, mean \pm alpha 0.05
- ACT_Collar06766_110721102514.ADF, X, mean \pm alpha 0.05
- ACT_Collar06767_120412140212.ADF, X, mean \pm alpha 0.05
- ACT_Collar06769_120413135629.ADF, X, mean \pm alpha 0.05



Appendix 1: Activity of all female red deer during telemetric observation displayed at interval of seven days. Processed in Activity Pattern software.



Appendix 2: The index of diurnality for selected male red deer during displayed interval. Processed in Activity Pattern software.