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Chapter 1

INFLUENCE OF ANTHROPOGENIC DISTURBANCES ON ACTIVITY, BEHAVIOR AND HEART RATE OF ROE DEER *(CAPREOLUS CAPREOLUS)* AND RED DEER *(CERVUS ELAPHUS)*, IN CONTEXT OF THEIR DAILY AND YEARLY PATTERNS

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ABSTRACT

Human recreation influences deer in various ways. To better understand these interactions three roe deer and two red deer were investigated during controlled disturbance trials. By means of implanted telemetry transmitters heart rate and positions of the head were recorded. Heart rates and behavior were compared before, while and after confronting the animals with various stimuli. Furthermore heart rate and activity of 14 roe deer and 8 red deer were continuously recorded to obtain their normal daily and yearly patterns without disturbance trials. Altogether 6.8 million minutes of data were analysed. For each registered minute a distinction between active and inactive behavior could be made.

Daily activity patterns of roe deer varied greatly within different seasons: From November to June the animals were more active in the daytime, whereas in late summer and early autumn they showed pronounced nighttime activity. In contrast, red deer showed a relative constant ratio of day to night activity. Both roe and red deer were most active during twilight, roe deer more so at dawn, red deer more at dusk. Resting heart rate of red deer was lowest in winter (~44 beats/min), and highest in May and June (~71 beats/min). Roe deer showed less pronounced seasonal differences of resting heart rate (65-76 beats/min). Lunar cycles influenced activity of red deer, but not of roe deer.

Both roe deer and red deer exhibited stronger behavioral reactions (“activation”) and heart rate increases towards optical stimuli (walking persons, dogs, equestrians and hang-gliders) than to acoustic stimuli (chain saw, radio music, dog barking) with exception of gunshots, which also elicited high reactions. Activation was associated with daytime and season. Both roe and red deer were more often activated in the morning hours and late afternoon than at noontime. Altogether the reactions of roe deer towards stimuli were short and strong, whereas red deer showed less obvious but persisting reactions. Behavior of red deer was disturbed for at least 10 minutes after gunshots and persons passing by, while equestrians, hang-gliders, tractors and most acoustic stimuli had milder reactions as consequence.

Roe and red deer showed different strategies of compensating after being disturbed. By roe deer the length of resting bouts were shortened on days with disturbance trials, but the number of resting bouts per day increased, so that the total activity budgets for daytime as well as for 24 hours were not influenced by disturbance trials. Red deer were more active during daytime when disturbed without changing their night activity (total daily activity increased), however, they had lower resting heart rates on days with disturbance trials. Recommendations are given to minimize disturbances of deer.

Keywords: human disturbance, hiking, horse riding, dogs, hang-gliders, gunshots, compensation strategies, controlled trials

1. INTRODUCTION

1.1. Objectives

Increasing human recreational activities lead to more and more disturbances of wild animals living in already size-reduced habitats that are additionally dissected by housing developments and traffic infrastructure (Jaeger et al., 2005; Jiang et al., 2009). The question arises to what extent animals are disturbed by recreationists and other land users such as foresters and hunters and how far their well-being is impaired. Particularly protected land areas should function as sanctuaries for native animal and plant species, but should also enable people to get in touch with nature. To harmonize both aims is one of the difficult tasks for ecologists, biologists and wildlife managers (Burch, 1988; Boyle and Samson, 1985). This study wants to improve the scientific basis for management decisions. The objectives are:

- to measure experimentally the impact of different anthropogenic disturbances on behavior and heart rate of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*);
- to relate the findings to the daily and yearly activity patterns of the deer species;
- to compare the results with the outcomes of other studies to this topic.

1.2. Fundamentals of Researching Stress in Wild Animals

1.2.1. Definition of Disturbance

“Disturbance” is interpreted very differently in literature, either as the cause of an occurrence, as the effect, or as both combined (Rykiel, 1985; Archer and Stokes, 2000). In this study the term “disturbance stimulus” is defined as the cause of changes in behavior, activity and heart rate of the animals and “disturbance effect” as their reaction to the disturbing agent.

Rykiel (1985) characterizes a disturbance effect by the *direction* of the impact, the *magnitude* and the *persistence*. A disturbance effect can either be *transient*, such as a temporary increase in the heart rate or it can be *permanent*, for example a change in the activity pattern of the animal. According to Reichholf and Schemel (1988) a disturbance can be specified by its intensity, its duration and its frequency. Christensen (1988) describes five parameters for disturbance: the *frequency*, the *return time* at a particular site, the *intensity* irrespective of its effect, its *severity*, i.e. its impact and its *predictability*. Horejsi (1976) distinguishes between active and passive harassment. Active harassment leads to obvious changes in behavior such as flight, whereas passive harassment shows only subtle changes in activity.

1.2.2. Definition of Stress

Seyle (1936) conceived stress as the nonspecific response of the body to any demand. These demands can be very different in nature: e.g. heat, injuries, hunger or toxins. Moberg (1985) later pointed out that stress reactions are not always nonspecific, but rather various stress factors can affect the same individual differently. Jenkens and Kruger (1973) discern between *psychological* stress (such as fear and frustration) and *somatic* stress (for instance injuries or hunger). Stress reactions depend on the responsiveness of the animal being exposed to the stressor (Porges, 1985). Different individuals can show varied reactions upon the same stressor and even one and the same individual responds dissimilar at different times. The reaction towards a certain stressor is modified by many factors, e.g. age, sex, condition, temperament of the animal, previous experiences or concurrent environmental conditions (Jenkens and Kruger, 1973).

Cannon (1929) was the first to recognize the relevance of the autonomic nervous system in stress procedures. During an “emergency state” triggered by pain or agitation, epinephrine is released and heart rate increases. Further physiological responses are increase of respiration rate, oxygen consumption, blood sugar and body temperature (Gabrielsen and Smith, 1995). Next to the short-term effects of the autonomic nervous system the behavior of the animal plays an important role in stress procedures. Behavioral reactions are often the most simple and economical way for animals to respond towards stress, for example finding a shady spot on a hot day (Moberg 1985).

1.2.3. Relevance of Investigating Stress in Animals

Stress reactions can generally be interpreted as adaption of the organism to changes in the environment. An environment poor in stimuli can at times even have an adverse effect (Fraser et al., 1975). But usually an excess of excitation is detrimental for the animal, yes, can even endanger its life (Geist, 1971). This is especially the case when more than one stress factor affect the animal simultaneously, e.g. harsh weather and harassment.

Due to the increased release of epinephrine the basic metabolic rate is raised, which leads to an increased energy consumption. Furthermore, the time the animal spends with forage intake is reduced when disturbed frequently, as could be observed e.g. in chamois (Cederna and Lovari, 1985) and red deer (Jayakody et al., 2008). Manor and Saltz (2003) observed that gazelles distinguished between nuisance disturbances, such as by recreationists, and direct threats to survival, such as feral dogs. Yet also nuisance disturbances may be detrimental to the animals, resulting in increased energy expenditure and vigilance at the expense of foraging activity.

Animals may respond to disturbance from humans by avoiding areas of high risk (Gill et al., 1996; Hewison et al., 2001; Rogala et al., 2011). Yet animals with no suitable habitat nearby may be forced to remain despite the disturbance (Mysterud et al., 1999), even if survival or reproductive success is reduced (Gill et al., 2001). Sometimes animals temporally shift into areas with unfavorable food supply, e.g. from open grassland into woodland as with chamois (Rauer-Gross et al., 1988), wapiti (Hernández and Laundré, 2005), or red deer (Jayakody et al., 2011). Particularly in winter this can lead to a negative energy balance, in which the animal expends more energy per time unit than it can ingest. Thus survival in winter is jeopardized (Geist, 1971). Also the digestion of ruminants is disordered when the animals are frequently disturbed, since sufficient resting periods for ruminating are necessary. With reduced chewing less saliva is produced inducing acidosis of the rumen. This leads to poorer condition of the animals (Barth, 1984).

Further negative effects of disturbance are reduced fertility and abortion. Squibb et al. (1986) observed a sudden decline in conception frequency in wapiti at the beginning of the hunting season. They assume an interference of the rut or early embryonic mortality. It is documented for reindeer that chasing heavily pregnant females through deeply crusted snow can precipitate abortion (Geist, 1971). Moving away into unfavorable calving areas results in higher mortality of young (Whitten et al., 1992).

In some cases wild animals migrate in other regions due to anthropogenic disturbances. For example wapiti were more easily driven off from their home range by firewood gatherers than the less sensitive mule deer (Ward, 1984) and wapiti also avoided a newly built road (Czech, 1991). White-tailed deer could be dispelled from their home range through high hunting activity (Sparrowe and Springer, 1970) and traditional winter habitats of red deer remained unused after high hunting pressure (Schmidt, 1992). Female fallow deer were more apt to abandon habitats frequently disturbed, whereas males tended to remain in these areas (Apollonio et al., 2005).

Yet usually cervids are philopatric and return to their home range after the disturbance has ended. According to Sweeney et al. (1971) white-tailed deer chased by dogs out of their home ranges usually returned within one day. Whereas male white-tailed deer migrated away when often disturbed through cattle drives, females showed higher fidelity to their home range (Hood and Inglis, 1974). Even after repeated targeted disturbances red deer would not abandon their home range (Georgii, 1980). Jeppesen (1984) observed that roe deer stayed within their home range under cover or left it only for a short time when disturbed by orienteering and driven hunts. After an extensive forest fire red deer returned to their home range despite the totally changed landscape and lacking forage (Raesfeld and Reulecke, 1988). Also caribous which were often chased and harassed by helicopters would not leave their home ranges (Bergerud et al., 1984).

Not only wild animals suffer through excessive disturbances, also the forest is indirectly damaged through bark peeling and browsing of young shoots. Two main reasons are relevant. On the one hand the animals seek hiding cover in the forest, but cannot find appropriate forage. Secondly, peeling can prevent rumen acidosis, in that more alkaline saliva is produced through the chewing motion (Onderscheka, 1979). Especially in winter harassment of deer can provoke bark peeling (Reimoser et al., 1987). How and to which extent disturbances of wild ungulates lead to game damage is poorly understood and should be more investigated (Völk and Gossow, 1997; Reimoser, 2005).

Overviews of effects of various disturbance stimuli on wildlife can be found in Knight and Gutzwiller (1995), Ingold (2005), Stankowich (2008) and Snetsinger (2009).

1.2.4. Measuring Stress

Many different physiological parameters can serve as indicator for stress and agitation (Levine, 1985; Pfaff, 1982). Some of them though are unsuitable for the investigation of targeted disturbance trials on wild animals. Measuring blood pressure, skin temperature, electrodermal activity, muscle tone, EEG and oxygen consumption is technically difficult. The concentrations of catecholamines, free fatty acids and corticosteroids in blood change with impact of stressors, yet since the capture and the taking of blood samples causes strain in wild animals, these parameters must also be discarded. Besides this, interpreting the concentration of corticosteroids in blood plasma is extremely difficult, since they can elevated or lowered depending on whether the situation is acute or chronic (Stott, 1981; Rushen, 1991). The isozyme LDH-5 proved to be a suitable parameter for measuring stress in fallow deer (Jones and Price, 1990), but is also associated with the problem of taking blood samples as above-mentioned. Cortisol levels can also be measured in faeces (Huber et al., 2003; Keay et al. 2006). This evades the problem of capturing the animal, but it is difficult to allocate the samples to an individual wild animal and if rendered possible it is still impractical to relate the variations in cortisol level to specific short-term disturbances (von der Ohe and Servheen, 2002).

Another characteristic connected to stress is the enlargement of the adrenal glands. Werner (1976) could find considerably enlarged adrenal glands as only pathological change in a roe buck which died during disturbance trials. Yet the measurement of the adrenal glands cannot give information about differing effects of various stress factors on the same animal and about the impact of short-term disturbances. Furthermore the individual variability of adrenal weights in roe deer is considerable (Georgii, 1976).

Heart rate in contrast is a very suitable parameter for this study. By collecting the data via telemetry the behavior of the animals is not additionally affected. Above all short-term reactions can also be measured. Harlow et al. (1987) state that remote monitoring cardiac frequency can be used to predict adrenal function as they found a linear relationship between heart rate and blood cortisol in bighorn sheep. The correlation of heart rate and energy consumption is also relevant, as was verified in the redshank (Ferns et al., 1979), caribou (Fancy and White, 1985) and white-tailed deer (Holter et al., 1976; Mautz and Fair, 1980). According to Freddy (1979) heart rate gives information on psychic strain of the animal even if the animal doesn’t show noticeable behaviorial reactions. Ferns et al (1979) observed a doubling of the heart rate in sleeping redshanks as soon as a person entered the laboratory, while the birds didn’t change their body position. Ball and Amlaner (1979) had similar results with herring gulls. Jacobsen (1979a) measured an increase of 50% of the normal heart rate in lying white-tailed deer calves, when alarmed. The heart rate was 2.4 times higher in moose and 2.7 times higher in caribou when agitated (Roshchevskii et al., 1976), and Freddy (1979) could also observe an increase in the heart rate of mule deer when persons passed by.

Arousal of animals does not necessarily lead to an increase of heart rate. Under certain circumstances the heart rate can also decrease. Red deer calves (Espmark and Langvatn, 1979), white-tailed deer calves (Moen et al., 1977; Jacobsen 1979b) as well as eastern cottontail rabbits

(Smith and Worth, 1979) showed the so-called “alarm bradycardia”. Normally this is the case with animal species that show the behavior of lying prone when alarmed (“freezing and hiding” in opposition to “fight and flight”). Stöhr (1982) observed that individual tupajas lowered their heart rate while other individuals increased it when confronted with the same stimulus. Animals that normally reacted with tachycardia could also show bradycardia when confronted with a very intense stimulus. Miller (1982) interprets these two contrary reactions as two different inherent behavioral patterns when in fear. But also animals without freezing behavior when alarmed can react with bradycardia when they are alert, e.g. wolves (Kreeger, 1990) and bighorn sheep (Stemp, 1983). Experiments analysing the reaction time of humans confirm the assumption that the heart rate slows down when the test person is attentive and in a state of anticipation (Zimmer et al., 1989).

Besides the so far mentioned examples of short-term (“phasic”) changes in heart rate through disturbances, also long-term (“tonic”) changes in heart rate can occur, as Stöhr (1982) could provide evidence in tupajas.

In addition to analysing heart rate, the monitoring of behavior is suitable for examining stress in wild animals. Both short term reactions as well as changes in activity patterns in the long run offer valuable clues to the agitation of the animals. Particularly, because heart rate is not only a criterion for the psychic status of the animal, but also strongly influenced by its activity and therefore insufficient as a sole measure (Stemp, 1983), it is important to include the behavioral composition and the overall activity before and after disturbance trials.

Berger et al. (2002) suggest analysing how far ultradian rhythms in activity patterns are synchronized with the external daily cycle as measure for stress. This was shown to be an indicator for drastic impacts on the animal, such as chases or immobilization, but it remains to be seen if disturbances on a fine-scale can also be detected.

Another approach to investigate habitat use and general activity patterns depending on disturbance impacts is the use of collars with GPS and activity sensor (e.g. Sibbald et al., 2001; Adrados et al., 2003; Sunde et al., 2009; Naylor et al. 2009; Duscher et al., 2009). Contrary to direct observation of flight distances, animals responding beyond the perceptive range of the observer can also be detected via GPS (Preisler et al., 2006).

To draw conclusions about the wellness of an animal, numerous parameters, such as health, fertility, physiological measurements and behavior should be dealt with (Blackshaw, 1986). Heart rate is only one aspect, however combined with behavioral monitoring a good indicator for disturbance of wild animals is available.

1.2.5. Habituation and Sensitization

If an identical stimulus is applied repeatedly the reaction of an individual toward this stimulus lessens, the animal habituates (Thompson and Spencer, 1966). Yet an animal's behavior is not simply habituated or non-habituated, but a matter of degree, and responses occur in differing magnitudes in different contexts (Whittaker and Knight, 1998).

An extraneous stimulus can disrupt the process of habituation, this is called dishabituation. If the stimulus repeatedly applied has an aversive character, the opposite of habituation can occur, the animal is sensitized towards this stimulus (Groves and Thompson, 1970).

Espmark and Langvatn (1985) could observe habituation as well as dishabituation regarding alarm bradycardia when confronting red deer calves with persons passing, stones thrown and dog barking. Gaisbauer (1988) noticed that the flight reaction of roe deer decreased when approached repeatedly. Albrecht (1988) differentiates between unspecific and person-specific habituation. After three months he could approach a group of chamois approximately 27 meters, whereas the flight distance towards other persons was in average 46 m. Altmann (1958) observed that moose had a shorter flight distance towards frequently encountered fishermen than to other persons.

But also the spatial arrangement plays an important role in habituation towards stimuli. When Schleidt and Shalter (1983) let dummies pass angel fish repeatedly from the same direction the first strong flight reactions declined. If the dummy was pulled from a different direction the original strong reaction took place again. Shalter (1984) came to similar results with domestic and jungle fowl. He deduced that animals in a natural environment don’t habituate towards predators contrary to the simulated experiments, since these always approach their prey from different, unaccustomed directions.

Miller and Gunn (1984) report that individual muskoxen habituate towards helicopter overflights while others are sensitized, and conclude that the tolerance threshold towards stimuli can be individually different. Moen et al. (1982) could not find any habituation of white-tailed deer towards snowmobiles, and MacArthur et al. (1982) noticed higher heart rate reactions when approached by persons repeatedly. This is in accordance with the observations of Freddy et al (1986), as they measured progressive higher heart rates in mule deer from the first to third approach. Contrary to his expectations Stemp (1983) also noticed a sensitization of heart rate reactions in bighorn sheep when repeatedly approached by humans. From this he concluded that frequent disturbances lead to sustained heart rate reactions.

In summary it can be said that animals react differently towards regularly recurring disturbances. Mostly they gradually habituate, but they can also show increased sensitivity to disturbing factors.

1.2.6. Vigilance

Potential prey can protect themselves from predators in being vigilant. The time spent in vigilance goes at the expense of other behavioral elements, which are vital for the animal such as forage intake (Turner, 1979; Frid and Dill, 2002, Benhaiem et al., 2008, Ciuti et al, 2012b). An alternative to reduce the vigilance time for the individual animal without reducing its security is to herd together. Turner (1983, cit. Kurt, 1991) compared the time budget of single roe deer compared to roe deer in groups. Detached animals spend about 26 minutes per hour in vigilance behavior, deer living in larger groups only about 12 minutes. Büttner (1980) and Lark and Slade (2008) could also observe a decrease of vigilance behavior for each individual with increasing group size, combined with time gained for forage intake.

Another alternative to lessen the time dedicated to vigilance behavior is in the use of terrain rich in hiding cover (Dimond and Lazarus, 1974). Whereas species in open fields often herd, woodland species respond to disturbances by hiding (Putman, 1988). According to Petrak (1996) red deer show three different strategies when disturbed: seeking hiding cover (mostly at daytime), increasing distance to the source of disturbance (mostly at night), or gaining overview. If hiding cover is sparse, e.g. in winter, it is also feasible for the animal to shift its activity into the night.

This matches the observations of Guthörl (1987) and Jeppesen (1989) for roe deer, Beier and McCullough (1990) and Kammermeyer and Marchinton (1977) for white-tailed deer and Jeppesen (1987) for red deer. Red deer studied by Georgii and Schröder (1981) showed evenly spaced activity bouts at daytime in terrain rich in hiding cover, but were mainly nocturnal if hiding cover was sparse. They conclude that the activity pattern of an animal is also regulated by habitat structure.

1.3. Activity Patterns

Activity patterns of animals are influenced by many factors. On the one hand endogenous factors, such as the momentary metabolic state and hereditary behavioral programmes, play an important role, on the other hand exogenous factors, such as weather, day length or disturbances. Silver et al. (1969) did research on the basic metabolic rate of hungry white-tailed deer in respiratory chambers. Despite constant temperature in the chamber the metabolic rate was much higher in summer (May to August) than in winter. This change was ascribed to changing endocrine activity triggered by day length.

1.3.1. Seasonal Activity Patterns

Activity is strongly influenced by season and daytime. In most investigations cervids were far less active in winter than in summer (Georgii and Schröder, 1978; Lieb, 1981; Green and Bear, 1990). Moreover the active and inactive bouts are longer in winter than in summer, where more frequent changes in activity occur (Cederlund, 1981; Jeppesen, 1989). According to Cederlund (1981) this is due to supply of forage. In summer with plenty of forage the rumen is quickly filled and the animal soon reclines to ruminate. The high-energetic, easily digestible food is quickly metabolized, the rumen is soon empty and the animal rises again to forage. In winter the expenditure of time to intake food is much longer, so the activity bouts are prolonged ("rumen fill theorie"). The forage is rich in crude fibers, requiring more time to chew the cud and leading to longer resting bouts.

In opposition to the above-mentioned findings, it was experimentally shown with roe deer (Ellenberg, 1978) and white-tailed deer (Ozoga and Verme, 1970) kept under steady conditions with constant food composition, that they also minimized food intake and activity in winter. This is an indication of a genetic fixation of the seasonal pattern.

Female red deer investigated by Georgii (1981) showed, contrary to roe deer, shorter, but more frequent activity bouts in winter. Wapitis were more nocturnal in winter according to Green and Bear (1990), whereas the same animal species investigated by Lieb (1981) were more active at daytime during the winter.

1.3.2. Circadian Rhythms

Bimodel daily activity patterns, e.g. intensified activity at dawn and dusk and an extensive inactive phase in the early afternoon, are very widely spread in many animal species (Aschoff, 1966). This rhythm is triggered by an endogenous, self-sustaining oscillation, as Aschoff (1966) could show in greenfinches, yet afterwards modified by so-called synchronizers or "zeitgebers". The environment can inhibit or emphasize parts of the activity pattern, but cannot generate a basic rhythm (Ozoga and Verme, 1970). Many investigated deer species showed a bimodal daily pattern (for red deer: Bützler, 1974; Georgii and Schröder, 1978; Georgii, 1981; for wapitis: Collins et al., 1978; Green and Bear 1990; Lieb, 1981; Lieb and Les Marcum, 1979; for white-tailed deer: Kammermeyer and Marchinton, 1977; for roe deer: Cederlund, 1981; Jeppesen, 1989; Mertens, 1984, Pagon et al. 2013). According to Jeppesen (1989) the bimodal pattern of roe deer is more pronounced in winter, the same is valid for wapitis (Green and Bear, 1990) and red deer (Georgii, 1984). Turner (1980) ascribes the crepuscular behavior to a better synchronization of the individual animals, since the change in light functions as "zeitgeber". With the individual variable digestion time the behavior desynchronizes at daytime.

2. MATERIAL AND METHODS

2.1. The Deer Investigated

14 roe deer and 8 red deer were investigated for their activity patterns and heart rate (Table 1). Of 9700 days of collected data, 4754 days (2839 days for red deer, 1915 days for roe deer) were considered as high quality data for activity analysis, with less than 60 minutes missing values per day and good signal strength. 3606 days were used in heart rate analysis.

Table 1. Details of study animals for activity patterns

No.	species	sex	age (years) when implanted	enclosure type[1]	trans-mitter type[2]	collected data (days)	heart rate data (days)	high quality activity data (days)[3]
1	roe deer	f	2	1,2	t	332	302	292
2	roe deer	f	2	1	h	35	30	29
3	roe deer	f	3	1,2,3	t	337	210	214
5	roe deer	f	2	1	h	57	13	13
7	roe deer	f	2	1	h	381	338	325
21	roe deer	m	3	1	h	133	116	110
22	roe deer	m	3	1,2,3	t	314	176	173
24	roe deer	m	?	1	h	67	35	29
27	roe deer	m	3	1	t	119	110	102
28	roe deer	m	4	1	h	18	15	14
29	roe deer	m	3	3	t	125	75	73
31	roe deer	m	2	1	h	261	179	185
32	roe deer	m	3	1	h	260	230	229
33	roe deer	m	1	1	h	141	135	127
102	red deer	m	1	4	r	914	325	190
106	red deer	f	3	4	r	1185	141	469
107	red deer	f	3	4	r	1155	185	337
113	red deer	f	2	4	r	1066	703	741
121	red deer	m	10	4	r	791	216	491
130	red deer	f	2	4	r	394	39	171
135	red deer	m	5	4	r	702	33	81
140	red deer	f	1	4	r	913	0	359

[1] enclosure type: 1=50m^2, 2=3500 m^2, 3=46ha, 4=37ha

[2] transmitter type: h = implanted transmitter for heart rate, t = transmitter for heart rate including tilt switch, r = repeater system

[3] high quality data for activity are days with less than 60 minutes missing values

Table 2. Details of study animals for disturbance trials

No.	species	sex	age (years)	weight (kg)	disturbance trials (season)
1	roe deer	female	2	20	Sep.10 – Nov.18
22	roe deer	male	3	25	Sep.16 – Nov.18
3	roe deer	female	3	20	Oct.26 – Nov.18
61	red deer	male	1½	75	Dec.10 – Mar.30
51	red deer	female	½	45	Dec.11 – Mar.30

Three roe deer and two red deer were investigated during the planned disturbance trials (Table 2). The animals were born in enclosures, but were not tame. To avoid interactions between the two species the trials were carried out at separate periods.

The animals for the disturbance trials were fitted with telemetry transmitters that were able to measure heart rate and the position of the head (up/down). Technical details of the devices are available in Schober et al. (1982). The transmitters were implanted on the left body side between peritoneum and the muscles of the abdominal wall and connected with two subcutaneous ECG-electrodes in the thoracal area and a subcutaneous tilt switch in the neck area (Figure 1, left). The cables to the electrodes and the tilt switch as well as the antenna ran subcutaneously.

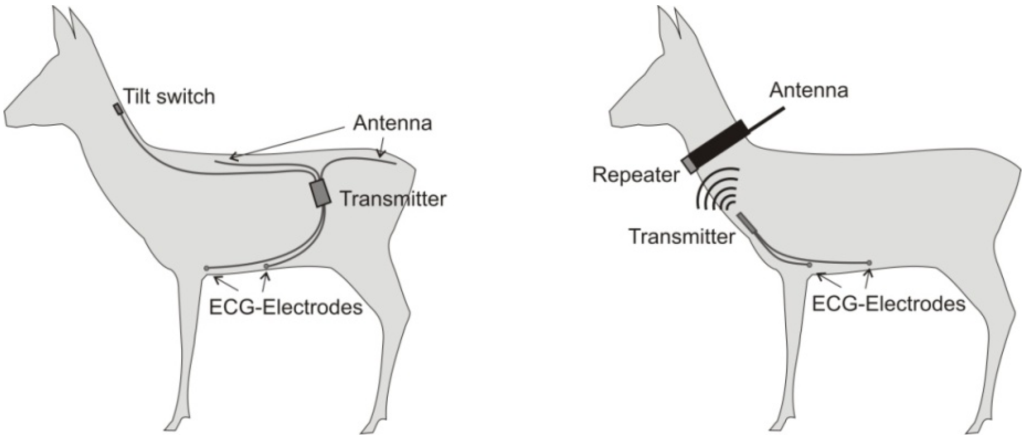


Figure 1. Left: Implanted Transmitter with tilt switch and ECG-electrodes; Right: Repeater system with implanted transmitter, ECG-electrodes and repeater neck collar.

Heart rate was transmitted by sending an impulse of several milliseconds for each QRS-complex of the ECG. The length of the impulse was modulated by the tilt switch depending on whether the head was up or down. The received signals were continuously recorded by two computers. The received field strength was dependent on the position of the implanted transmitters to the receiver and gave information on movements of the animals.

For the general activity and heart rate patterns only 5 roe deer had tilt switches, which allowed identifying feeding while active and “sleep” phases while inactive. The red deer had a repeater system with neck collars carrying larger batteries necessary for transmitting the signals for farther distances (Figure 1, right). With this system the transmitter implanted could be smaller since it only needed the energy to send signals to the neck collar, from where the signals were sent to the receiving station. Details about the repeater system can be found in Schober and Fluch (1995) and Giacometti et al. (2001).

2.2. Enclosure for Disturbance Trials

The disturbance trials were carried out in a 3500m^2 large enclosure (Figure 1) located in the research preserve of the Research Institute for Wildlife Ecology, Vienna. It encloses a meadow with a slight north-facing slope next to a mixed forest (beech-oak-pine) and is situated near the institute buildings.

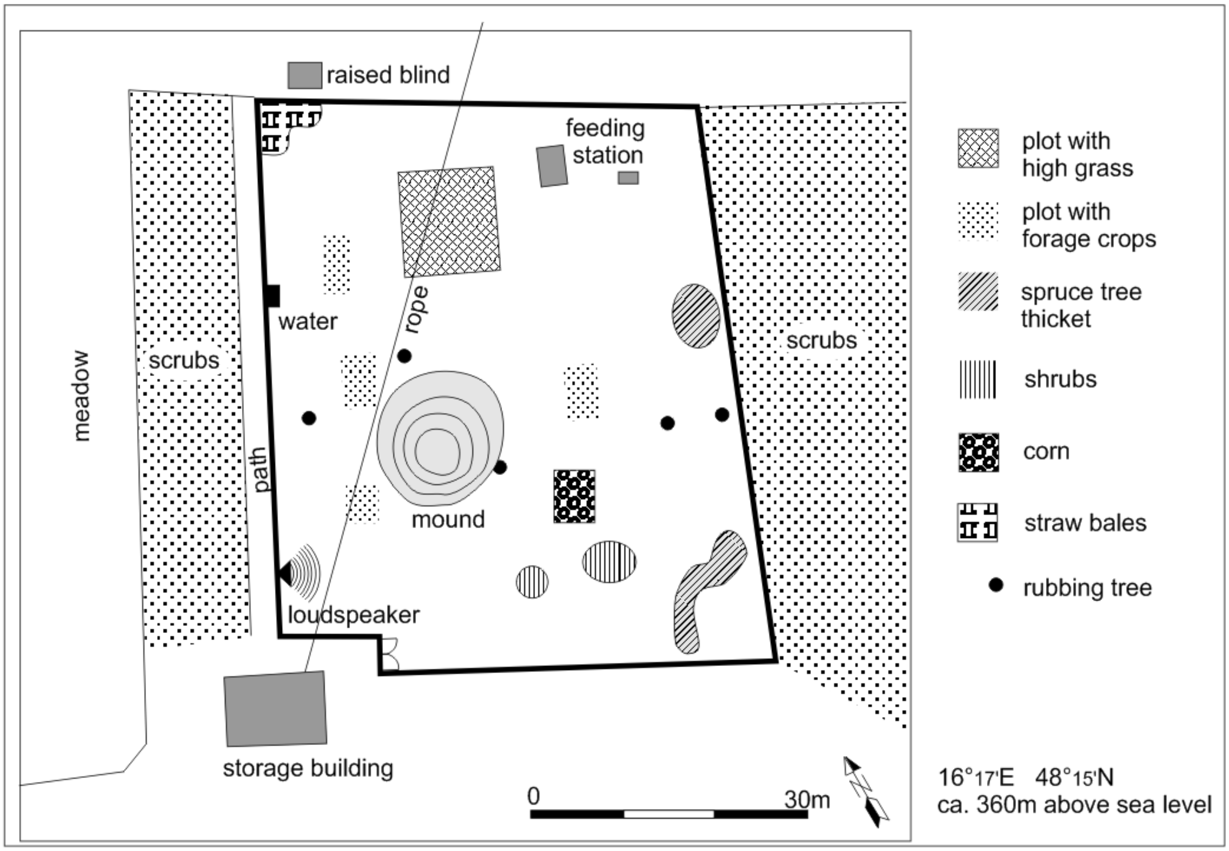


Figure 2. Enclosure.

The meadow was mown twice a year except for one larger patch of high grass and some small patches planted with forage crops (alfalfa, corn, rape, collard greens). In addition small groups of shrubs and young spruce trees provided hiding cover. Videos could be made from the window of a storage building near to the enclosure. A rope for the hang-glider was spanned across the enclosure 4-5m above ground level.

2.3. Disturbance Trials

Different standardized disturbance stimuli were applied in random order with at least half an hour time intervals in between. Heed was paid that each type of stimuli was placed at different times of the day. Subsequent the stimuli and the number of experiments carried out for roe and red deer respectively:

Optical stimuli

- round tour of a single person: One person walks along the fence inside of the enclosure (duration 3-4 minutes; n = 29/32)
- round tour of a person with dog: One person walks with a dog on leash along the fence inside of the enclosure (duration 3-4 minutes; n = 17/17)
- round tour of a group of people (Figure3): at least three persons walk along the fence inside of the enclosure talking at normal sound intensity (duration 4-5 minutes; n = 12/14)
- round tour with a horse (Figure 3): one person rides either a white or brown horse in slow tempo or in trot and gallop along the fence inside of the enclosure (duration 2-4 minutes; n = 19/31)
- round tour with a group of horses (Figure 3): three horses are ridden in slow tempo along the fence inside of the enclosure, with riders talking to each other (duration 4-5 minutes; n = 5/10)
- hang-glider (Figure 3): a model of a hang-glider (1.5m wing span) glides about 4-5 m above the ground on a rope (duration 2-3 minutes; n = 10/14)
- tractor: a small tractor is driven outside the enclosure next to the fence (duration 2-3 minutes; n = 10/14)
- ascent of raised blind: one person climbs a ladder up to a raised blind next to the enclosure (duration 1-2 minutes; n = 12/-)
- feeding: the animals are fed by the same person daily at 3 p.m. (duration 3-5 minutes; n = 31/29)

Optical and olfactory stimuli

- fire: a straw bale is set to fire inside of the enclosure (duration 8-10 minutes; n = -/5)

Acoustical stimuli

- radio music: music is played for 3 minutes from a loudspeaker fixed to the fence of the enclosure (n = 12/12)
- dog barking: a sequence of 20 seconds barking, 30 seconds pause and 40 seconds barking is played from a tape recorder (n = 6/12).
- chain saw: a chain saw is turned on about 20 m from the enclosure for 3 minutes (n = 11/11)
- gun shot: a cracker is lit near the enclosure (n = 24/17)

With all acoustical disturbance trials care was taken that the animals could not perceive the person conducting the trial.

Figure 3. Disturbance trials. Above left: group of persons, above right: hang-glider, below left: group of horses riders, below right: single equestrian.

2.4. Data Acquisition and Interpretation of the Data

Video recordings made during the disturbance trials, as well as the stored telemetry signals showing field strength, head position and heart rate of the animals were drawn upon for the investigation. The received telemetry data were aggregated to entities of one minute and stored on magnetic tapes (“offline data”) and were the basis for long-term analysis. Simultaneously non-aggregated data from heart beat to heart beat could be observed on the computer screen and were also stored (“online data”). These data were very suitable for short-term investigations when analysed in playback. With the high temporal resolution each single heart beat could be reconstructed.

2.4.1. Analysis of the Long-Term Recordings

The offline-data gave information about the activity of the animals over a long period of time. For every minute it could be discriminated if the animal was active or inactive. Inactive was defined as the animal lying, all other behaviour types were classified as active. For each individual an actogram was plotted showing active and inactive phases in a resolution of one minute.

In the analysis of the offline-data, the animal was considered active when the field strength changed often indicating movements of the animal. In addition, the heart rate was higher than in inactive animals, and often the head position changed (Figure 4 and 5).

Typically when browsing the head is down most of the time (Figure 4), while very high heart rates and many changes in field strength are characteristic when the animal is running (Figure 5). The transition towards an active phase was indicated by changes in field strength, changing head positions and a marked increase in the mean heart rate. After a while the heart rate dropped to a lower level, but still stayed higher than the rate in the inactive phase prior to standing up (Figure 6). When changing from active to inactive (lying down) the heart rate decreased gradually (Figure 7). In the inactive state changes in field strength are minimal and the heart rate is steady and low. Few head changes can occur when the animal is grooming itself or browsing while laying, yet the heart rate stays very low (Figure 8). "Sleeping" is defined as an animal lying with its head on the ground. In this state the heart rate decreases even more (Figure 9).

Day: 26.1.
Hour: 22

Minute	9	10	11	12	13	14	15	16	17	18	19	20	21	22
heart frequency: mean	82	82	86	96	98	98	92	94	96	94	92	92	94	92
heart frequency: maximum	90	92	110	112	106	110	108	108	110	108	104	106	110	114
heart frequency: minimum	74	74	76	86	88	84	80	78	88	80	86	82	80	76
head changes (up/down)	---	2	4	4	---	2	---	---	---	---	---	2	---	4
head down (sec)	60	49	42	41	60	59	60	60	60	60	60	59	60	48
max. contin. head down time	60	44	18	28	60	47	60	60	60	60	60	48	60	26
max. contin. head up time	---	11	10	13	---	1	---	---	---	---	---	1	---	8
number of signal adjustments	---	---	9	12	21	6	---	---	4	5	6	18	11	17
signal strength: mean	54	54	55	55	46	53	53	54	56	54	54	52	48	55
signal strength: maximum	54	54	58	62	60	57	53	54	57	56	55	58	57	59
signal strength: minimum	54	54	44	47	31	48	53	54	52	48	47	47	39	46

Figure 4. Example of an offline-file of an animal in active state. The long phases with head down and signal adjustments in middle range are typical for browsing or olfactory control of the ground surface.

Day: 27.1.
Hour: 21

Minute	43	44	45	46	47	48	49	50	51	52	53	54	55	56
heart frequency: mean	98	142	120	176	138	160	172	118	98	116	162	166	176	124
heart frequency: maximum	130	308	150	172	172	288	368	136	112	146	410	308	304	206
heart frequency: minimum	82	86	100	116	116	124	120	102	90	90	104	146	130	102
head changes (up/down)	9	8	2	6	11	9	12	4	4	10	9	11	16	5
head down (sec)	12	8	8	6	17	10	19	25	9	10	3	7	11	5
max. contin. head down time	4	2	8	2	5	4	8	23	8	4	1	3	3	3
max. contin. head up time	19	26	46	26	13	19	20	19	21	22	32	22	30	24
number of signal adjustments	26	32	10	36	31	35	21	11	6	37	28	39	7	9
signal strength: mean	57	32	10	36	31	35	21	11	6	37	28	39	7	9
signal strength: maximum	98	68	40	96	90	99	54	53	47	97	62	97	52	48
signal strength: minimum	42	44	29	48	28	40	39	39	39	38	38	41	38	31

Figure 5. Example of an offline-file of an animal during locomotory activity. Heart rates are high and signal strength is frequently adjusted.

Day: 28.1.
Hour: 19

							↓							
Minute	28	29	30	31	32	33	34	35	36	37	38	39	40	41
heart frequency: mean	74	72	78	82	80	76	88	100	104	106	104	88	88	94
heart frequency: maximum	84	82	96	108	96	82	136	136	124	124	114	114	102	112
heart frequency: minimum	70	68	68	70	70	68	74	68	74	92	94	76	74	84
head changes (up/down)	---	---	---	---	---	---	1	3	6	3	1	4	9	3
head down (sec)	---	---	---	---	---	---	9	10	30	32	38	20	21	11
max. contin. head down time	---	---	---	---	---	---	9	9	16	19	38	10	14	7
max. contin. head up time	60	60	60	60	60	60	51	30	18	21	22	25	12	42
number of signal adjustments	---	---	---	---	---	---	9	10	21	1	5	2	3	16
signal strength: mean	51	51	53	50	53	50	53	55	54	46	46	33	32	31
signal strength: maximum	51	51	53	50	53	50	62	57	59	100	51	34	35	41
signal strength: minimum	51	51	53	50	53	50	53	48	46	46	37	32	30	17

Figure 6. Offline-data of an animal standing up at 19:34.

Day: 26.1.
Hour: 17

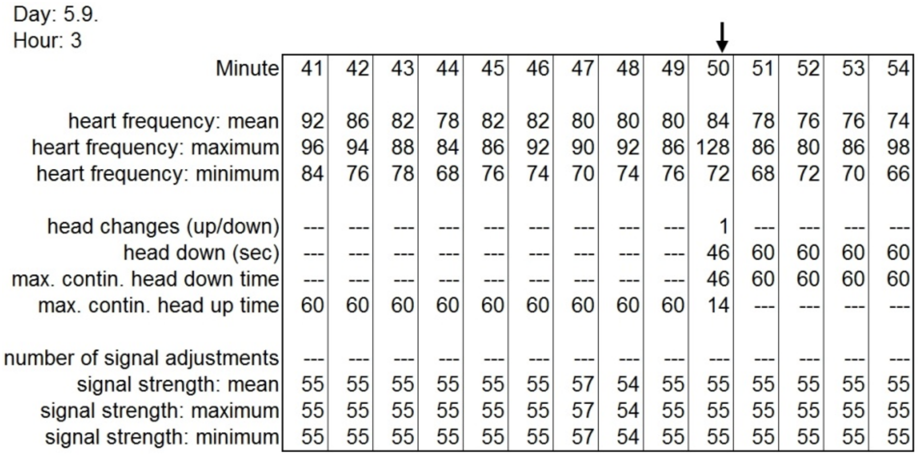
				↓										
Minute	42	43	44	45	46	47	48	49	50	51	52	53	54	55
heart frequency: mean	94	98	88	88	76	74	74	72	74	72	72	72	72	72
heart frequency: maximum	192	112	104	110	82	84	78	76	86	76	76	78	76	76
heart frequency: minimum	80	84	82	76	72	70	68	68	66	68	70	66	70	70
head changes (up/down)	8	7	4	2	---	---	---	---	---	---	---	---	---	---
head down (sec)	26	39	23	23	---	---	---	---	---	---	---	---	---	---
max. contin. head down time	10	25	20	23	---	---	---	---	---	---	---	---	---	---
max. contin. head up time	21	11	26	26	60	60	60	60	60	60	60	60	60	60
number of signal adjustments	25	8	6	16	---	2	---	---	---	---	---	---	---	---
signal strength: mean	58	58	58	51	42	36	32	35	35	35	35	35	35	35
signal strength: maximum	62	60	59	58	42	100	32	35	35	35	35	35	35	35
signal strength: minimum	51	51	50	43	42	33	32	35	35	35	35	35	35	35

Figure 7. Offline-data of an animal lying down at 17:45.

Day: 7.9.
Hour: 15

								↓						
Minute	40	41	42	43	44	45	46	47	48	49	50	51	52	53
heart frequency: mean	66	64	66	68	64	64	66	68	62	60	60	62	74	60
heart frequency: maximum	70	70	72	76	72	68	72	120	66	68	70	78	96	68
heart frequency: minimum	62	56	64	62	60	62	58	58	74	54	52	58	60	56
head changes (up/down)	---	---	---	---	---	---	---	1	1	2	4	3	4	2
head down (sec)	---	---	---	---	---	---	---	2	50	55	46	34	8	44
max. contin. head down time	---	---	---	---	---	---	---	---	50	37	28	26	6	44
max. contin. head up time	60	60	60	60	60	60	60	58	10	5	10	22	25	8
number of signal adjustments	---	---	---	---	---	---	1	5	---	---	---	---	---	---
signal strength: mean	52	51	54	51	52	52	57	53	53	54	54	54	54	54
signal strength: maximum	52	51	54	51	52	52	54	53	53	54	54	54	54	54
signal strength: minimum	52	51	54	51	52	52	---	45	53	54	54	54	54	54

Figure 8. Offline-data of a resting animal. At 15:47 there are slight adjustments in signal strength and some head changes. The heart rate remains at a low level. This can be interpreted as browsing or grooming in resting posture.



Day: 5.9.
Hour: 3

Minute	41	42	43	44	45	46	47	48	49	50	51	52	53	54
heart frequency: mean	92	86	82	78	82	82	80	80	80	84	78	76	76	74
heart frequency: maximum	96	94	88	84	86	92	90	92	86	128	86	80	86	98
heart frequency: minimum	84	76	78	68	76	74	70	74	76	72	68	72	70	66
head changes (up/down)	---	---	---	---	---	---	---	---	---	1	---	---	---	---
head down (sec)	---	---	---	---	---	---	---	---	---	46	60	60	60	60
max. contin. head down time	---	---	---	---	---	---	---	---	---	46	60	60	60	60
max. contin. head up time	60	60	60	60	60	60	60	60	60	14	---	---	---	---
number of signal adjustments	---	---	---	---	---	---	---	---	---	---	---	---	---	---
signal strength: mean	55	55	55	55	55	55	57	54	55	55	55	55	55	55
signal strength: maximum	55	55	55	55	55	55	57	54	55	55	55	55	55	55
signal strength: minimum	55	55	55	55	55	55	57	54	55	55	55	55	55	55

Figure 9. Offline-data of a resting animal laying its head on the ground (“sleep”) at 3:50.

The interpreted offline-data was compared with synchronous video recordings of three roe deer and 4 red deer. The percentage of falsely classified minutes was between 1.4% and 4.0% for the female roe deer. These errors occurred almost always with short active or inactive bouts under five minutes. Falsely active were situations when the animal lay down and stood up again shortly afterwards. Falsely inactive were situations when the animal stood motionless several minutes (for example standing alert), since the field strength remained unchanged, the head was incessant up and the heart rate was unusually low (alarm bradycardia). The roe buck often stood still for long times, instead of lying down, but showed all signs of inactive behavior, sometimes ruminating while standing. In 13.2% of the offline-data classified as inactive the buck was standing, thereof 40.2% standing and ruminating and 40.2% standing alert.

Estimating the number of activity changes (from active to inactive and vice versa) misclassifications ranged between 11.1% and 16.7%. These errors resulted from short active or inactive phases under five minutes length that weren’t identified. In relation to the total daily activity time these errors could be neglected, yet other parameters such as number of activity bouts or mean duration of activity bouts were influenced.

With red deer the falsely classified minutes were 3.7% and 4.7% for two animals observed under controlled conditions in a smaller enclosure (n=14326 minutes). Food intake was falsely classified in 5.5% of all minutes for animal No. 130 and 18.4% for No. 106. The high values for No. 106 is based on the fact that the head was more up than down while eating from a feeding station in the smaller observation enclosure. It can be expected that the error ratio is less high when the animal is eating grass at ground level which was the case in the large enclosure. From random video recordings (n=480 minutes) in the large enclosure falsely classified minutes lay between 1.1% and 6.7% for three animals. A source of error was also with the dominant male stag (No. 121). In one video observation the old stag lifted his head only twice in 1½ hours during browsing due to the fact that he was accompanied by a younger stag that took over the vigilant behaviour necessary. In such cases the old stag was sometimes falsely classified as being inactive.

To compare daytime and nighttime activity the time span from one hour after sunrise until one hour before sunset was defined as daytime, and one hour after sunset until one hour before sunrise as nighttime. On days with more than 5% missing values (no signal received or signal could not be interpreted correctly) the day was not evaluated for activity. For analysis of bout length only phases with no preceding or following missing values were incorporated. Also the first nine days after capturing and handling the animals were omitted. Such procedure is also recommended by Morellet et al. (2009).

2.4.2. Analysis of the Short-Term Recordings

The online data were suited for making statements about short-term changes of heart rate after applying disturbance stimuli. Both the magnitude of heart rate changes and the time span until the heart rate drops back to the resting values are indicators of the intensity of agitation for the animals. The moment the heart rate attained more than twice the standard deviation of the mean heart rate before the disturbance trial was defined as the outset of the disturbance effect. The ending of the disturbance effect was defined as the moment the heart rate dropped and remained at least one minute between the thresholds of double standard deviation before the trial (Figure 10).

The disturbance intensity was defined as the number of additionally performed heart beats compared to undisturbed behavior and was computed from the area compromising the heart rate curve from outset to ending of the disturbance effect and the mean heart rate before the disturbance trial began (Figure 10). The intensity of disturbance is a particularly important parameter since it is closely connected to the energy expenditure of the animals. Cases with animals changing from inactive to active behavior after the disturbance trial were omitted from analysis since it was not possible to determine the exact ending of the disturbance effect, because heart rate shifted to a higher level when active. The heart rate would fall back under the original threshold only after lying down again, which could be hours later (Figure 10, right diagram).

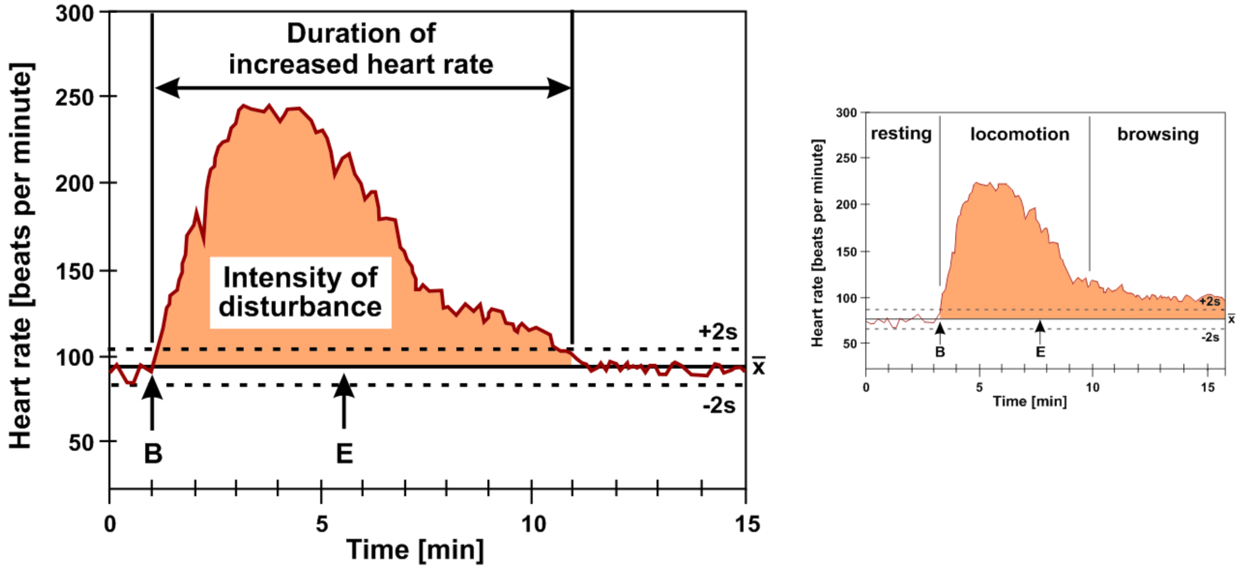


Figure 10. Model of disturbance intensity with heart rate as criterion: heart rate before, during and after a disturbance trial; B = beginning of trial; E = end of trial; shaded area = number of additionally performed heart beats. Large model on left hand shows a situation with the animal in the same state (active or inactive) before and after the disturbance. Small model on the right shows a situation with an inactive animal changing to active behavior after the disturbance. These cases were omitted from heart rate analysis.

2.4.3. Analysis of Video Recordings

The animals were video-recorded during the disturbance trials as well as five minutes (roe deer) to ten minutes (red deer) before and after the trials. An inventory of all exhibited actions of the animals (ethogram) was compiled (Figure 11) and used as the basis for the analysis of the video recordings. The beginning of each change in behavior was written down and the duration to the next change in seconds calculated. Since the clockwork of the videorecorder was daily matched to the computer, the actual behavior could be correlated with the corresponding heart rate.

48 different behavior types were identified, which were later on aggregated to 7 main categories:

- *Lying:* All behavior types in which the animal is lying on the ground are included: lying with and without ruminating, lying with the head on the ground, lying rolled up, while grooming, browsing or checking the surroundings with the sense of smell.
- *Standing:* The animal stands without vigilance behavior. Standing can be with and without ruminating.
- *Standing alert:* The preceding behavior is interrupted and the animal raises its head. Characteristic is increased vigilance, testing the surroundings with the three senses: scent, hearing and sight. The disposition for flight is heightened.
- *Locomotion:* This category includes walking, trotting and running (gallop), but also turning around on the spot and going backwards.
- *Olfactory control:* This behavior is defined as using the sense of smell. Generally the head is lowered, the muzzle moves just above ground level. This behavior pattern can easily be mistaken with foraging, but the mouth stays closed and chewing motion is missing. Also sniffing at higher grasses belongs to this category, in this case the head is held somewhat higher. This behavior can also be displayed while walking or trotting. When controlling the air the head is tilted upwards, sometimes twisting the neck. Only classified for red deer, since roe deer in comparison rarely showed this behavior type (and was then classified under miscellaneous).
- *Food intake:* While browsing the head is lowered, unless higher grasses and twigs are browsed. Contrary to olfactory control the head movements are jerky due to the plucking of plants. Also chewing movements can be seen. When the head is suddenly raised in alertness plant stems often hang from the jaw. Food intake at the feeding station (hay, supplemental pellets, fodder beets) also belongs to this category.
- *Miscellaneous:* Comfort behavior includes grooming the coat with tongue, teeth, hooves and antlers, furthermore shaking the head or whole body, stretching of neck or legs and wallowing. Other types of behavior that were recorded are: scraping, urinating, head rubbing, bark peeling, drinking, bucking, jumping, combating, lip curling and yawning.

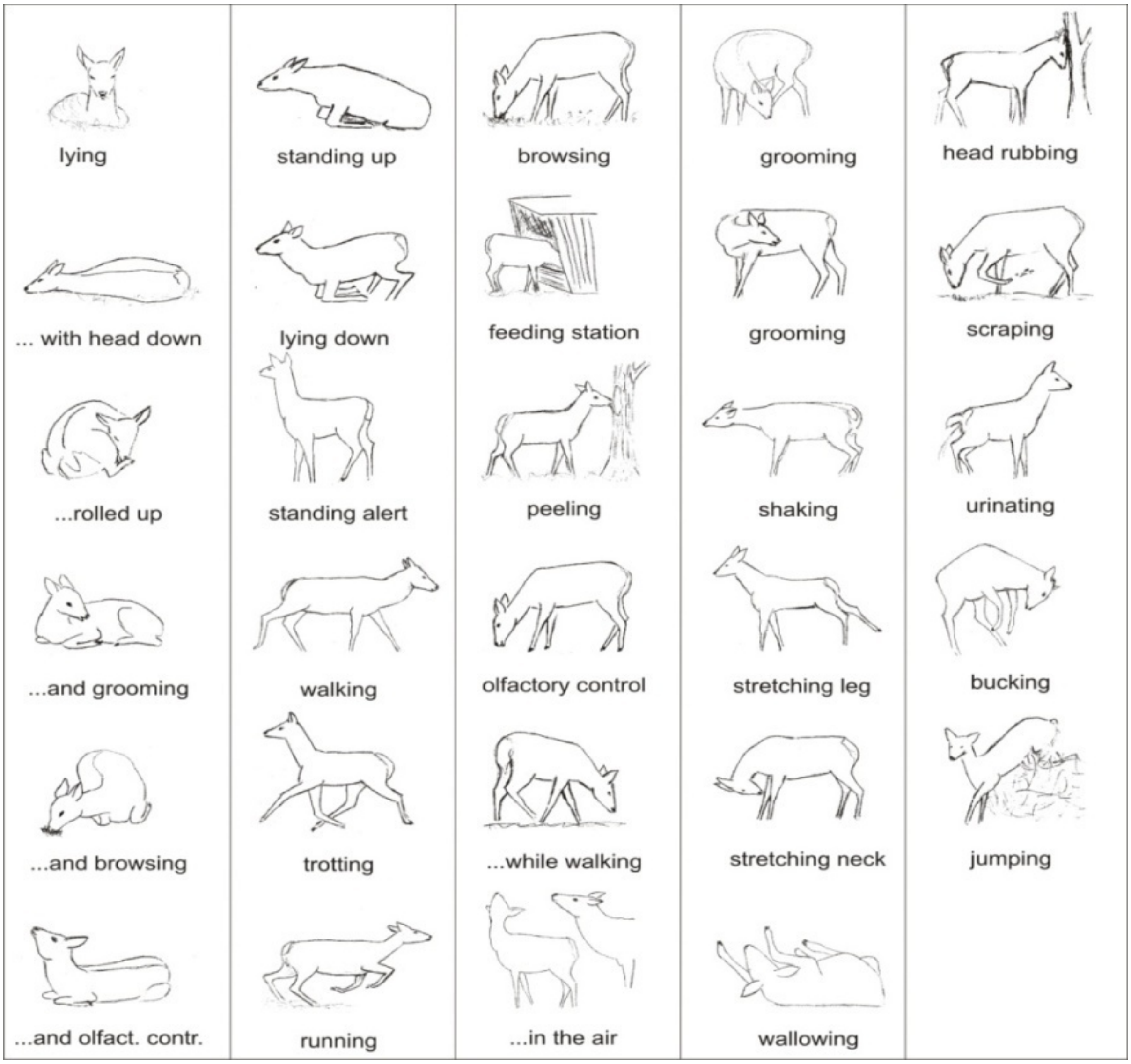


Figure 11. The most common behavioral patterns of roe deer and red deer during the disturbance trials (olfactory control, stretching, wallowing, bucking and jumping were only recorded with red deer). The first column is related to inactive behavior, all other columns to active behavior.

3. RESULTS

First the basic activity patterns of roe and red deer will be presented, afterwards the results of the disturbance trials.

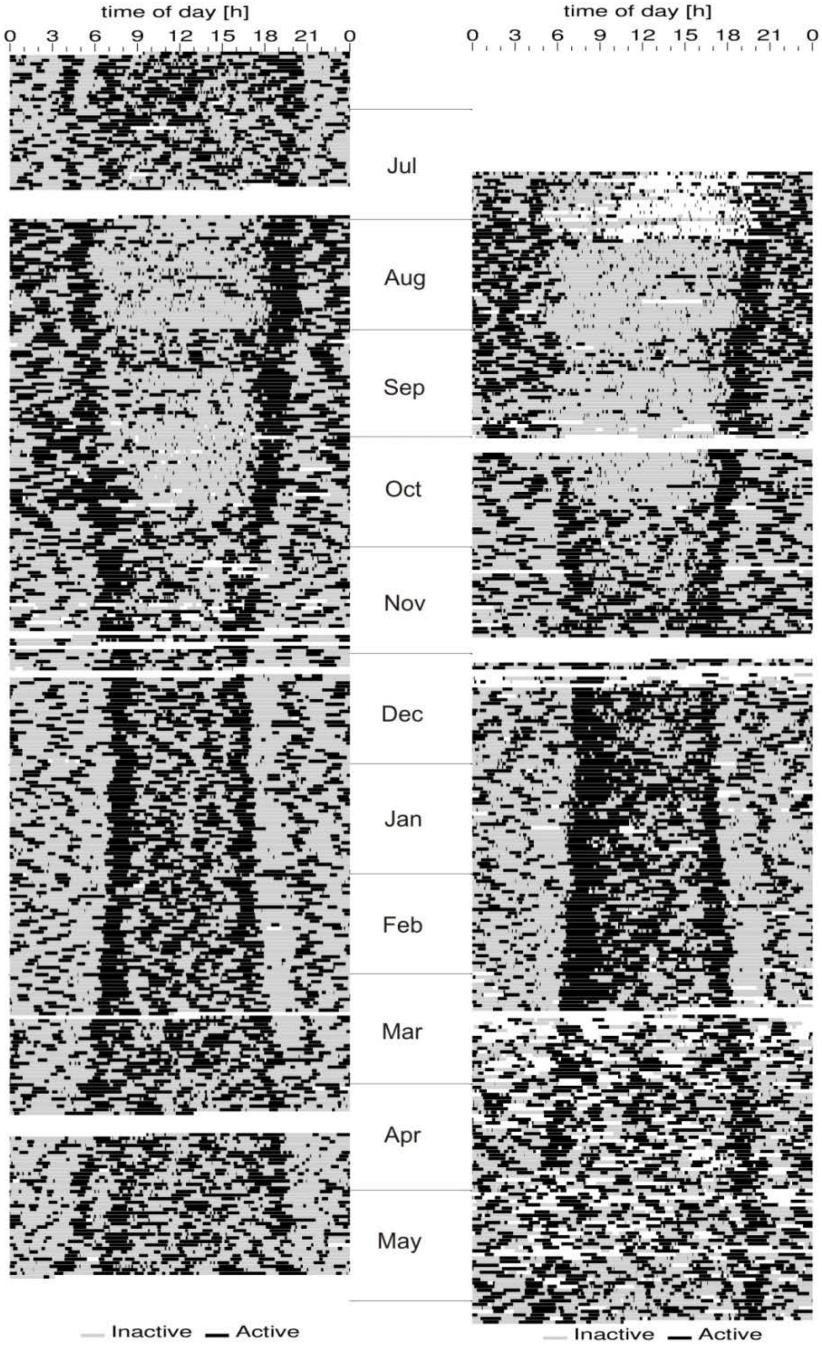


Figure 12. Actograms of two roe deer with a resolution of 1 minute (left: 3-year old male; right: 2-year old female), gray = inactive, black = active, white = missing values.

3.1. Basic Activity and Heart Rate Patterns

3.1.1. Roe Deer

3.1.1.1. Circadian and Seasonal Rhythms of Activity and Heart Rate

All individuals had similar activity patterns. The roe deer showed main activity in the morning and evening twilight. In winter the animals were more active in the daytime than at night. In late summer and early autumn (August-mid October) they were mainly inactive in the daytime (Figure 12 and 13).

Daily activity peaks occurred half an hour after sunrise (82.3% active) and half an hour after sunset (69.6%). Activity minimum was 1½ hours before sunrise (24.9%) and 2½ hours after sunset (23.4%). In average activity was higher at daytime than at night (Figure 14).

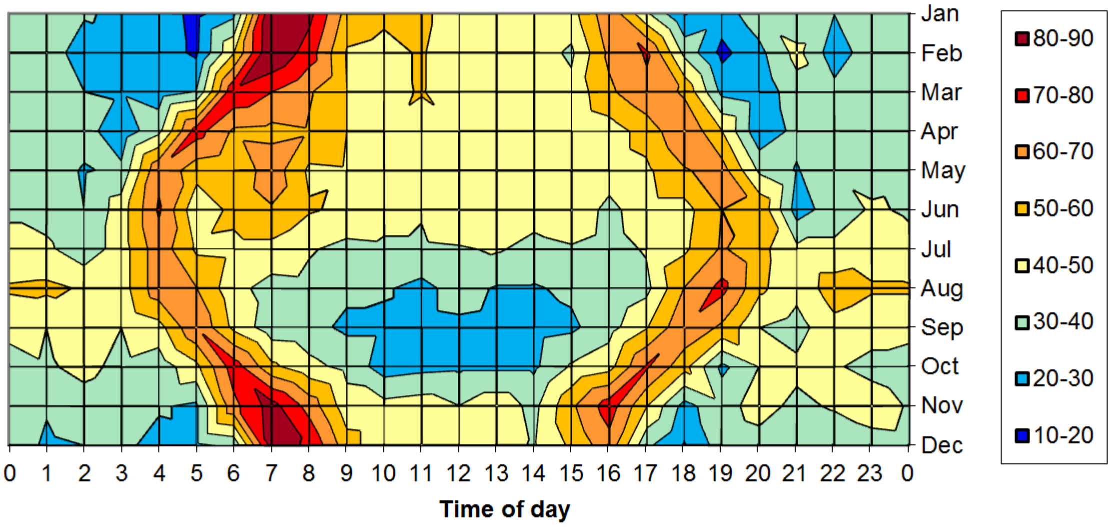


Figure 13. Activity of 14 roe deer (in % of time).

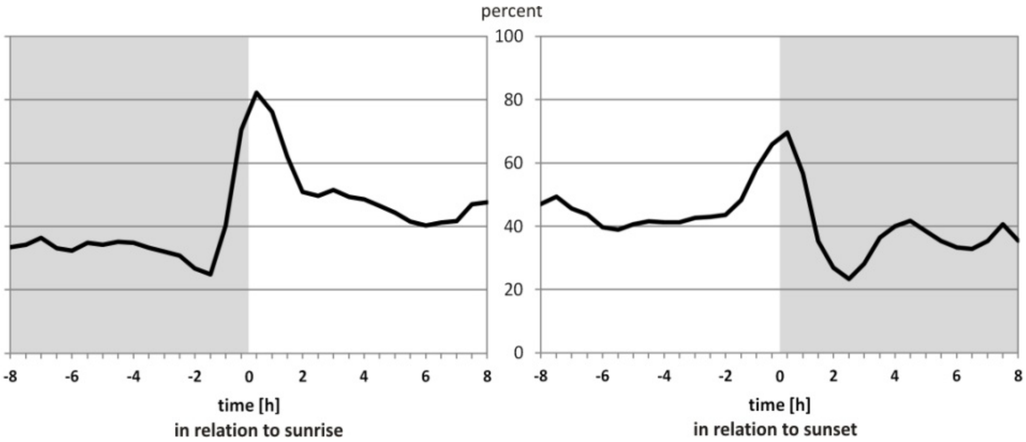


Figure 14. Daily activity of roe deer in relation to sunrise and sunset. Gray shaded areas are night.

The mean monthly activity throughout the year varied greatly among individual roe deer (Figure 15). Roe deer No. 1 (2 year-old female) hardly showed any seasonal fluctuations in activity (39-47%). The animal was mostly kept in a small pen except for September to November when it was transferred to a medium-sized enclosure for disturbance trials. Roe deer No. 3 (3 year-old female) was mainly in a large enclosure and showed great variation in mean monthly activities ranging from 41% in January to 63% in May. The animal was transferred to the medium-sized enclosure for disturbance trials from mid-October until mid-November, which may be the reason for the increase of activity in this time of the year. Male roe deer were in general less active than females (Figure 16). Roe deer No. 22 (3 year-old buck) showed low activity after the rut from August to October (35%) although the buck was involved in the disturbance trials from mid-September to mid-November. Highest activity was in April (49%). Roe buck No. 31 showed little variations ranging from 36% to 45%.

In general the roe deer kept in small pens showed less variation in amount of activity than roe deer in large enclosures (Figure 17).

Although the seasonal changes in activity varied greatly between individuals, all animals showed very similar circadian patterns. In late summer and early autumn roe deer were less active at daytime compared to the rest of the year. They were more active at night in this time of the year (Figure 13).

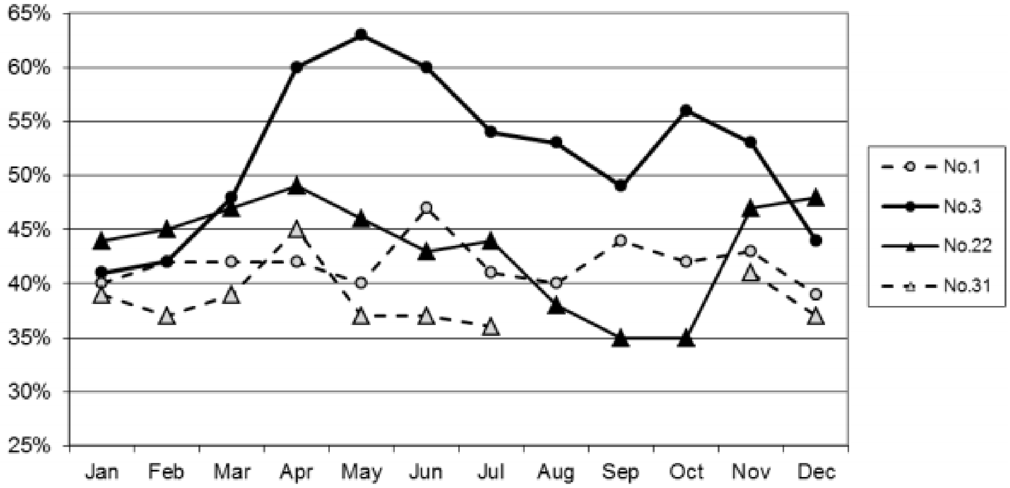


Figure 15. Mean monthly activity (in %) of 4 individual roe deer. (round marks = female, triangle marks = male, dotted line = mainly in small pen, continuous line = mainly in large enclosure). Disturbance trials were carried out from Sep-Nov for Nos. 1 and 22, and Oct-Nov for No.3.

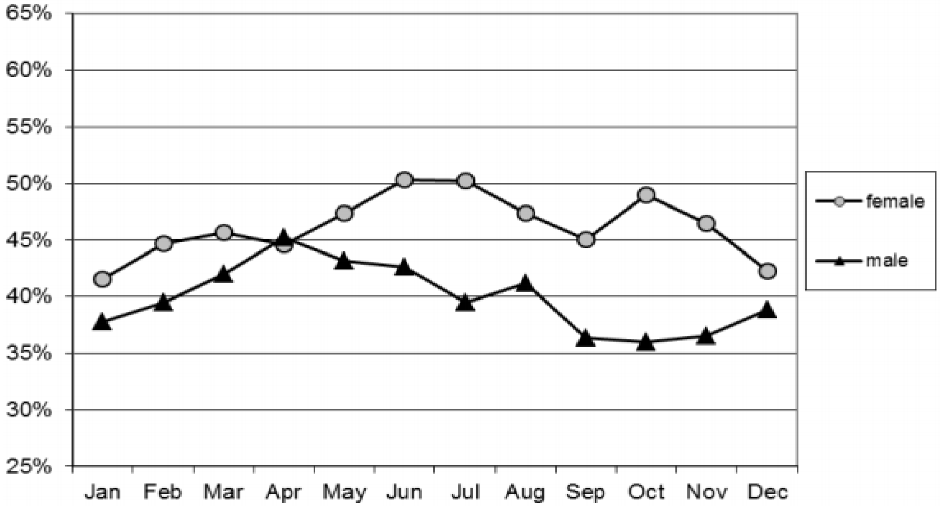


Figure 16. Mean monthly activity (in %) separately for male and female roe deer.

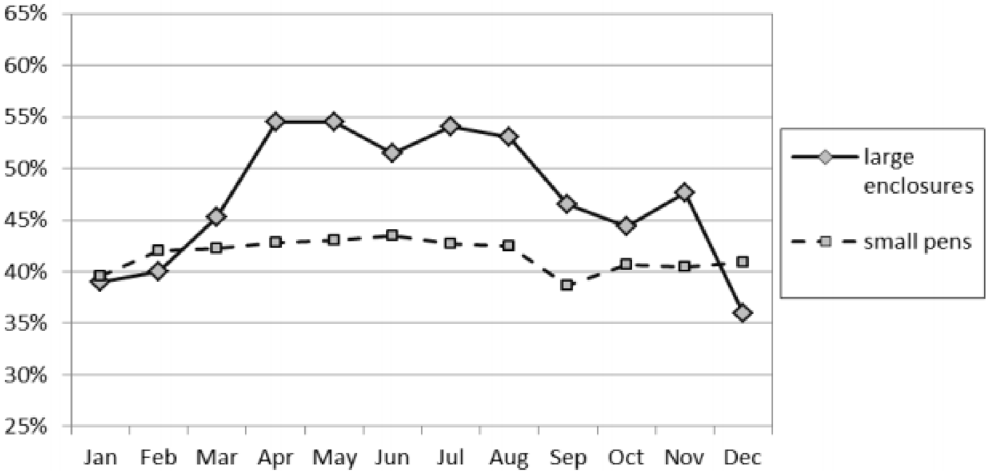


Figure 17. Mean monthly activity (in %) separately for roe deer in large enclosures and in small pens.

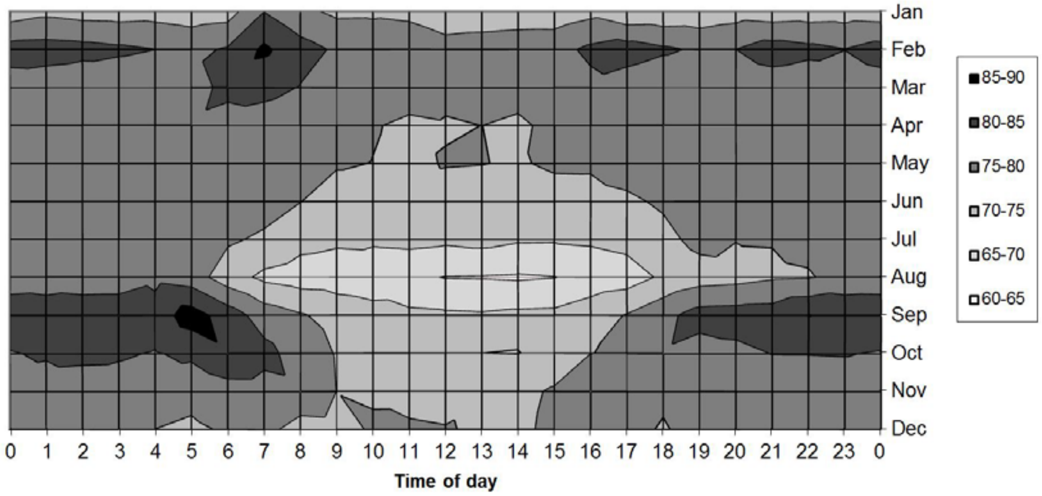


Figure 18. Resting heart rate (beats/minute) of 14 roe deer.

In winter and spring resting heart rate showed very little variations during the day. In late summer and autumn resting heart rate was in contrast much higher at night than at daytime (Figure 18).

3.1.1.2. Influencing Factors on Activity and Heart Rate

A variance analysis was carried out incorporating the input factors daytime, season, sex, size of enclosure, and weekday/weekend (i.e. more/less human activity). All factors had a highly significant influence on activity ($p<0.001$), influence on resting heart rate was significant for all factors except for weekend/weekday. The by far greatest impact was daytime, followed by sex, enclosure type and season.

Roe deer were most active at twilight. In general they were more active during daylight than at night (Table 3).

Table 3. Activity and heart rate of roe deer differentiated by time of day

(twilight = 1 hour before to one hour after sunrise/-set)

	night	twilight	daylight
activity	33.8	64.9	45.9
heart rate	83.8	89.1	81.4
resting heart rate	76.5	76.6	72.4

Table 4. Activity and heart rate of roe deer differentiated by sex

	male	female	total
total activity	39.7	46.0	43.4
daytime activity	41.7	48.9	45.9
night activity	31.8	35.2	33.8
ratio day/night	1.3	1.4	1.4
heart rate	95.2	75.6	83.9
resting heart rate	85.9	67.0	75.0

Altogether does were more active than bucks, yet heart rate of does was lower (Table 4). Both bucks and does were more active during daytime.

Strong interactions exist between daytime and season and between daytime and enclosure type. Roe deer in the large enclosure were in total more active than those in the small pen, yet at daytime activity was higher in the small pens (located next to the research institute with more human activity) (Table 5).

The influence of workdays (with many disturbances) versus weekends (undisturbed) was tested only for daylight time (9 – 15h) when the most disturbances took place (Table 6). Roe deer were more active on weekdays than on weekends (less personal at the research institute and therefore less disturbances). However, the influence on activity was considerably less than the other factors mentioned. Resting heart rate was independent of day in the week (Table 6).

Table 5. Activity and heart rate of roe deer differentiated by enclosure size

	small pen	large enclosure
activity	43.3	47.5
daytime activity	46.4	44.9
night activity	31.2	39.4
ratio day/night	1.5	1.1
heart rate	82.8	83.7
resting heart rate	73.0	72.7

Table 6. Activity and heart rate of roe deer differentiated by weekday/ weekend

	weekday	weekend
day activity (9h-15h)	43.8	38.4
heart rate	82.4	80.3
resting heart rate	73.0	73.1

Total activity was highest during fawning and rut (Table 7). Daytime activity was highest in spring (establishment of territories) and during fawning and very low post rut. In rut, and especially after rut roe deer were more nocturnal.

Table 7. Activity and heart rate of roe deer differentiated by season
(spring = March/April, fawning period = May/June, rut = July/mid August,
post rut = mid August - October, winter = November – February)

	spring	fawning	rut	post rut	winter
activity	43.2	47.4	46.5	41.8	42.5
daytime activity	49.1	51.4	42.7	31.8	48.9
night activity	28.8	32.8	44.2	44.3	30.4
ratio day/night	1.7	1.6	1.0	0.7	1.6
heart rate	78.6	81.6	74.7	86.3	81.8
resting heart rate	69.5	71.4	65.4	76.0	73.8

Particularly for roe bucks during rut and post rut the ratio daytime/nighttime activity was negatively correlated with ambient temperature. For the other seasons correlation was negligible (Table 8, Figure 19).

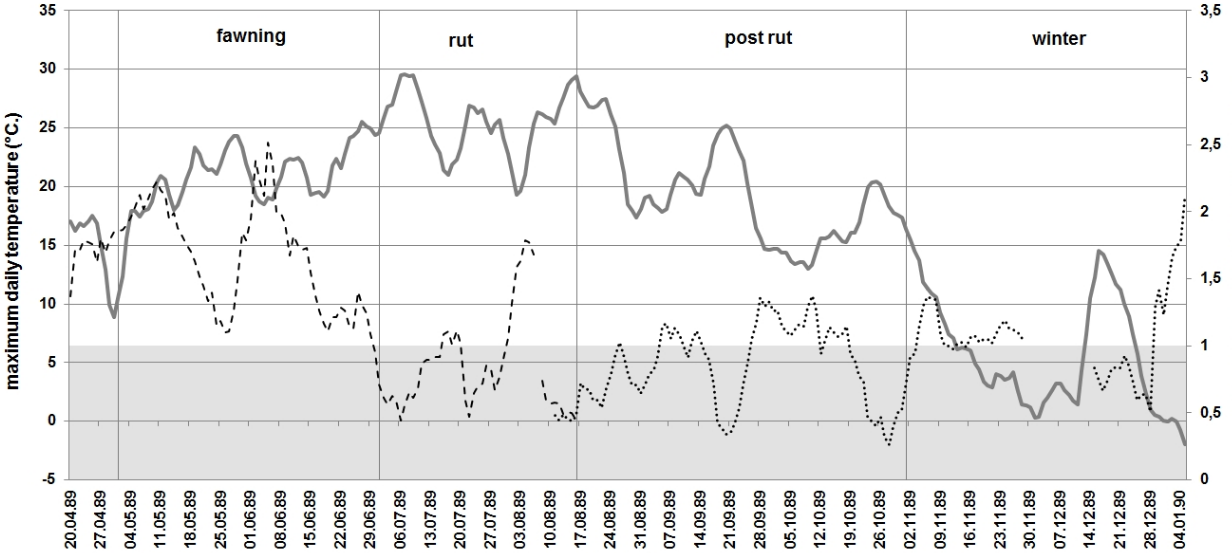


Figure 19. Ratio daytime/nightime activity of two roe deer individuals plotted against maximum daily air temperature. Values are 5-day running means. Gray full line: temperature, dashed line: roe deer No. 27, dotted line: roe deer No. 21. Values under 1 indicate nocturnal, above 1 diurnal behavior.

Table 8. Pearson product-moment correlation coefficient of ratio daytime/nighttime activity of roe deer and daily maximum air temperature, averaged for all individuals

	spring	fawning	rut	post rut	winter
female	-0.07	-0.20	-0.17	-0.29	-0.02
male	0.12	-0.10	-0.60	-0.51	-0.08
total	0.01	-0.15	-0.42	-0.41	-0.06

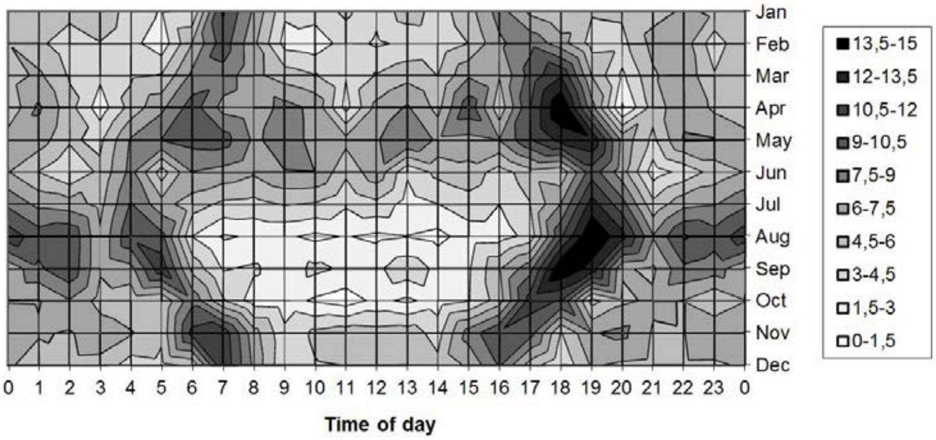


Figure 20. Food intake (index) of 5 roe deer. Values for March were interpolated from February and April.

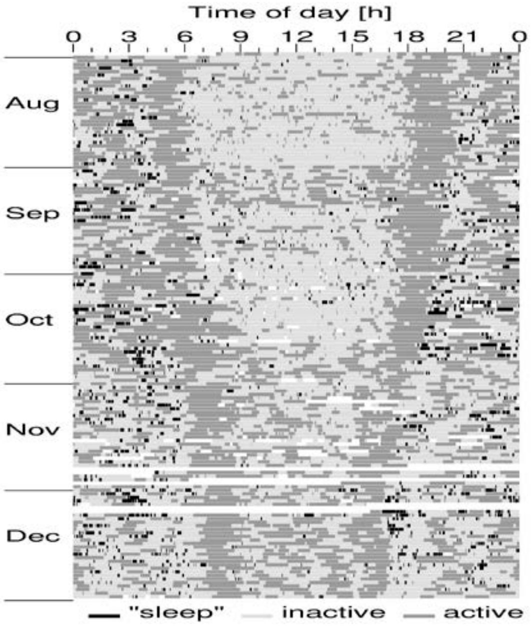


Figure 21. Example of an actogram including sleep phases (2-year old female), black = sleep phases, light gray = inactive phases without sleep, dark gray = active, white = missing value.

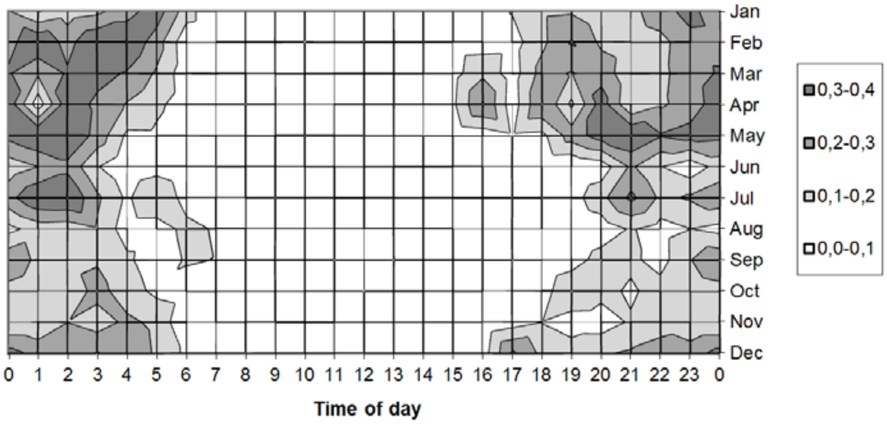


Figure 22. Sleep (in %) of 5 roe deer. Values for March were interpolated from February and April.

Activity for the time periods night (21-3), morning (3-9), daytime (9-15) and evening (15-21) was compared for full moon (±2 days) and new moon (±2 days). No significant differences could be found for roe deer in any of the time periods (Mann-Whitney-U-Test).

3.1.1.3. Food Intake

Feeding of roe deer was defined as being active with the head at least 20 sec/min down. This can be only seen as index of feeding, not as absolute feeding time. Feeding patterns are similar to overall activity patterns (Figure 20). Whereas in winter feeding was more evenly spread during daytime and at night, in April and May distinct peaks can be seen at 1:00, 6:00 (dawn), 9:00, 13:00, 15:00, 18:00 (dusk) and 22:00.

3.1.1.4. Sleep

"Sleep" was defined as lying (inactive) with the head on the ground. Sleep could only be discriminated in animals with implanted tilt switch or with repeater system (Table 1 in methods section).

Sleep mostly occurred only in the night even in August and September when the deer were mostly inactive in the daytime (Figs. 21 and 22).

3.1.2. Red Deer

3.1.2.1. Circadian and Seasonal Rhythms of Activity and Heart Rate

Just as roe deer the red deer showed strong crepuscular activity. Whereas roe deer had higher activity in the dawn than at dusk, red deer were more active at dusk (Figure 23 and 19). In summer red deer had increased activity in late afternoon, and most of the year also around midnight. Only in the short nights of July there was no increased phase of activity.

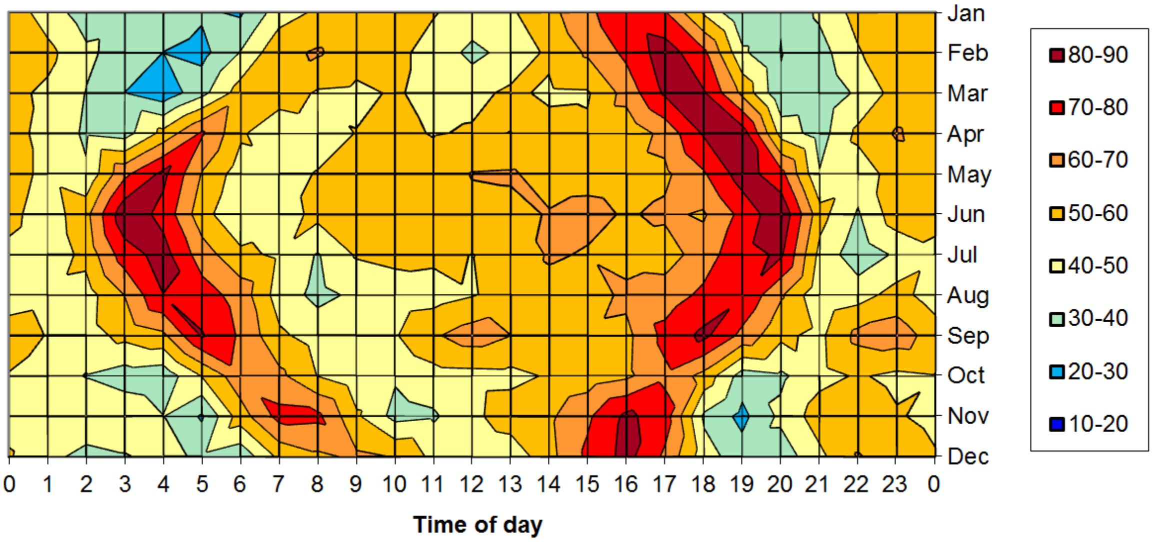


Figure 23. Activity (in %) of 8 red deer.

Daily activity peaks occurred half an hour after sunrise (71.1% active) and half an hour after sunset (84.8%). Activity minimum was 2 hours before sunrise (34.9%) and 3 hours after sunset (34.6%). In average activity was higher at daytime than at night (Figure 24).

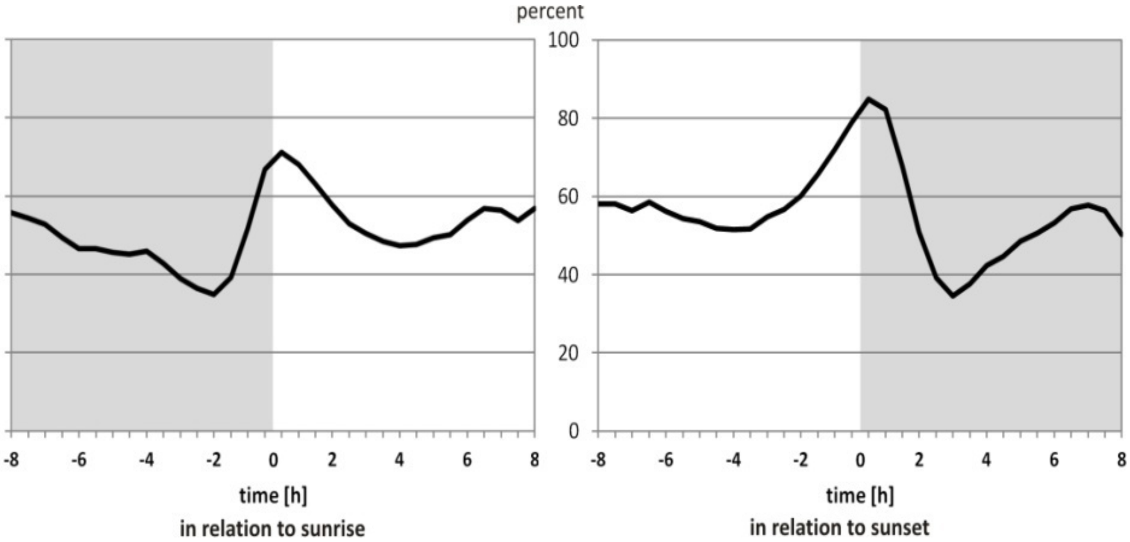


Figure 24. Daily activity of red deer in relation to sunrise and sunset. Gray shaded areas are nighttime.

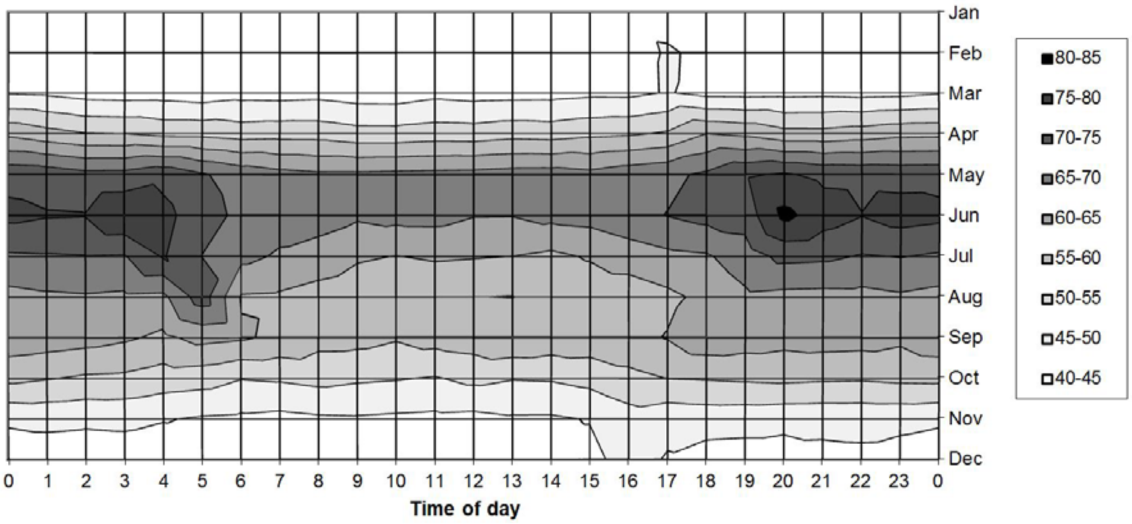


Figure 25. Resting heart rate (beats/minute) of 8 red deer.

Resting heart rate was considerably higher in summer than in winter (Figure 25). Whereas mean resting heart rate was about 44 beats/minute from December to February, resting heart rate averaged 71 beats/minute in June.

3.1.2.2. Influencing Factors on Activity and Heart Rate

Red deer were most active at twilight (Table 9). Mean heart rate was higher at dawn and dusk due to the activity peaks in this time.

Table 9. Activity and heart rate of red deer differentiated by time of day
(twilight = 1 hour before to one hour after sunrise/-set)

	night	twilight	daylight
activity	46.4	74.4	54.5
heart rate	59.0	66.8	61.6
resting heart rate	54.1	55.0	55.4

Altogether hinds were more active than stags, especially in the daytime (Table 10). The ratio of daytime activity and night activity was higher for hinds. In contrast to hinds, stags were more nocturnal.

Table 10. Activity and heart rate of red deer differentiated by sex

	male	female	total
total activity	46.0	56.9	53.8
daytime activity	39.2	60.5	54.5
night activity	47.3	46.0	46.4
ratio day/night	0.8	1.3	1.2
heart rate	61.3	61.6	61.4
resting heart rate	53.7	56.4	54.8

Total activity was highest during calving, summer and rut, and lowest in winter (Table 11). Unlike roe deer the ratio daylight activity to night activity was quite balanced throughout the year.

Table 11. Activity and heart rate of red deer differentiated by season
(spring = March/Mid. May, calving period = Mid May/Mid. June, summer = Mid June-August, rut = September-Mid October, post rut = Mid October - November, winter = December – February)

	spring	calving	summer	rut	post rut	winter
activity	52.8	61.6	59.6	58.3	51.3	49.2
daytime activity	53.2	59.5	57.2	57.7	51.6	53.0
night activity	45.0	53.1	50.1	51.7	44.9	42.8
ratio day/night	1.2	1.1	1.1	1.1	1.1	1.2
heart rate	60.6	80.1	73.3	65.9	55.3	48.2
resting heart rate	54.2	70.7	64.6	56.7	48.0	43.5

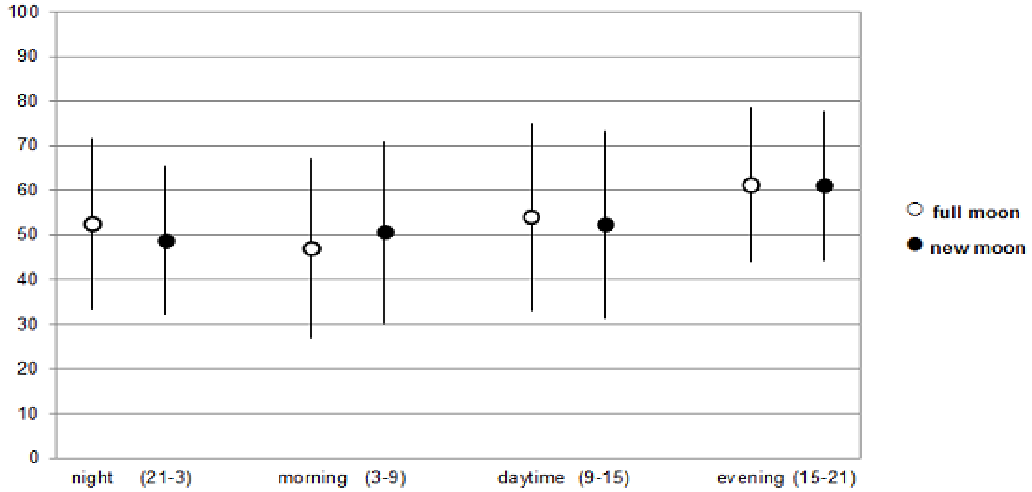


Figure 26. Mean activity in % of red deer at full moon ±2 days and new moon ±2 days for four time periods (n=511 days full moon, 572 days new moon). Bars indicate standard deviation. Differences for night and morning are significant.

Activity for the time periods night (21-3), morning (3-9), daytime (9-15) and evening (15-21) was compared for full moon (±2 days) and new moon (±2 days). In full moon nights red deer were more active (Mann-Whitney-U-Test, $p < 0.01$) than in new moon nights and in the morning of full moon nights red deer were less active ($p < 0.001$). No significant differences could be found for daytime and evening hours (Figure 26).

3.1.2.3. Food Intake

Feeding of red deer was defined as being active with the head at least 40 sec/min down. Feeding patterns are similar to overall activity patterns. Highest feeding activity was mainly in the evening (Figure 27).

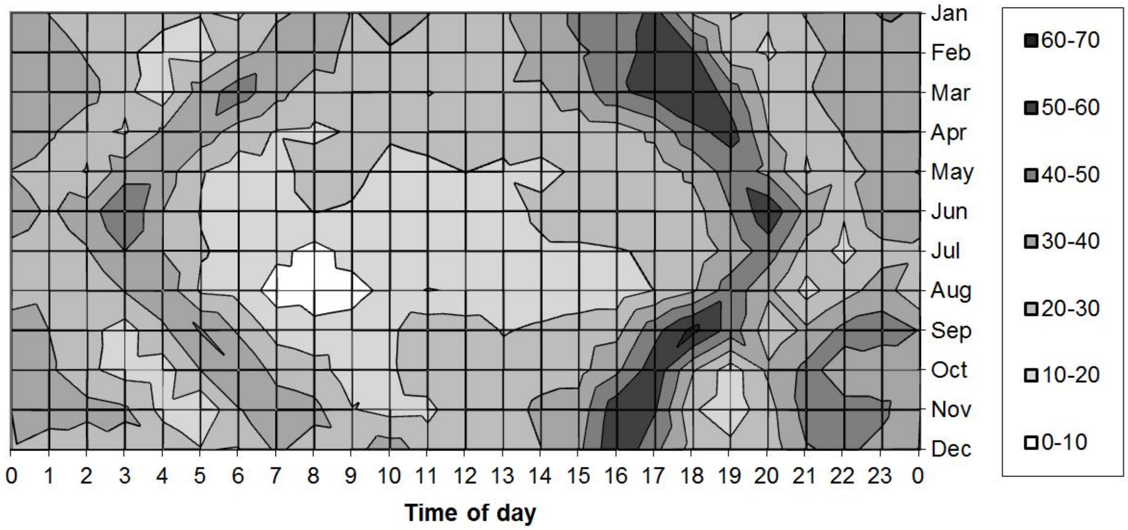


Figure 27. Feeding (in %) of 8 red deer.

3.1.2.4. Sleep

Sleep (lying with head on the ground) covered only a few percent of the daily time budget (highest in October and lowest in May, Figure 28).

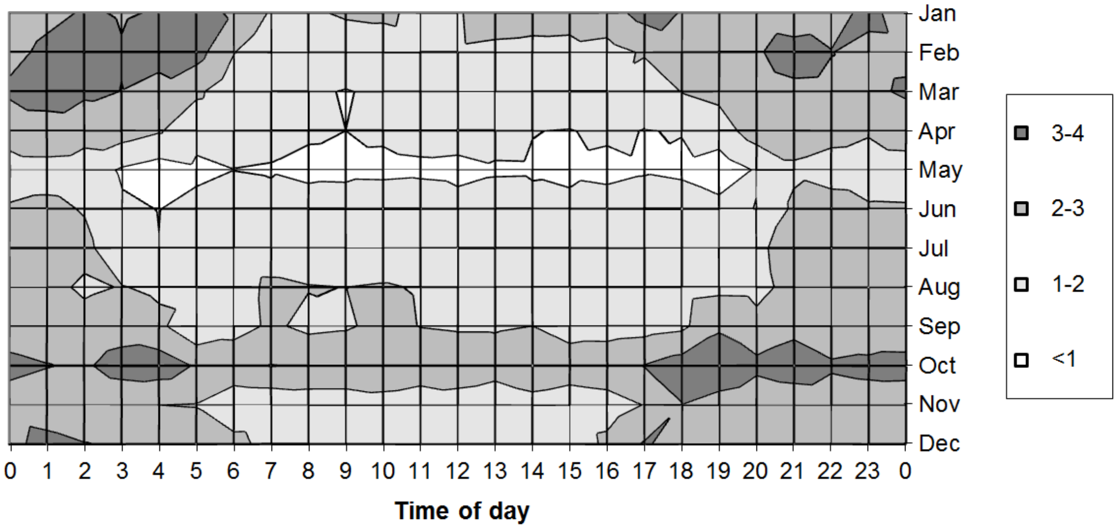


Figure 28. Sleep (in %) of 8 red deer.

3.2. Disturbance Trials

3.2.1. Roe Deer

Since the roe deer showed an abrupt change in general activity in autumn, first being mainly nocturnal and suddenly changing to diurnal behavior on Oct. 21th, the disturbance trials were interpreted separately for both time periods.

3.2.1.1. Choice of Bedding Site

The resting sites of the animals were located in the video recordings. With one exception the three roe deer always bedded in or next to the unmown grass patch from Sept. 20th until Oct. 24th noon (Figure 29). After this they rarely lay down in this field, but rather preferred either the small spruce stand or the northeast corner of the enclosure as resting site (Figure 29).

When disturbed in early autumn the roe deer always returned to the large grass patch where they had bedded before the disturbance trial. In late autumn in contrast they chose a new bedding place in 35.3% of the cases when they were disturbed.

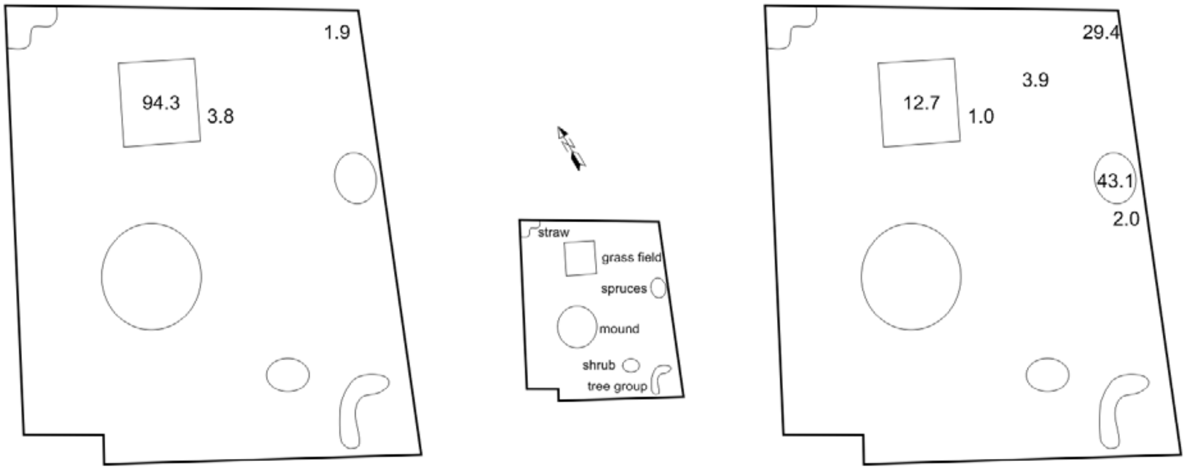


Figure 29. Distribution of roe bedding sites in percentage. Left: Sept.10th to Oct.24th, noon (n = 53); right: Oct.24th, noon to Nov.18th (n=102).

3.2.1.2. Activity

Analyses of roe deer were done separately for early autumn (Sept.10 - Oct.20) and late autumn (Oct.21- Nov.18).

Circadian Rhythm

No difference was found in daily activity rhythms between days with disturbance trials (Figure 30) and days without (Figure 31) (Kruskal-Wallis-Test).

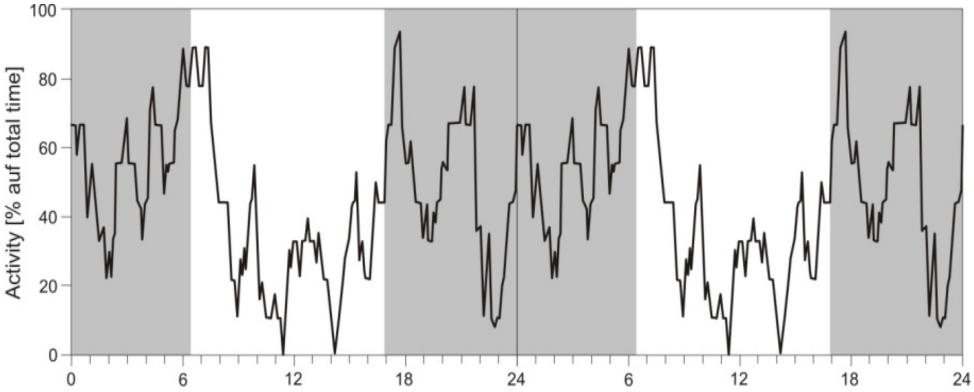


Figure 30. Daily activity pattern of roe deer No. 1 on undisturbed days. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

Total Activity

Both roe deer Nos. 1 and 21 were mainly nocturnal in early autumn, independent if disturbance trials were held on that day or not (Tables 12 and 13). The roe buck was less active than the doe (Mann-Whitney-U-Test, $p < 0.05$), both at daytime and in 24 hours. From October 21st on both animals showed an increase in daytime activity ($p < 0.05$). Also roe deer No. 3, which was brought into the enclosure on October 25th was more active at daytime. Contrary to the roe buck ($p < 0.001$) roe deer No. 1 did not change its total amount of activity from early to late autumn. Roe deer No. 3 was more active than the other two deer ($p < 0.01$).

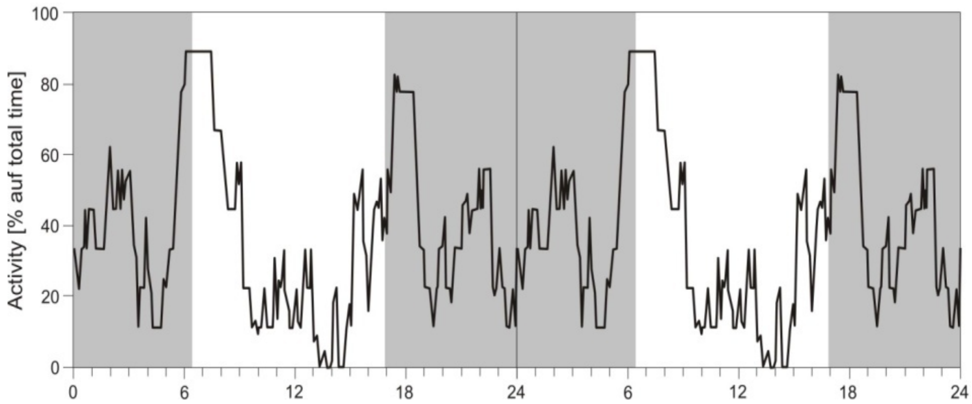


Figure 31. Daily activity pattern of roe deer No. 1 on days with disturbance trials. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

Table 12. Share of time roe deer were active during 24 hours

(No. = animal number, n= number of days, med = median,

x̄ = arithmetic mean, s = standard deviation, min-max = extrema)

Season	No.	Days without disturbance trials					Days with disturbance trials				
		n	med	x̄	s	min-max	n	med	x̄	s	min-max
Early autumn	1	12	42.4	40.2	7.5	39.2-53.2	15	39.8	40.7	5.9	32.5-52.6
	22	9	29.1	28.4	4.6	19.9-35.9	7	28.0	28.2	4.5	27.0-36.5
Late autumn	1	7	43.7	42.4	4.3	33.8-47.4	14	41.6	43.0	5.2	33.9-53.0
	22	6	36.6	40.9	5.9	35.6-50.0	17	43.3	43.6	7.0	31.8-62.9
	3	4	53.0	51.6	3.5	46.5-54.1	15	54.5	54.9	3.9	54.2-60.8

Table 13. Share of time roe deer were active during daytime

(No. = animal number, n= number of days, med = median,

x̄ = arithmetic mean, s = standard deviation, min-max = extrema)

Season	No.	Days without disturbance trials					Days with disturbance trials				
		n	med	x̄	s	min-max	n	med	x̄	s	min-max
Early autumn	1	12	25.9	29.8	14.5	11.2-60.5	15	28.3	28.1	8.8	14.7-50.1
	22	9	17.5	16.5	5.9	0.5-26.8	7	12.3	14.0	6.3	7.7-24.7
Late autumn	1	7	52.8	49.9	8.3	35.2-59.5	14	48.3	49.9	7.7	63.5-37.6
	22	6	44.1	45.2	7.4	36.0-53.3	17	50.6	49.5	8.0	31.2-62.0
	3	4	57.6	56.4	9.5	46.3-64.8	15	63.5	62.0	7.5	51.9-71.7

Both the total activity as well as the amount of daytime activity was not altered by disturbance trials in any of the three roe deer, neither in early nor in late autumn (Tables 12 and 13).

Number and Length of Resting Phases

In early autumn the roe deer had only slightly shorter resting phases on days with disturbance trials (Table 14), whereas in late autumn the mean duration of resting phases was considerably shorter (Kruskal-Wallis-Test).

With increasing number of disturbance trials the resting phases shortened (Table 14). Likewise the number of resting phases at daytime increased with increasing number of disturbance trials (Table 15). A significant difference (Mann-Whitney-U-Test) could only be found in late autumn. The number of resting phases did not differ significantly between early and late autumn on undisturbed days.

Table 14. Duration of diurnal resting phases of roe deer (in minutes) on days without, with few (2-4) and with many (5-10) disturbance trials

(No. = animal number, n= number of resting phases, $\bar{x}$ = arithmetic mean of duration, s = standard deviation, min-max = extrema)

		no disturbance trials				few disturbance trials				many disturbance trials			
Season	No.	n	$\bar{x}$	s	min-max	n	$\bar{x}$	s	min-max	n	$\bar{x}$	s	min-max
Early autumn	1	21	86	65	4-276	33	70	51	3-202	69	65	47	4-207
	22	35	108	114	6-408	11	133	122	10-415	53	85	88	3-367
Late autumn	1	25	78	41	5-151	19	51	39	7-108	63	43	39	1-155
	22	31	87	52	6-167	46	43	35	5-138	104	33	27	2-108
	3	14	56	37	15-139	15	39	39	4-110	63	31	27	3-91

Table 15. Number of diurnal resting phases of roe deer on days without, with few (2-4) and with many (5-10) disturbance trials

(No. = animal number, n= number of days, $\bar{x}$ = arithmetic mean of number resting phases/day, s = standard deviation, min-max = extrema)

		no disturbance trials				few disturbance trials				many disturbance trials			
Season	No.	n	$\bar{x}$	s	min-max	n	$\bar{x}$	s	min-max	n	$\bar{x}$	s	min-max
Early autumn	1	7	6.0	2.8	3-9	4	8.3	1.3	7-10	7	8.0	2.0	6-11
	22	9	7.6	3.4	3-18	2	6.0	0	6	7	7.6	2.0	5-11
Late autumn	1	6	4.5	0.8	4-6	3	6.3	1.5	5-8	7	8.3	2.4	6-12
	22	6	5.3	2.0	2-8	7	7.3	2.2	5-11	11	9.6	3.4	6-18
	3	3	4.7	1.2	4-6	2	7.5	0.7	7-8	8	7.4	2.1	6-10

Resting Phases during the Course of the Day

Length of resting phases was shorter in the morning and evening hours compared to daytime and at night.

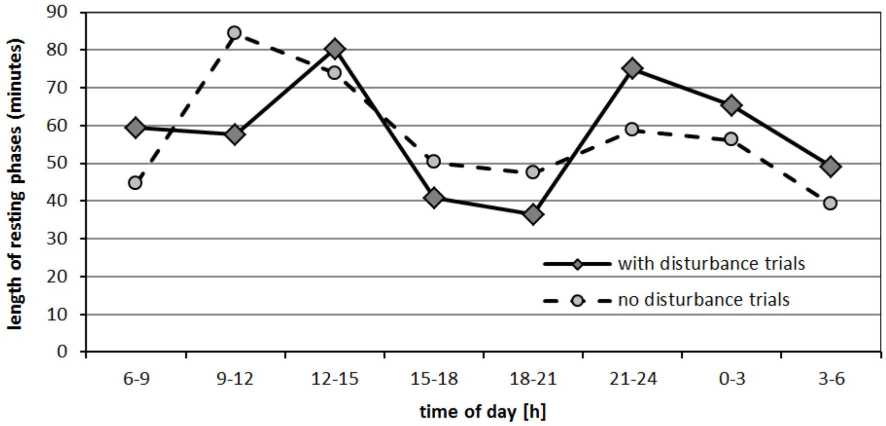


Figure 32. Mean length of resting phases (in minutes) of roe deer during the course of the day on days with and days without disturbance trials in early autumn.

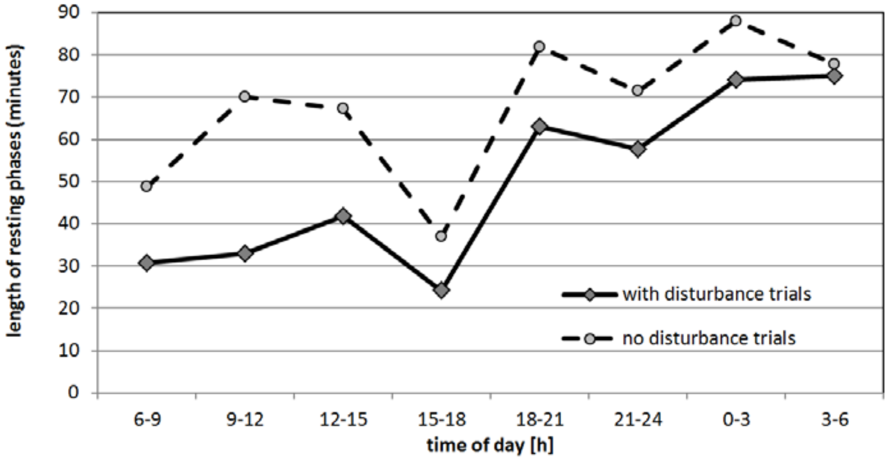


Figure 33. Mean length of resting phases (in minutes) of roe deer during the course of the day on days with and days without disturbance trials in late autumn.

In early autumn no significant differences were found between days with and days without disturbance trials (Figure 32), whereas in late autumn daylight (9-15) resting phases were shorter on days with disturbance trials (Figure 33).

Activation through Disturbance Trials

"Activation" was defined as cases in which an animal`s resting phase is interrupted due to a disturbance and the animal changes over to active behavior. "Activation length" is the length of time an activated animal spends before lying down again. Also with disturbance trials in which video recordings were missing, the activation time could easily be recognized in the transmitted offline data. Disturbance trials in which the animals inevitably had to escape (e.g. the observed animal was lying on the predetermined route of the walking circuit), were omitted from the analysis of activation.

The association of activation among the studied roe deer was rather low in early autumn (Cole's coefficient of association = +0.38 ± 0.11 between roe deer Nos. 1 and 22). The same applies for late autumn with the coefficients lying in a range between +0.22 ± 0.15 (Nos. 22 and 3) and +0.56 ± 0.18 (Nos. 1 and 3).

Influence of Daytime and Season on Activation of Roe Deer

Both in early and late autumn activation was influenced by time of day (χ^2-Test, $p < 0.05$). The roe deer could be more easily activated in the morning and evening hours than at noon (Figure 34). Roe deer was also more frequently activated in late autumn (55.4%) than in early autumn (27.3%, χ^2-Test, $p < 0.001$).

Dependence of Roe Deer Activation on Type of Disturbance

In early autumn there appears to be a difference of activation frequency by optical (31.4%) and acoustical stimuli (18.8%), yet this discrepancy was not statistically significant. In late autumn roe deer were significantly more often activated by optical (68.0%) than by acoustical stimuli (21.4%). Furthermore activation by optical stimuli were more frequent in late than in early autumn, whereas acoustical stimuli did not show a significant difference between these two time periods (χ^2-Test).

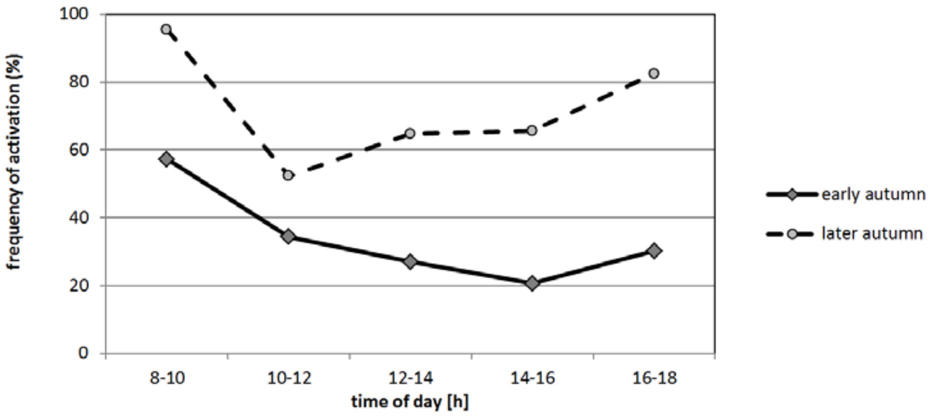


Figure 34. Activation through disturbances in dependence on daytime in early and late autumn. The relative frequency of activation is pooled for two roe deer in early autumn and three roe deer in late autumn.

Table 16. Activation (in %) in dependence on disturbance type and season.
Numbers of samples are specified in brackets respectively for early and late autumn

Disturbance type (*n*)	Early autumn	Late autumn
Round tour of single person (21/6)	19.0	66.7
Round tour of person with dog (11/8)	54.5	100.0
Round tour of group of persons (14/-)	92.9	---*
Round tour with horse(s) (-/6)	---*	66.7
Hang-glider (-/13)	---*	76.9
Tractor (5/10)	20.0	40.0
Ascent of raised blind (12/5)	0.0	40.0
Feeding (23/28)	13.0	71.4
Radio music (9/11)	22.2	9.1
Dog barking (2/11)	0.0	0.0
Chain saw (11/9)	9.1	0.0
Gunshot (17/10)	23.5	80.0

*corresponding trials were not carried out.

Both in early and late autumn the type of disturbance stimuli had different intense effects on activation (χ^2-Test). Generally activation was more easily provoked by the same disturbance type in late than in early autumn (Table 16).

Duration of Activation

Individual differences in the length of activation between single roe deer could not be identified, neither in early nor in late autumn (Kruskal-Wallis-Test). In early autumn length of activation was on average 2.7 minutes (median 1 min), in late autumn about 26 minutes (median 16 min.). The difference was highly significant (Kruskal-Wallis-Test, $p < 0.0001$). The duration of activation was independent of the length of the resting phase directly before it. Also there was no relationship between the type of disturbance and the length of the provoked activity phase following.

Yet there was a close connection between time of day and duration of activation (Figure 35).

The lengths of active bouts following activation were longer in morning and late afternoon and shorter at noon in late autumn. But these differences were not statistically significant, probably owing to the small number of samples. The activation initiated by feeding is presumably not responsible for the increase of activation length between 14 and 16h, as the duration of activation caused by feeding and the duration brought about by other disturbance types did not differ significantly for this time period (Mann-Whitney-U-Test).

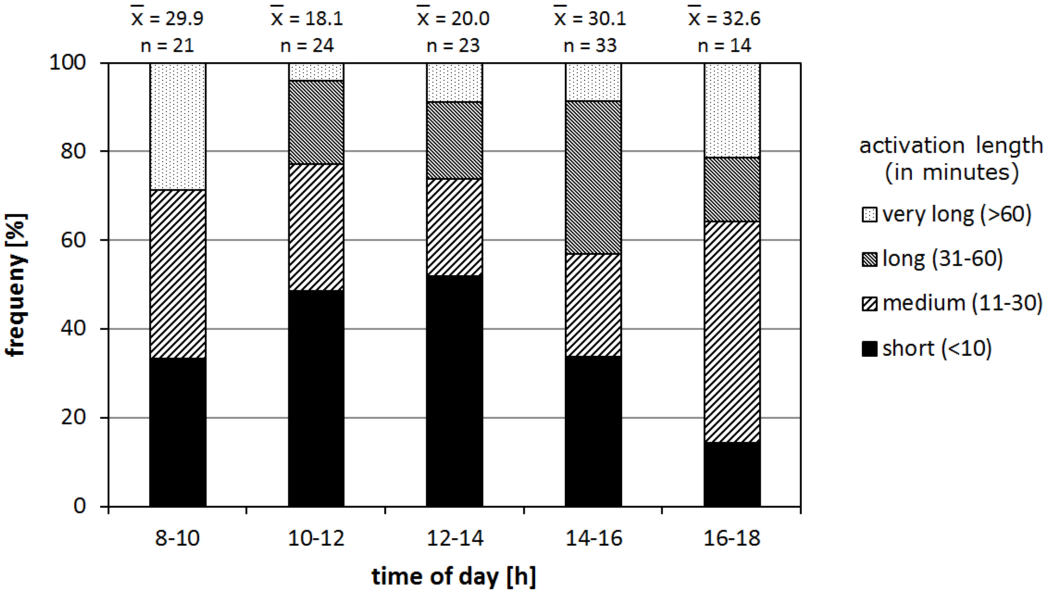


Figure 35. Dependence of activation length on time of day averaged for three roe deer. Above the column the number of samples and the mean duration of activation (in minutes) for each class are specified.

It was also compared to which extent the duration of activation differed between two simultaneously activated roe deer, to draw conclusions on synchronization of behavior. The variation between the length of activation of single roe deer was comparatively high (Table 17).

Mostly the roe buck (No. 22) had lain down at first, in 68.8% of all cases before roe deer No. 1 and in 76.2% of the cases before No. 3. Roe deer No. 3 mostly had lain down as last, only 29.4% of the cases it had lain down before No. 1.

Table 17. Variation in duration of activation (in minutes) between two roe deer

Animal Nos.	n	median	$\bar{x}$	s	extrema
1/22	28	5	17.2	26.4	0-87
1/3	17	14	25.8	29.9	1-89
22/3	21	15	33.0	40.0	1-162

Dependence of Duration of Activation on Type of Disturbance

No significant differences in length of activation of roe deer could be found between varying disturbance stimuli. Generally there was also no difference between duration of activation provoked by optical or by acoustical stimuli.

3.2.1.3. Behavior

The behavioral patterns after disturbance trials were dissected in minute entities and compared with the behavior before applying the disturbance stimuli.

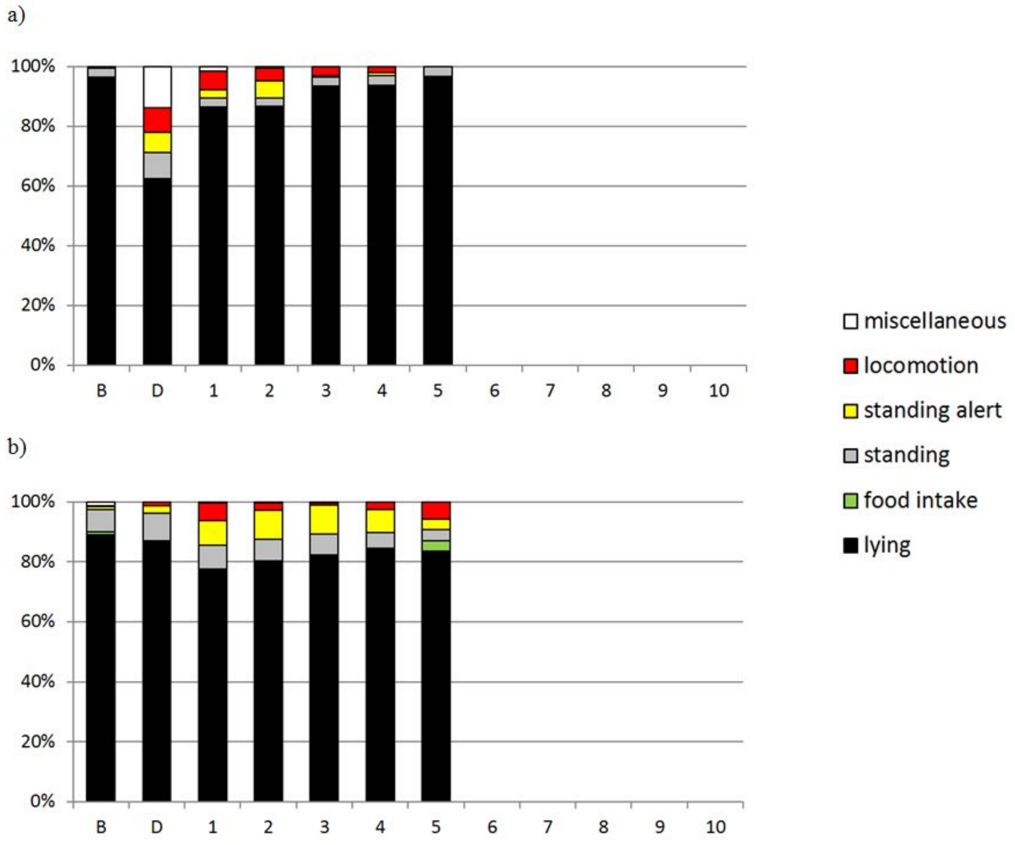


Figure 36. Behavioral pattern of roe deer Nos. 1 and 22 in early autumn (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after a) optical disturbances trials (504 minutes observation time in total) and b) acoustical disturbances trials (315 minutes observation time in total).

Undisturbed (normal) behavior after disturbance trials returned in the moment when the behavioral pattern did not differ anymore from the pattern before the disturbance. The relative share of time for each behavioral class was calculated for each minute after the disturbance and opposed to the corresponding values of the undisturbed behavior before the disturbance. 250 disturbance trials were analysed. For the time period before disturbance trials 1065 minutes were evaluated, for the period after trials 1142 minutes were drawn upon. In early autumn the behavior of roe deer was only marginally affected (Figure 36).

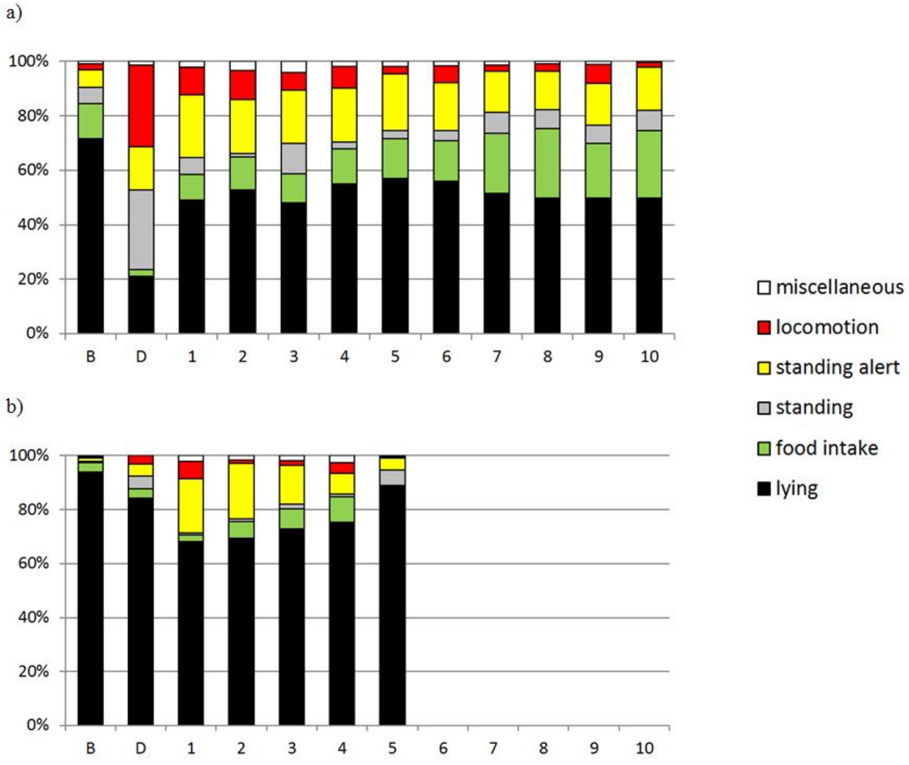


Figure 37. Behavioral pattern of three roe deer in late autumn (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after a) optical disturbances trials (1275 minutes observation time in total) and b) acoustical disturbances trials (317 minutes observation time in total).

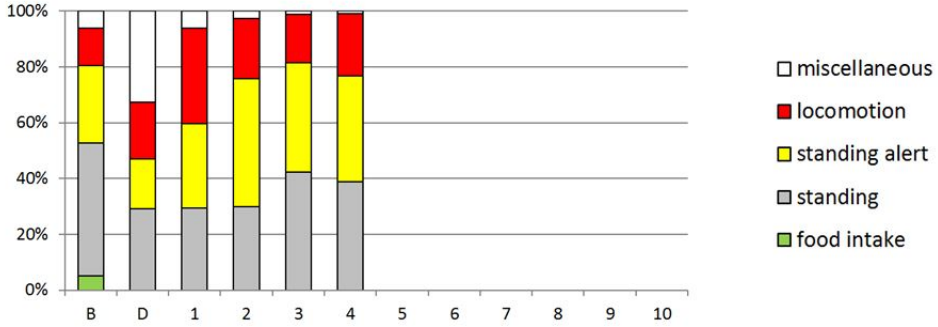


Figure 38. Behavioral pattern of active roe deer in early autumn (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after optical and acoustical disturbances trials (101 minutes observation time in total).

In late autumn the behavior was affected more intensely and longer than in early autumn (Figure 37). After being disturbed the deer lay less and expended more time in standing alert. After acoustical disturbances roe deer showed only minor changes in their behavioral pattern.

To assess the length of disturbance effect in an animal that was "activated" but did not lie down after the disturbance trials, the behavior of the afterwards active animal was compared with the undisturbed activity of the animal when not exposed to the disturbance stimulus. In the few cases in early autumn, when activated animals did not lie down again, they reacted with increased locomotion and alert standing (Figure 38).

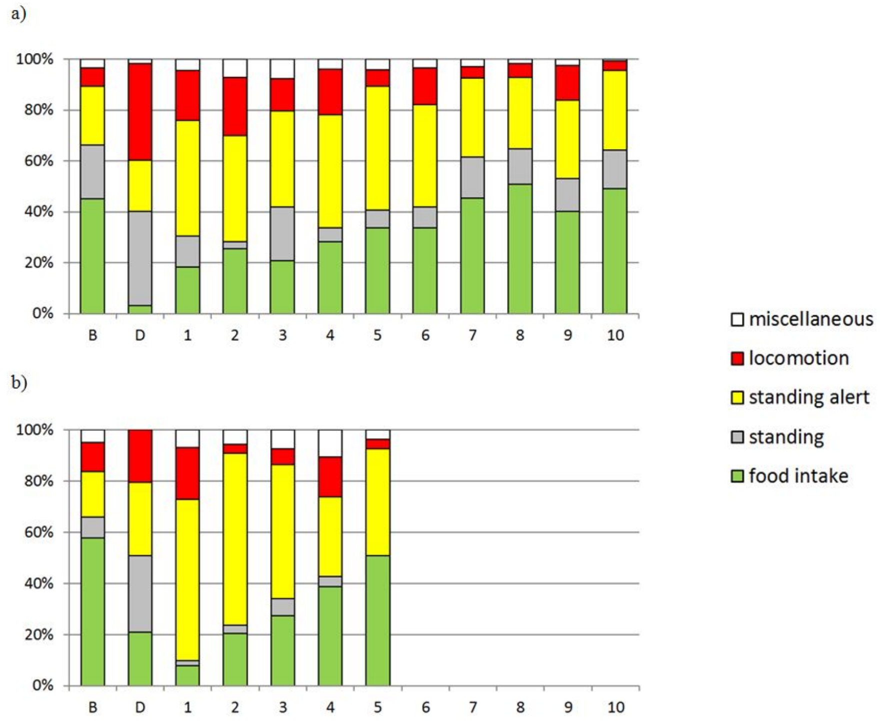


Figure 39. Behavioral pattern of active roe deer in late autumn (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after a) optical disturbances trials (906 minutes observation time in total) and b) acoustical disturbances trials (49 minutes observation time in total).

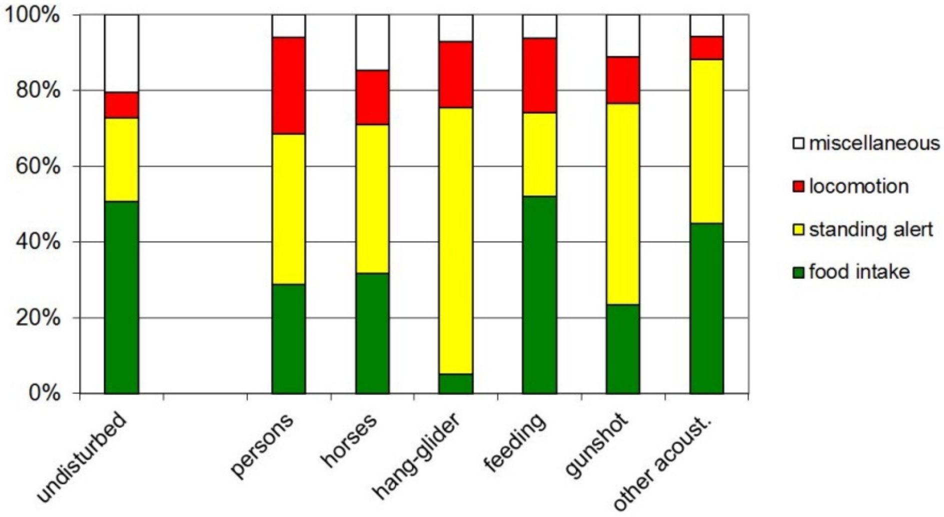


Figure 40. Behavioral pattern of active roe deer (relative share of time for each behavior class) in late autumn before (undisturbed) and after different disturbances trials.

In late autumn the food intake after optical disturbance trials was analog to an undisturbed animal after seven minutes (Figure 39a). After acoustical disturbances the feeding activity reached a normal level within five minutes. Yet the time standing alert was still considerably heightened (Figure 39b).

Regarding the varying disturbance stimuli, different behavioral categories were affected in various ways. Locomotion was more pronounced after persons walked by, standing alert after hang-gliders (Figure 40).

3.2.1.4. Heart Rate

Influence of Season on Heart Rate

Daily heart rate was calculated as the arithmetic mean of all heart rate values across 24 hours. The heart rate of the roe buck (No. 22) was on a higher level than the two roe does (Figure 41).

Circadian Rhythm

The mean heart rate of undisturbed roe deer showed periodic changes during the course of the day. It was highest in the morning and lowest in the afternoon (Figure 42). On days with disturbance trials the heart rate showed the same daily pattern as on undisturbed days (Figure 43).

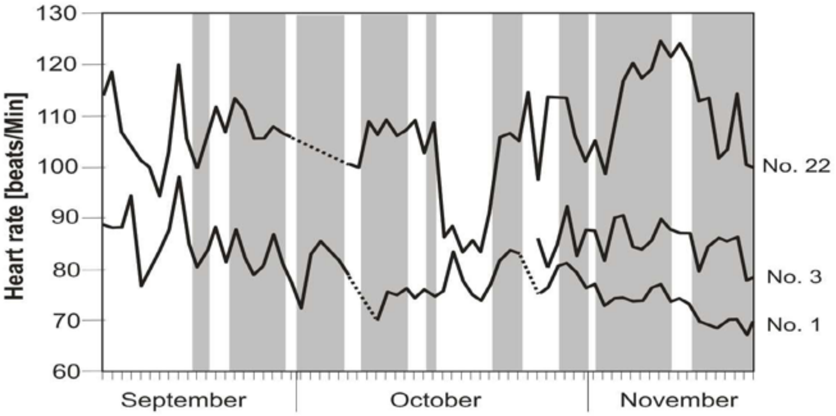


Figure 41. Mean daily heart rate of three roe deer during disturbance trial test period. Days with disturbance trials are highlighted in gray.

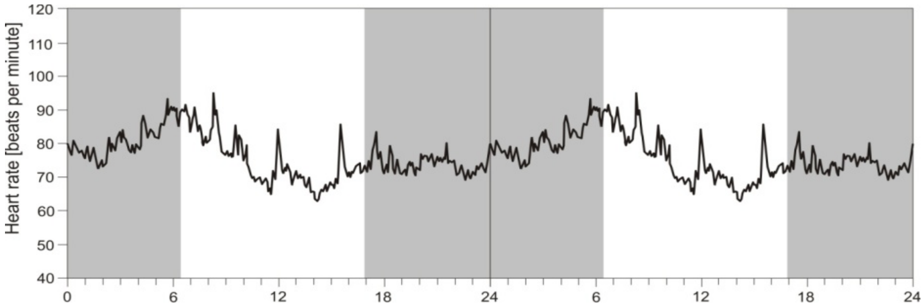


Figure 42. Daily heart rate pattern of roe deer No. 1 on undisturbed days. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

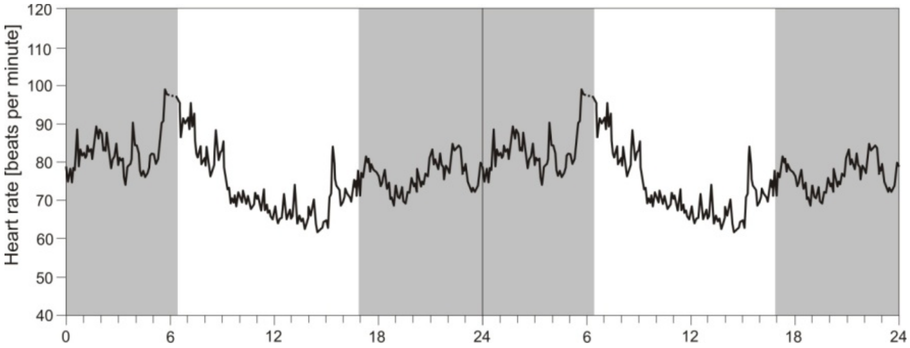


Figure 43. Daily heart rate pattern of roe deer No. 1 on days with disturbance trials. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

Resting Heart Rate

For each resting bout the arithmetic mean of heart rate for each minute was calculated. 1262 resting bouts were taken into account. Kruskal-Wallis-Test was applied to the data. The individual differences in resting heart rate were significant between the three roe deer. Highest heart rate was measured in the roe buck No. 22 (100.8 ± 18.8 beats/min). Doe No. 1 and doe No. 3 had 71.0 ± 6.4 beats/min and 80.3 ± 5.0 beats/min respectively.

Influence of Daytime and Season on Resting Heart Rate of Roe Deer

In early autumn the resting heart rate changed significantly during 24 hours.

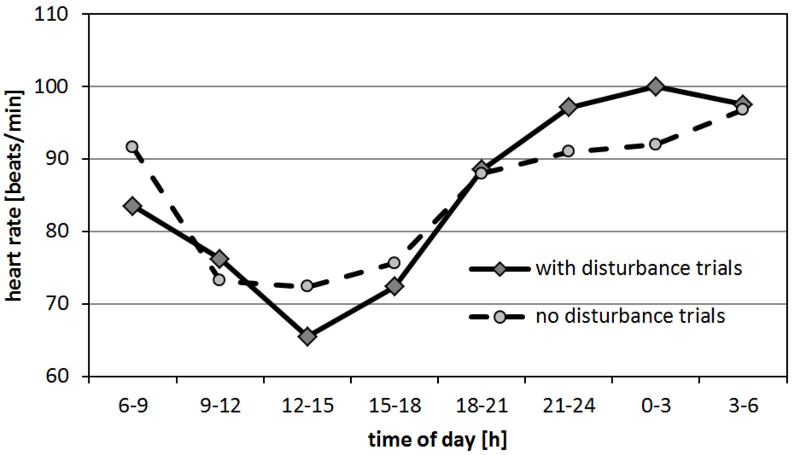


Figure 44. Daily heart rate pattern of roe deer on days with and without disturbance trials in early autumn. 24 hours were subdivided in 8 time segments and the mean heart rate during resting bouts for each fraction calculated.

Resting heart rate was highest in the night and lowest at noon in early afternoon (Figure 44). In late autumn daily fluctuations were not significant (Figure 45). No significant differences could be found in resting heart rate of roe deer between days with and without disturbance trials, neither in early nor in late autumn (Figs. 44 and 44).

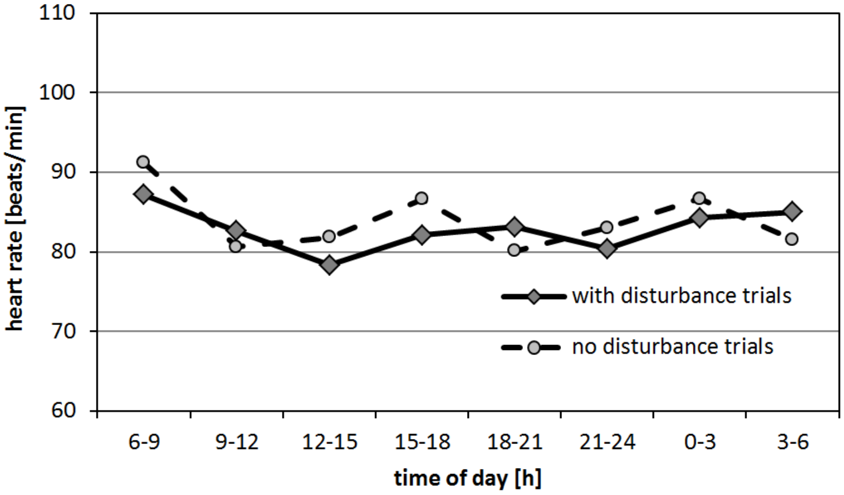


Figure 45. Daily heart rate pattern of roe deer on days with and without disturbance trials in late autumn. 24 hours were subdivided in 8 time segments and the mean heart rate during resting bouts for each fraction calculated.

Influence of Number of Disturbance Trials Per Day on Resting Heart Rate of Roe Deer

There was no significant relationship between number of disturbance trials carried out per day and resting heart rate of roe deer (Kruskal-Wallis-Test).

Intensity of Disturbance and Increase of Heart Rate

In general resting roe deer showed less heart rate reactions towards disturbances than active animals. The magnitude of heart rate reactions towards disturbances increased in late autumn (Tables 18 and 19).

Table 18. Heart rate reactions of roe deer during disturbance trials in early autumn (2 individuals)

Status of roe deer during disturbance trial	Number of additional heart beats	Duration of increased heart rate (in seconds)	Magnitude of heart rate increase (beats/min)	n
Lying	50	265	11	70
Active	181	378	29	59

Table 19. Heart rate reactions of roe deer during disturbance trials in late autumn (3 individuals)

Status of roe deer during disturbance trial	Number of additional heart beats	Duration of increased heart rate (in seconds)	Magnitude of heart rate increase (beats/min)	n
Lying	137	263	31	9
Active	316	680	28	95

Influence of Disturbance Type on Heart Rate Reactions of Roe Deer

In early autumn the strongest heart reactions were caused by gunshots. Despite shorter duration of the disturbance effect compared to the other disturbance trials, the strong increase of heart rate caused by gunshots resulted in 119 extra heart beats in the roe buck. Other acoustical disturbances showed the lowest heart rate reactions (Table 20).

In late autumn heart rate reactions were higher than in early autumn. Highest heart rate reactions were caused by persons walking the tour (Table 21).

Table 20. Heart rate reactions of roe deer during disturbance trials in early autumn separated for different disturbance types and roe deer individuals

	Roe buck (No. 22)				Roe doe (No. 1)			
Disturbance type	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*
Persons	59	246	14	*25*	96	240	24	*29*
Feeding	40	293	8	*11*	19	141	8	*12*
Gunshot	119	110	65	*6*	97	119	49	*10*
Other acoust.	7	186	2	*13*	31	250	7	*11*

Table 21. Heart rate reactions of roe deer during disturbance trials in late autumn separated for different disturbance types and roe deer individuals

	Roe buck (No. 22)				Roe doe (No. 3)			
Disturbance type	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*
Persons	275	515	32	*8*	288	608	28	*5*
Horse riders	127	380	20	*9*	173	464	22	*6*
Hang-glider	66	197	20	*4*	51	205	15	*5*
Feeding	155	409	23	*6*	176	569	19	*4*
Gunshot	291	641	27	*3*	66	251	16	*4*
Other acoust.	19	152	8	*7*	23	131	11	*4*

Table 22. Heart rate reactions of roe deer in early autumn (2 individuals) during disturbance trials with persons walking, separated for three subgroups

Disturbance type	Number of additional heart beats	Duration of increased heart rate (in seconds)	Magnitude of heart rate increase (beats/min)	*n*
Single person	46	198	14	*26*
Person with dog	80	268	18	*16*
Group of persons	150	306	29	*12*

If disturbance trials with persons walking the round tour are evaluated separately for its subgroups the heart rate reactions are by far higher when a group of persons (at least 3 people) are involved than for single persons ($p<0.01$). A single person with a dog on leash also elicits higher heart rate reactions (Table 22) than a person without dog, but the differences were statistically not significant.

3.2.2. Red Deer

3.2.2.1. Choice of Bedding Site

Red deer did not show special preferences for their bedding sites (Figure 46). Contrary to the roe deer they often lay on the upper end of the enclosure which is nearer to human activities. Often they lay under an elder shrub and on top of the small grass covered mound.

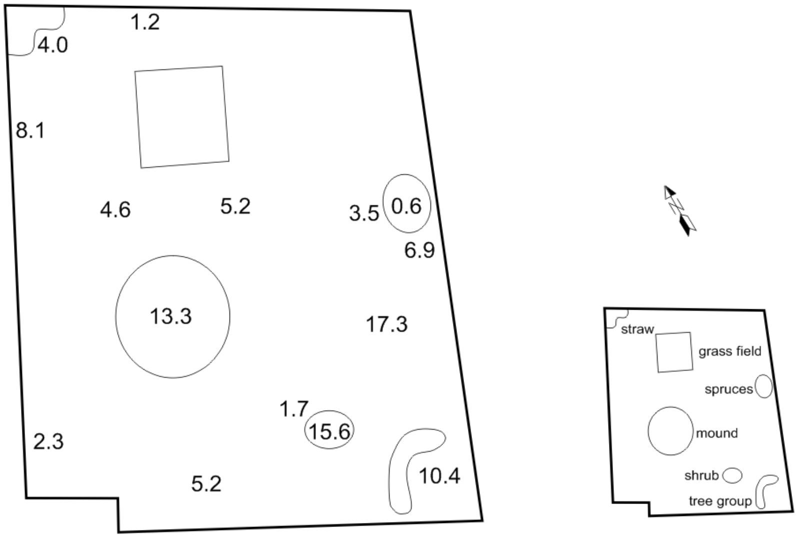


Figure 46. Distribution of red deer bedding sites in percentage (n=173).

Choice of Bedding Site after Disturbances

In 53.6% of all cases in which the animals were activated through disturbance trials a different bedding site was chosen after the trial.

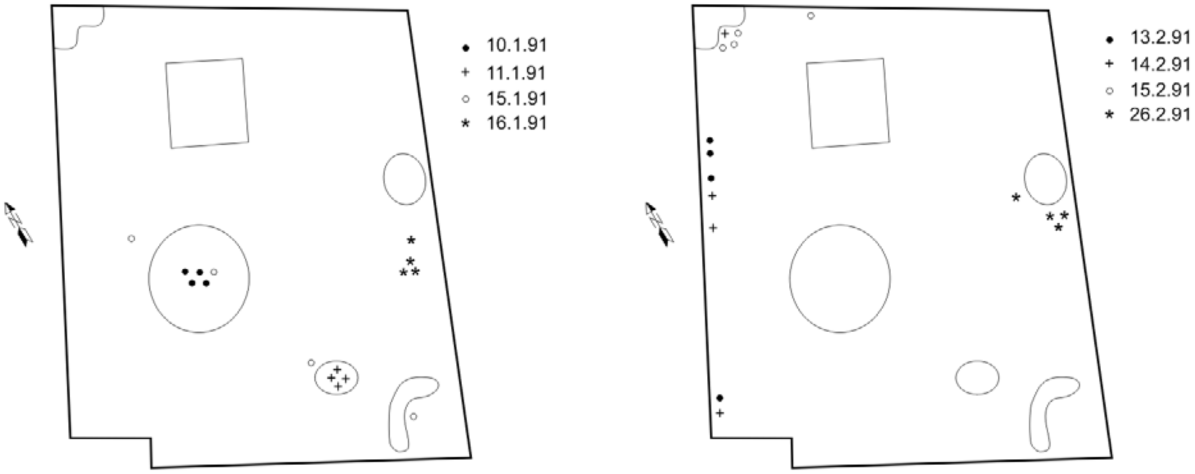


Figure 47. Bedding sites of red deer bedding sites on specific days (each day mapped had at least four disturbance trials).

It is noteworthy that on certain days a favoured bedding site was frequented again for the rest of day even if disturbance trials were carried out, but on the following day a different bedding site was chosen (Figure 47).

3.2.2.2. Activity

Circadian Rhythm

On undisturbed days main activity peaks were in the morning and evening hours with a smaller activity peak in the early afternoon (Figure 48). On days with disturbance trials daytime activity was on a higher level than on undisturbed days. Also nighttime activity showed modifications in rhythm when disturbed at daytime (Figure 49).

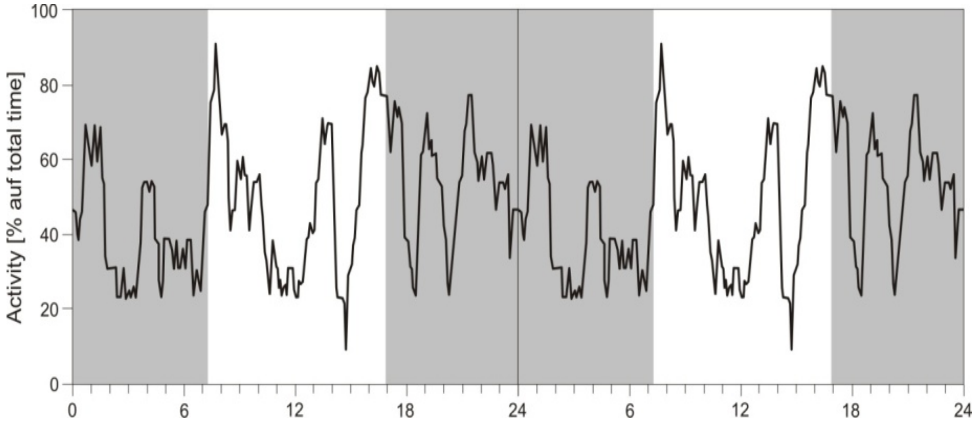


Figure 48. Daily activity pattern of red deer No. 61 on undisturbed days. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

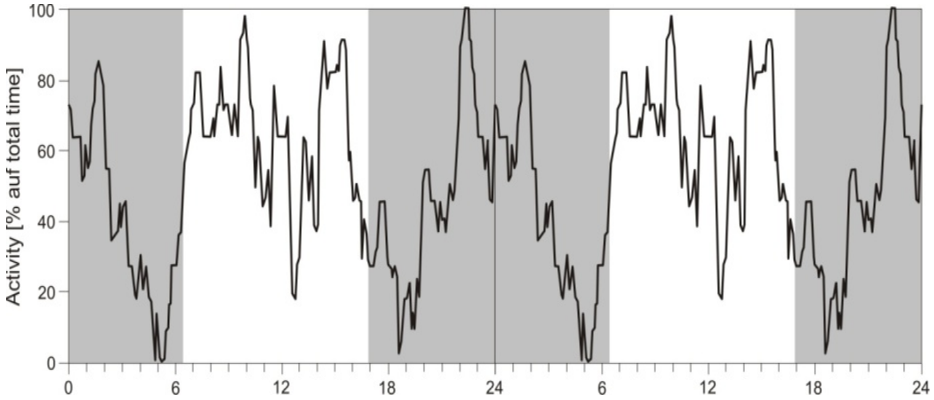


Figure 49. Daily activity pattern of red deer No. 61 on days with disturbance trials. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

Total Activity

On days with disturbance trials the total activity time was slightly increased with the animals spending half an hour less resting per day. The difference was only significant for the calf (No. 51) in January (Table 23). Relating to daylight time the animals reduced the time spent resting by

10 percent (Table 24). The reduction of resting time in 24 hours is effected practically only in the daytime and not compensated for at nighttime.

Table 23. Share of time red deer are active during 24 hours
(No. = animal number, n= number of days, med = median,
x̄ = arithmetic mean, s = standard deviation, min-max = extrema)

		Days without disturbance trials					Days with disturbance trials				
Month	No.	n	med	x̄	s	min-max	n	med	x̄	s	min-max
Dec	51	13	48.6	48.2	6.7	32.5-61.1	--	---	---	--	-----
	61	18	51.6	48.7	6.4	35.0-55.6	2	50.6	50.6	11.9	42.2-59.0
Jan	51	9	50.0	49.8	4.1	42.9-56.2	11	55.9	55.1	6.6	44.4-65.5
	61	13	46.4	47.2	4.0	38.6-53.6	18	48.5	49.4	5.9	40.2-63.4
Feb	51	9	53.4	52.9	3.8	46.9-57.7	9	57.5	56.9	7.0	47.3-67.3
	61	14	47.9	47.1	5.0	39.6-55.3	14	50.2	54.7	7.1	45.2-65.6
Mar	51	4	58.1	58.0	1.5	56.1-59.6	4	52.9	61.8	6.9	57.4-72.1
	61	4	54.6	53.5	3.6	48.5-56.5	5	49.7	56.1	7.6	49.2-67.8

Table 24. Share of time red deer are active during daytime
(No. = animal number, n= number of days, med = median,
x̄ = arithmetic mean, s = standard deviation, min-max = extrema)

		Days without disturbance trials					Days with disturbance trials				
Month	No.	n	med	x̄	s	min-max	n	med	x̄	s	min-max
Dec	51	14	53.3	52.1	7.4	45.2-62.8	1	59.8	59.8	--	-----
	61	19	56.8	59.1	8.6	39.3-74.4	2	72.5	72.5	2.1	71.0-74.0
Jan	51	9	53.1	52.1	9.5	40.3-69.2	15	68.4	61.2	7.9	54.2-77.7
	61	12	47.1	49.1	7.3	41.7-64.2	18	61.1	62.2	9.7	48.0-84.0
Feb	51	12	56.9	57.0	7.9	50.3-72.3	8	68.5	67.5	9.8	50.6-80.5
	61	12	51.7	51.1	7.6	40.4-66.3	12	62.6	60.7	11.5	43.0-78.9
Mar	51	5	59.0	54.5	4.3	49.8-59.7	4	61.7	60.3	4.5	53.9-63.1
	61	5	55.3	49.3	4.1	54.2-42.8	5	58.2	56.0	5.2	50.0-60.3

Number and Lengsth of Resting Phases

On days with disturbance trials the duration of resting phases was significantly reduced during the daytime (Mann-Whitney-U-Test; Table 25).

Table 25. Duration of diurnal resting phases of red deer (in minutes) on days without, with few (2-4) and with many (5-10) disturbance trials
(No. = animal number, n= number of resting phases,
x̄ = arithmetic mean, s = standard deviation, min-max = extrema)

	no disturbance trials				few disturbance trials				many disturbance trials			
No	n	x̄	s	min-max	n	x̄	s	min-max	n	x̄	s	min-max
51	208	52.6	37.0	6-200	33	39.5	24.0	10-95	154	37.4	24.6	2-122
61	218	61.8	37.3	3-174	34	42.5	29.2	7-116	151	42.4	30.3	5-144

The number of resting phases was the same on days with and without disturbance trials (Table 26).

Table 26. Number of diurnal resting phases of red deer on days without, with few (2-4) and with many (5-10) disturbance trials

(No. = animal number, n= number of days, x̄ = arithm. mean, s = stand. dev., min-max = extrema)

	no disturbance trials				few disturbance trials				many disturbance trials			
No	n	x̄	s	min-max	n	x̄	s	min-max	n	x̄	s	min-max
51	35	5.0	1.5	2-8	6	4.7	1.6	3-7	17	5.7	2.1	3-10
61	30	4.9	1.6	3-8	8	5.0	1.1	4-7	27	5.4	1.8	1-8

Resting Phases during the Course of the Day

Length of resting phases was shorter during the daytime than at night (Figure 50). On days with disturbance trials resting phases were particularly shorter during daytime (Kruskal-Wallis-Test).

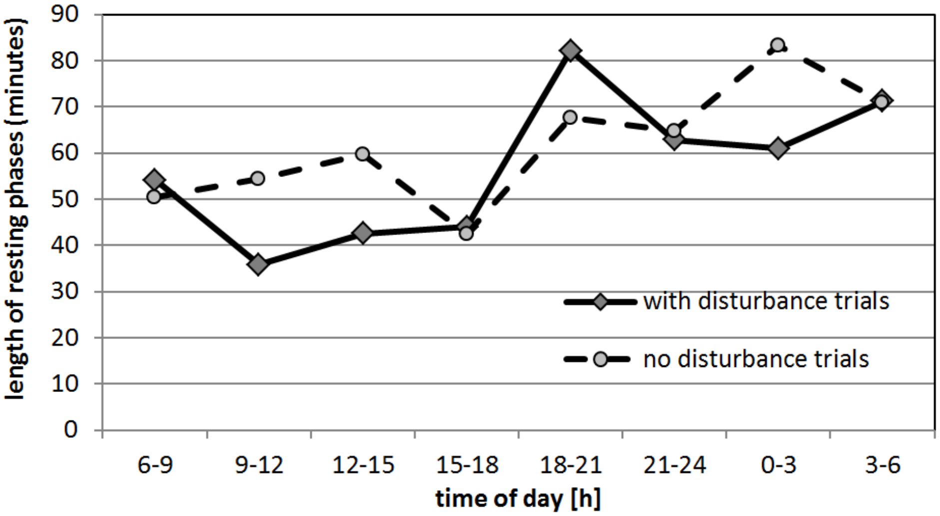


Figure 50. Mean length of resting phases (in minutes) of red deer during the course of the day on days with and days without disturbance trial.

Activation through Disturbance Trials

The association of activation among the two red deer was very high (Cole's coefficient of association = +0.915 ± 0.14). With both animals no seasonal change in activation could be found during the test period (December – March). The red deer calf tended to be more easily activated (76.7%) by optical and acoustical disturbances than the male deer (65.9%), but the difference was not significant (χ^2-Test).

Influence of Daytime on Activation of Red Deer

Both red deer were least activated between 12:00 and 14:00 (Figure 51), although the circadian differences were not significant.

Dependence of Red Deer Activation on Type of Disturbance

Both red deer were significantly more often activated by optical (87%) than by acoustical stimuli (28%; χ^2-Test, $p<0.01$). All optical stimuli led to 90-100% activation (Table 27), aside from tractor (28.6%) and hang-glider (33.3%). Of the acoustical stimuli only gunshots caused high activation (53.3%), but this could not be statistically verified.

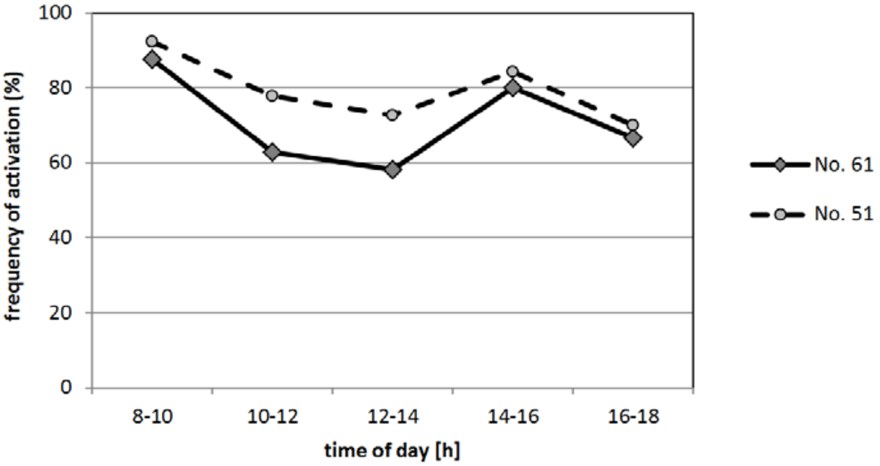


Figure 51. Activation through disturbances in dependence on daytime for red deer nos. 51 and 61.

Table 27. Activation (in %) in dependence on disturbance type.

(n = number of samples)

Disturbance type	% activated	n
Round tour of single person	100.0	27
Round tour of person with dog	100.0	14
Round tour of group of persons	100.0	14
Round tour with horse(s)	92.0	25
Hang-glider	33.3	12
Tractor	28.6	7
Fire	100.0	10
Feeding	90.9	11
Radio music	12.5	8
Dog barking	25.0	8
Chain saw	9.1	11
Gunshot	53.3	15

Duration of Activation

Length of activation was on average 38.5 minutes. Individual differences in the length of activation between both red deer could not be identified (Kruskal-Wallis-Test).

There were also no significant differences in length of activation between the months, although there was a trend of decreasing activation length toward end of the winter.

Activation length in dependence of daytime was significant (Kruskal-Wallis-Test). Activation length was longest in the evening (Figure 52)

Differences in length of activation between two simultaneously activated red deer were minimal ($\bar{x}$=10.5 min, median = 5 min, extrema 0-57 min). In equal number of cases one animal was longer active than the other.

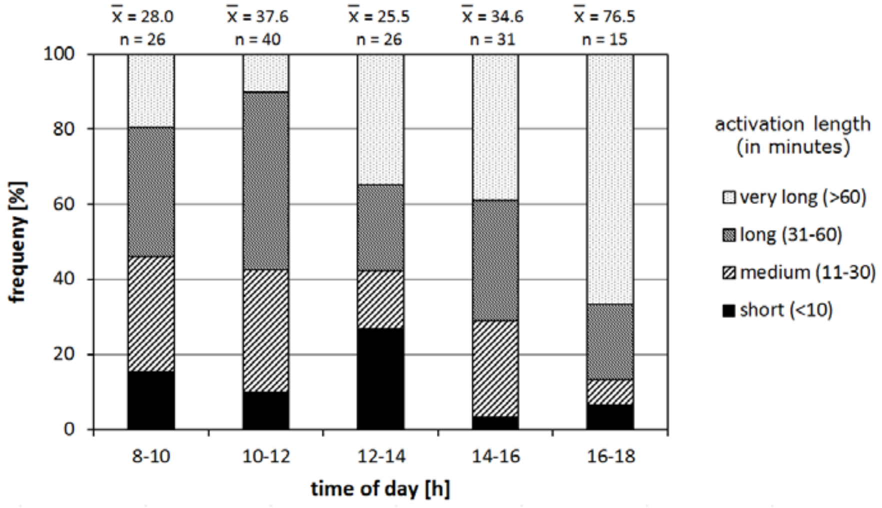


Figure 52. Dependence of activation length on time of day averaged for both red deer. Above the column the number of samples and the mean duration of activation (in minutes) for each class are specified.

Dependence of Duration of Activation on Type of Disturbance

Basically there was also no difference between duration of activation provoked by optical or acoustical stimuli. Yet between individual disturbance stimuli there were very significant differences in length of activation (Table 28; Kruskal-Wallis-Test).

Table 28. Activation length (in minutes) in dependence on disturbance type (n=number of samples)

Disturbance type	median	n
Round tour of single person	34.5	24
Round tour with single person and leashed dog	51.0	15
Round tour of group of persons	55.0	9
Round tour with one horse (walk-gallop)	21.0	24
Round tour with group of horses (walk)	12.0	11
Hang-glider	32.5	4
Tractor	19.0	5
Fire	35.5	6
Feeding	42.0	9
Radio music	3.0	1
Dog barking	18.5	2
Chain saw	3.0	1
Gunshot	68.0	3

3.2.2.3. Behavior

Just as with roe deer the behavioral patterns of red deer before disturbance trials were compared with the time after. Undisturbed behavior returned as soon as the behavior after the trials did not differ significantly from the behavior before the trial. 244 disturbance trials were analysed on basis of seconds. The time span before setting the disturbance stimulus compromised 2484 minutes, after the trial 1869 minutes were analysed.

In the first week of the test period red deer were disturbed at least 10 minutes after finishing the disturbance trial with optical stumuli (Figure 53a), however with acoustical disturbance trials there was no significant change to undisturbed behavior after six minutes (Kruskal-Wallis-Test; Figure 53b).

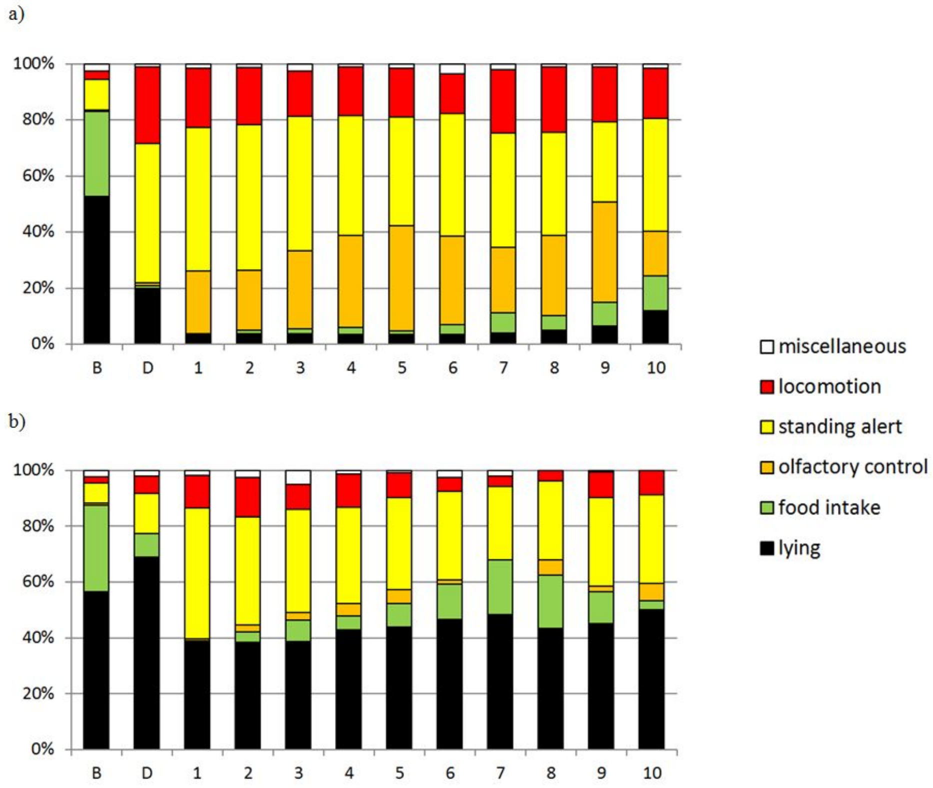


Figure 53. Behavioral pattern of red deer in the first test week (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after a) optical disturbances trials (642 minutes observation time in total) and b) acoustical disturbances trials (410 minutes observation time in total).

In the last test week the animals showed undisturbed behavior after optical disturbances within 10 minutes (Figure 54a). After acoustical disturbances the behavior was already in a normal range in the following first minute (Kruskal-Wallis-Test; Figure 54b).

When comparing the behavior of animals that stayed active after the disturbance trials with undisturbed active animals, the behavior in the first week was still deviant after 10 minutes both for optical and acoustical stimuli (Figure 55)

In the last week active red deer showed at least 8 minutes disturbed behavior after optical stimuli and at least 6 minutes disturbed behavior after acoustical stimuli (Figure 56). The data was not sufficient to evaluate the ninth and tenth or respectively the seventh to tenth minute.

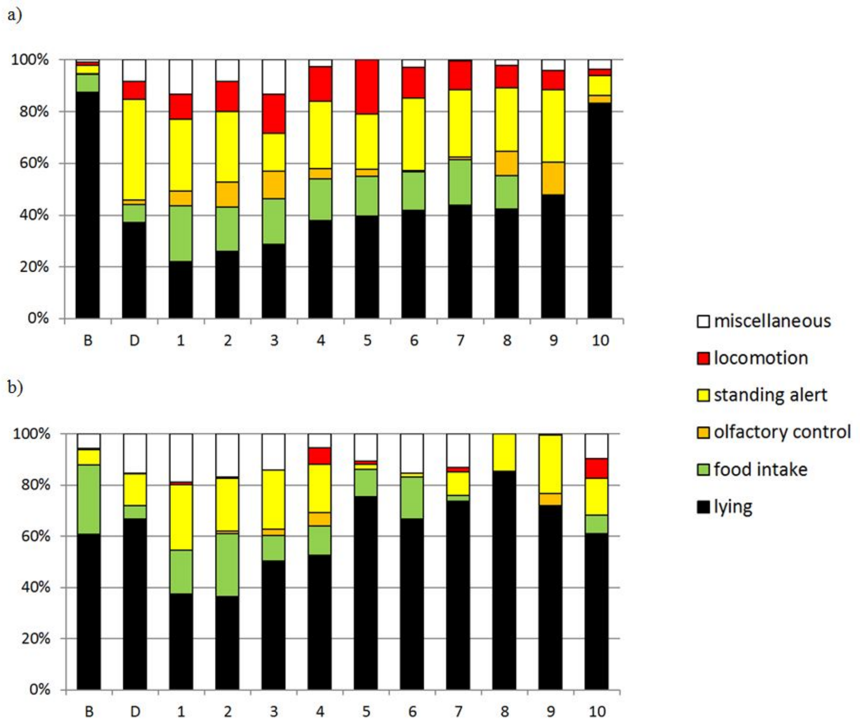


Figure 54. Behavioral pattern of red deer in the last test week (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after a) optical disturbances trials (476 minutes observation time in total) and b) acoustical disturbances trials (172 minutes observation time in total).

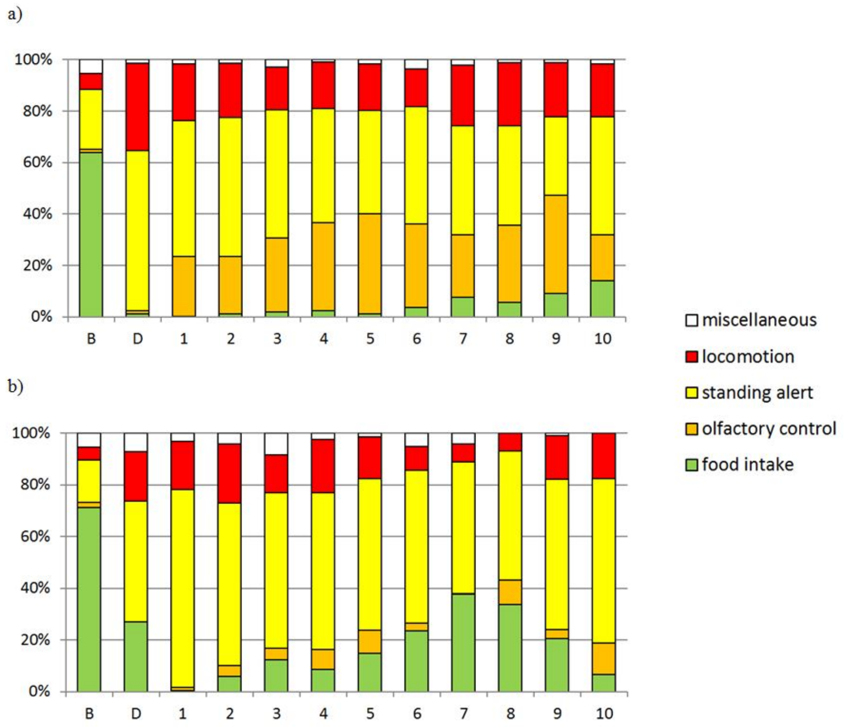


Figure 55. Behavioral pattern of active red deer in the first test week (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after a) optical disturbances trials (466 minutes observation time in total) and b) acoustical disturbances trials (201 minutes observation time in total).

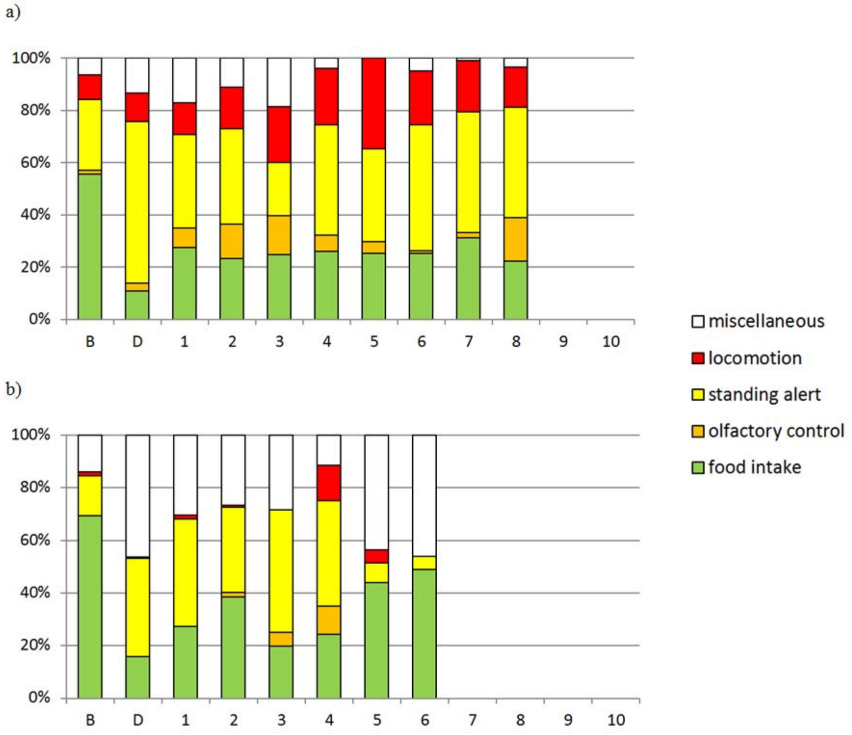


Figure 56. Behavioral pattern of active red deer in the last test week (relative share of time for each behavior class) before (B), during (D) and in the single minutes (1,2,3…) after a) optical disturbances trials (173 minutes observation time in total) and b) acoustical disturbances trials (66 minutes observation time in total).

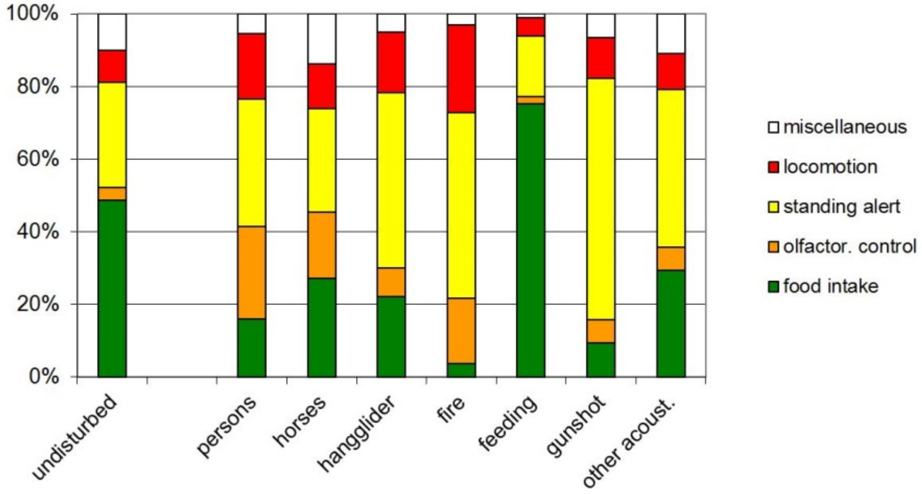


Figure 57. Behavioral pattern of active red deer (relative share of time for each behavior class) before (undisturbed) and after different disturbances trials.

Regarding the varying disturbance stimuli, different behavioral categories were affected in various ways. Olfactory control was most pronounced after persons walked by, standing alert after gunshots. With fire locomotion was more pronounced, after filling the feeding station, food intake increased (Figure 57).

The time span until there was no significant deviation from undisturbed behavior varied with disturbance types. With persons walking in the enclosure and gunshots the behavior still differed significantly after 10 minutes (maximum observation time) in several behavioral classes from undisturbed behavior (Table 29). With other acoustical stimuli, but also with hang-gliders, tractors, and equestrians the behavior was virtually the same after the disturbance as before.

Table 29. Time span (in minutes) after completion of the disturbance trial, in which still significant differences to undisturbed occur in at least one behavioral category

Disturbance trial	Lying	Locomotion	Food intake	Standing alert	Olfact. Contr.	Miscell.
Single person	9	10	4	10	9	---
Person with dog	9	8	9	10	9	---
Group of persons	---	4	---	---	9	---
Horse rider(s)	---	---	---	---	---	---
Hang-glider	---	---	---	1	---	---
Tractor	---	---	---	---	---	---
Gun shot	---	---	10	4	---	---
Other acoust.	---	---	---	---	---	---

3.2.2.4. Heart Rate

Influence of season on heart rate:

The mean heart rate decreased continuously from December to mid-March and started to increase afterwards. The heart rate of the male red deer was consistently higher than the female calf deer (Figure 58)

Circadian rhythm:

The mean heart rate of undisturbed red deer showed periodic changes during the course of the day. It was highest in the late afternoon (Figure 59). On days with disturbance trials the heart rate was considerably lower, especially between 10:00 and 14:00. At nighttime there was no noticeable change in heart rate between disturbed and undisturbed days (Figure 60).

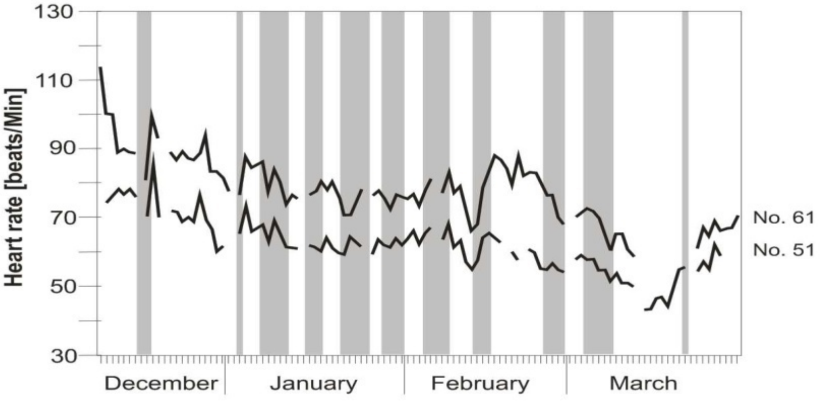


Figure 58. Mean daily heart rate of red deer nos. 51 (female calf) and 61 (male, spike) during the disturbance trial test period. Days with disturbance trials are highlighted in gray.

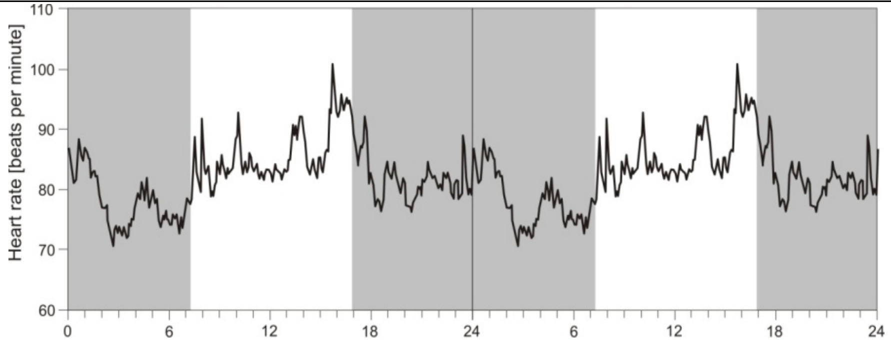


Figure 59. Daily heart rate pattern of red deer No. 61 on undisturbed days. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

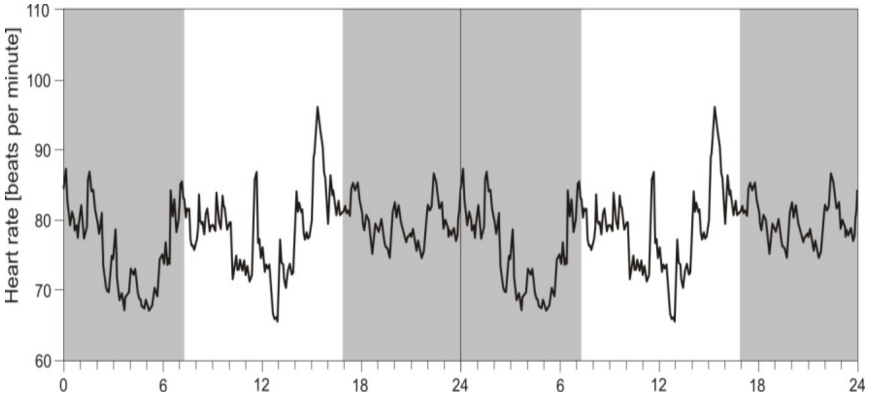


Figure 60. Daily heart rate pattern of red deer No. 61 on day with disturbance trial. Moving average of 5 consecutive minutes averaged over 10 days. The data are double plotted to better illustrate the circadian rhythm.

Resting heart rate:

Resting heart rate was calculated as for roe deer, with 1262 resting bouts taken into account. The data was testet with Kruskal-Wallis. The resting heart rate of the male deer (No. 61) was significantly higher (73.9 ± 10.7) than the female calf (58.1 ± 7.6).

Influence of daytime and season on resting heart rate of red deer:

Resting heart rate decreased gradually from December (73.2 ± 11.6) over January and February (63.4 ± 10.7) until March (53.7 ± 8.1). Resting heart rate was lower at night and in the morning and highest in the evening (Figure 61). On undisturbed days these fluctuations were not significant in contrast to days with disturbance trials. Generally the circadian variations had a similar pattern for disturbed and undisturbed days, yet the resting heart rate was on a lower level when disturbance trials were carried out (Figure 61).

Influence of number of disturbance trials per day on resting heart rate of roe deer:

On days with disturbance trials mean resting heart rate (60.6 ± 9.1) was significantly lower than on days without disturbances (66.0 ± 12.2).

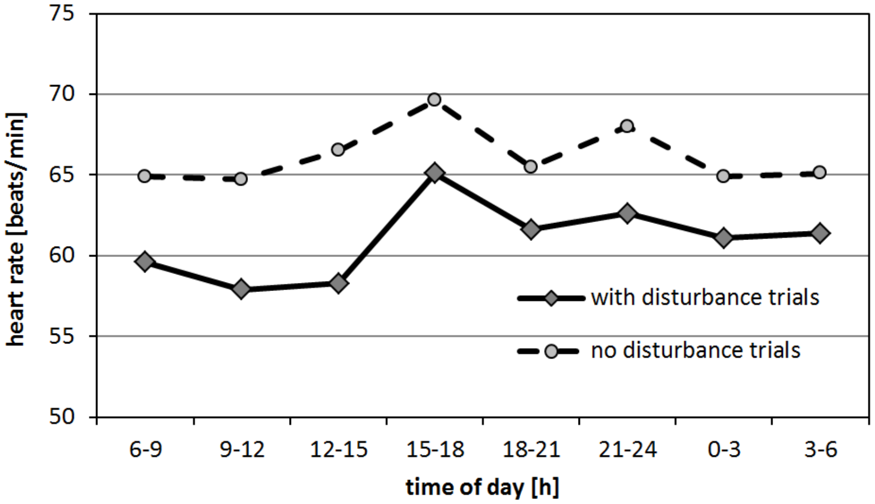


Figure 61. Daily heart rate pattern of red deer on days with and without disturbance trials. 24 hours were subdivided in 8 time segments and the mean heart rate during resting bouts for each fraction calculated.

Table 30. Heart rate reactions after disturbances of red deer (2 individuals)

Status of red deer during disturbance trial	Number of additional heart beats	Duration of increased heart rate (in seconds)	Magnitude of heart rate increase (beats/min)	n
Lying	9	102	5	25
Active	257	760	20	201

Increase of heart rate and intensity of disturbance:

Resting red deer showed less heart rate reactions to disturbances than active animals (Table 30).

Influence of disturbance type on heart rate reactions of red deer:

The greatest heart rate reactions were caused by feeding, especially for the female calf (Table 31). Acoustical stimuli and the hang-glider caused only weak reactions.

Table 31. Heart rate reactions of red deer during disturbance trialsseparated for different disturbance types and individuals

	female (No. 51)				male (No. 61)			
Disturbance type	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*
Persons	110	363	18	*16*	173	454	23	*15*
Horse riders	89	387	14	*12*	137	607	14	*8*
Hang-glider	40	183	13	*6*	45	253	11	*6*
Feeding	525	1118	28	*9*	174	579	18	*8*
Gunshot	47	214	13	*10*	14	64	13	*7*
Other acoust.	32	245	8	*12*	29	268	6	*14*

Heart rate reactions were higher at the beginning of the test period (first nine days) than at the end (last nine days), both for optical and acoustical disturbances (Table 32). The decline in extra heart beats result mainly from less magnitude of heart rate increase, only to a lesser extent from a shorter duration of the disturbance effect. However only the trial type “horse riding” had a significant ($p<0.001$) decrease in heart rate reactions with advancing number of disturbance trials (regression equation … $y = 793 – 3.5x$; coefficient of correlation … $r^2 = 0.304$).

Table 32. Heart rate reactions of red deer during disturbance trials for time period 1 (Jan.7th to Jan. 16th) and time period 2 (Feb. 27th to Mar. 8th)

	Period 1				Period 2			
Disturbance type	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*	Extra heart beats	Duration of heart rate increase	Mean increase (beats/ min)	*n*
Optical	135	395	21	*23*	42	339	7	*18*
Acoustical	36	195	11	*19*	16	158	6	*11*

If disturbance trials with persons walking the round tour are evaluated separately for its subgroups the heart rate reactions are much higher when a group of persons (at least 3 people) walks the tour than a single person (only marginally significant, $p<0.05$). There was no difference between a single person with a dog on leash and a person without dog (Table 33). If a rider gallops past the deer, heart rate increase is higher than with a single rider or group of riders staying at a low pace; these differences were statistically not significant.

Table 33. Heart rate reactions of red deer (2 individuals) during disturbance trials with persons walking separated for three subgroups and for horse riding trials separated for three subgroups

Disturbance type	Number of additional heart beats	Duration of increased heart rate (in seconds)	Magnitude of heart rate increase (beats/min)	*n*
Single person	103	387	16	*16*
Person with dog	117	344	20	*12*
Group of persons	440	766	35	*3*
Single horse walking	62	413	9	*10*
Single horse trot/gallop	168	466	22	*7*
Group of horse riders	122	703	10	*3*

3.2.2.5. Mountain Bike Trial

A series of 10 trials with a mountain biker crossing the enclosure was carried out. Each trial lasted about 2 ½ minutes, after a 5 minute break the next trial was carried out. Heart rate showed the highest increase during the second trial. With each following trial the heart rate peak was reduced until in the 7th trial no noticeable peak could be observed. From the 8th to 10th trial heart rate peaks increased with each trial (Figure 62).

Behavioral analysis showed that standing alert and locomotion were predominant during each trial. During the 7th trial the animals stood alert most of the time (Figure 63).

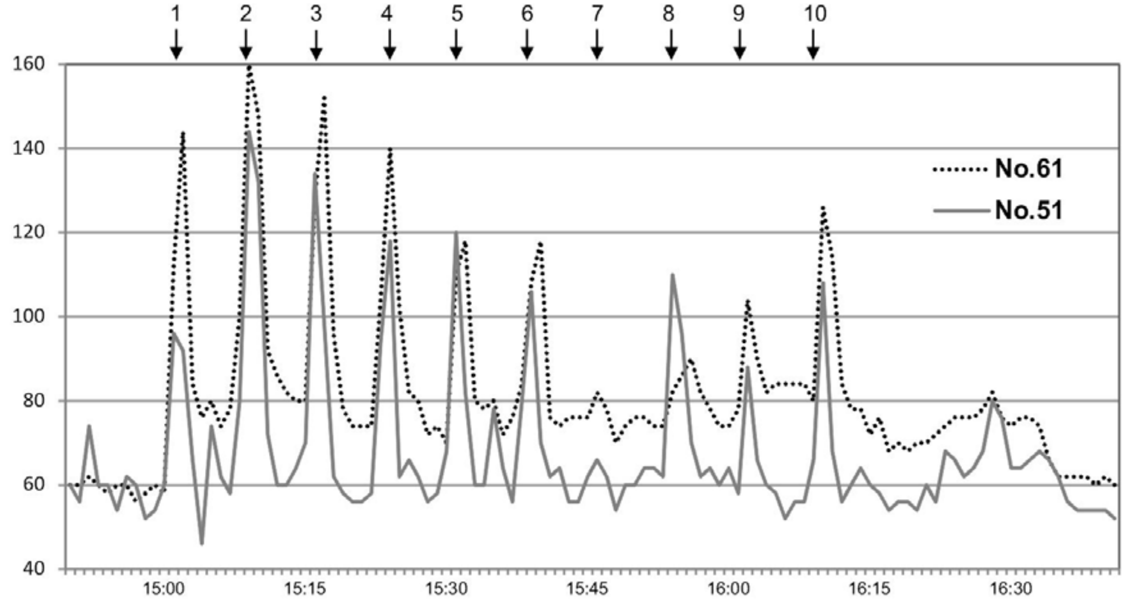


Figure 62. Heart rate of of red deer nos. 51 (female calf) and 61 (male, spike) during the mountain bike trial series.

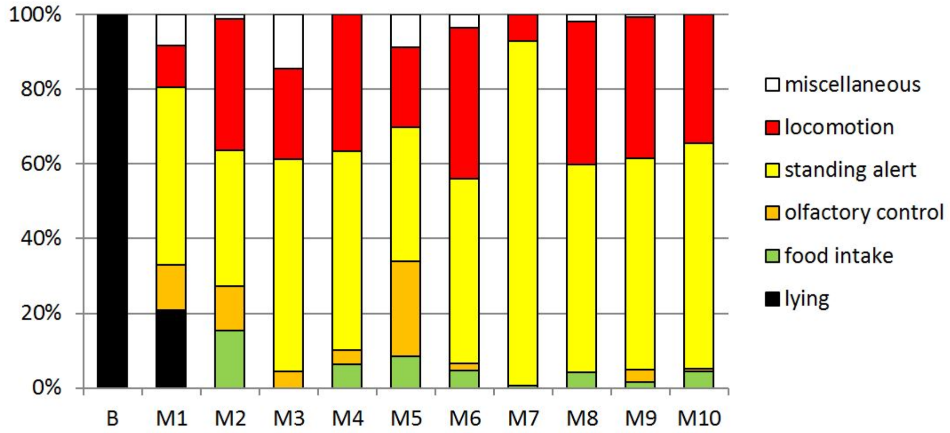


Figure 63. Behavioral pattern of red deer before (B) and during 10 mountain bike trials (M1, M2,…), each lasting 7-8 minutes.

4. DISCUSSION

Aim of this study was to measure and analyze the effects of anthropogenic disturbances on the behavior and heart rate of roe and red deer under controlled conditions. An essential precondition for this purpose is the knowledge of the natural circadian and seasonal activity rhythms and corresponding heart rates of the undisturbed animals.

4.1. Circadian and Seasonal Rhythms of Activity and Heart Rate

Roe Deer

Roe deer had a conspicuous period of inactivity at daytime in late summer and early autumn. They seem to have a strong need for resting during daytime in this time of the year and spent most of the time lying in hiding cover. In late autumn the roe deer were much more active during daylight time.

This change to increased daytime activity was quite abrupt. Both roe deer used in the disturbance trials changed their activity pattern on October 21st. Several factors were taken into account as cause. The only temporally concordant incident was a sudden temperature drop on October 21st, in which the primary temperature range of 9°C to 19°C declined to a range of -3°C to 8°C. Presumably this change in activity triggered by the weather change is based on an endogenic process, since all other roe deer in this investigation showed similar activity patterns, although the exact date of activity change differed each year, depending on ambient temperature. Diurnal activity in winter and nocturnal behavior of roe deer in summer and early autumn were also found in other studies (Krop-Benesch et al. 2013; Pagon et al. 2013).

Heart rate fluctuated strongly between daytime and nighttime in early autumn. The distinct variations in early autumn may indicate a high sensitivity of the cardiovascular system. This can partly be related to shedding hair, and shifting towards winter metabolism.

During rut and post rut roe deer, particularly bucks showed a negative correlation between ambient temperature and the ratio of daytime to nighttime activity. In late summer and autumn roe deer shifted their activity into the night on warm days. In springtime marking and defending the territories and later on fawning seems to overrule these temperature effects. In winter on the other hand, roe deer make use of most of the short daylight time for activity, regardless of the ambient temperature. This also has consequences for hunting in summer and late autumn: the chances of observing roe deer during daytime is increased on cooler days.

Male roe deer tended to be less active than females. Mean activity was 46% for females and 40% for male roe deer. Seasonal fluctuations of mean daily activity were very dependent on the individual. One female roe deer in the large enclosure, which approximates the normal home-range size of roe deer, showed strong seasonal fluctuations with highest activity around May (63%) and lowest activity in winter (41%), one buck in the large enclosure varied between 35% in September/October and 49% in April. Guthörl (1994) measured about 49% activity in three free-ranging female roe deer, without any pronounced seasonal variations. Wallach et al. (2010) also could not observe significant differences between activity of roe deer in a Mediterranean environment in summer (47%) and winter (48%). Cederlund (1989) in contrast observed strong seasonal variations in activity of northern boreal roe deer ranging from 30-40% in winter to 57% in late May-early June. Chapman et al. (1993) found quite high mean annual activity rates of 56% for roe deer.

Red Deer

Red deer were more active in summer and autumn than in winter. In general red deer was slightly more active at daytime than at night, especially in winter and spring. Contrary to most investigations including this one, Kamler et al. (2007) could not observe increased activity of red deer during twilight. They explain this with the absence of human hunting, negligible human activities and the presence of large carnivores in the study area.

Heart rate was highest during calving and lactation time and was markedly lower in winter. Not only heart rate but also peripheral body temperature was reduced in cold winter periods (Arnold et al., 2003). Seasonal changes in heart rate are often described in literature. Freddy (1984) measured lowest heart rate in mule deer end of January, and Moen and Chevalier (1977) observed lowest heart rates in white-tailed deer in February. Lieb and Les Marcum (1979) found a negative correlation of heart rate and ambient temperature in wapitis.

4.2. Lunar Cycles

Findings on lunar rhythms in deer are rather inconsistent. Reasons may be different methods for measuring activity (observability vs. biotelemetry), choice of time spans (morning hours, daylight hours, days near full moon or longer phases) or different habitats. Some authors mention increased night activity of roe deer near full moon (Kurt, 1991; Prior, 1968, cited in Turner, 1980). Other studies could not confirm a noticeable effect of the lunar cycle on roe deer activity (Turner, 1980; Pagon, 2010). Whereas Kjær et al. (2008) noticed increased contact rates near full moon, Beier and McCullough (1990) and Webb et al. (2010) could not find any influence of moonlight on nighttime activity or habitat use of white-tailed deer. Buss and Harbert (1950) found a strong correlation between lunar phases and occurrence of mule deer at a salt lick, but both Hayes and Krausman (1993) and Kufeld et al. (1988) observed no differences in activity of mule deer between full and new moon phases. According to Bonchev (2010) the moon affects the reproduction of red deer.

For roe deer no significant differences between activity at full moon and new moon could be found in this study. In contrast red deer showed significant increase of activity at night during full moon and highly significant increase of activity in the morning during new moon phases.

4.3. Disturbance Trials

Roe deer and red deer had quite different reactions towards anthropogenic disturbances.

4.3.1. Impact of Stimuli Types

Roe Deer

Groups of persons created the strongest heart rate and behavioral reactions in roe deer, followed by persons with dogs and gunshots. Reactions towards single persons and equestrians were less and of all optical stimuli tractors elicited the least reactions. Acoustical stimuli other than gunshots hardly provoked any reactions. Roe deer were easily activated by hang-gliders and feeding, but heart rate reactions were only mild. Regarding the single disturbance stimuli types, different behavioral categories were affected in various ways. Locomotion was more pronounced after persons walked by, standing alert after hang-gliders.

Red Deer

Similar to roe deer, persons caused greatest activation and heart rate reactions in red deer. Only feeding caused higher heart rate reactions in the female calf, which will be discussed later on. Equestrians had less impact on behavior and heart rate than persons on foot. Hang-gliders and tractors provoked only mild reactions, and acoustical stimuli other than gunshots had very little influence. Heart rate reactions after gunshots were mild in red deer, which was in contrast to the strong behavioral reactions.

Species Comparison (Parallels, Differences, and General Reaction Patterns of the Species after Disturbances)

Some parallels could be found in the behavior of roe and red deer after disturbances. For both species optical stimuli had a by far higher influence on heart rate and behavior than acoustical stimuli. This result is in accordance with disturbance trials that Hoffmeister (1979) conducted with roe and fallow deer. An exception is the gunshot which elicited very strong heart rate reactions, even though the incidence lasted only a split second, compared to one to three minutes for the other acoustical stimuli. The studied animals were non-hunted, but at single days of each year the surplus of the population was reduced through gun shots. Herbold (1990) could also observe higher flight distances of roe deer after gunshots than through disturbances caused by forest workers or recreationists. The mild heart rate reactions in red deer after gunshots could be a sign of bradycardia, since in more than half of all cases red deer were activated by gunshots, and their behavior was still significantly impacted after 10 minutes (less food intake and more standing alert). Ward and Cupal (1979) in contrast measured a dramatic increase of heart rate in wapiti after gunshots.

After optical disturbances roe deer mostly reacted with standing alert, red deer with increased locomotion. The reactions of roe deer were intense but short, the reactions of red deer longer-lasting. Roe deer showed normal behavior within seven minutes after optical disturbances. After acoustical stimuli they showed the same share of time browsing as undisturbed animals within five minutes, but still spent more time standing alert. Red deer still showed disturbed behavior, both for optical as well as acoustical stimuli, 10 minutes after the disturbance trial. Activated red deer did not compensate the shortened resting bouts, not even in the following night, whereas roe deer rested more after disturbances. Sibbald et al. (2011) observed that the disturbance effect on red deer caused during days with many recreationists tended to last over full 24 h, even when the following night was quiet. In contrast farmed red deer investigated by Hodgetts et al. (1998) returned to pre-stimulus levels of alertness 15 minutes after presenting a disturbance stimulus, and park deer observed by Langbein and Putman (1992) only showed very short-term reactions when disturbed (but it is not mentioned if the population is hunted).

For roe deer both behavioral and heart rate reactions were higher when a person was accompanied by a dog. For red deer there were no differences between a single person walking the tour with a dog on leash or walking without a dog. It should be mentioned that in the present study the dog used in the disturbance trials was a dachshund, and a larger dog breed might have a different effect on the animals. According to Ueckermann et al. (1975) dogs accompanying persons do not effect red deer, fallow deer or wild boar considerably, but in most cases agitate roe deer. This may be that the smaller roe are more prone to fall prey to feral canines. In other studies dogs accompanying a person did not present a special threat in opposition to loose canines, which can cause maximal heart rates and intense flight reactions (for bighorn sheep MacArthur et al., 1979; for roe deer Stadler, 1985; Gaisbauer, 1988). Miller et al. (2001) measured greater flush distances of mule deer when confronted with pedestrians accompanied by a dog on leash than with persons walking alone and Scottish red deer were more vigilant when dogs were present (Jayakody et al., 2008). Yet some studies indicate that humans evoke flushing of wild ungulates more easily than canines (Stankowich, 2008) and elk responded to human-predation risk more intensely than to wolf-predation risk (Proffitt et al, 2009).

After persons walked the round tour with and without a dog, red deer spent much time nosing the ground (olfactory control). In doing so they often walked along the route the persons went. Interestingly the red deer hardly showed this behavior after horses were ridden along the route. It might be that the hooves of the horses leave less traces of scent behind than the soles of dogs or shoes. As mentioned in the methods section, olfactory control was investigated only for red deer (since this behavior was not obvious with roe deer).

Both for roe and red deer reactions towards equestrians were less than towards persons walking without horse. At the first encounter with equestriansthe roe deer reacted with intense flight, whereas red deer were much less disturbed compared to persons on foot, even though they never were confronted with horses before. Ueckermann et al. (1975) state that single riders riding quietly do not disturb deer, but agitate them when moving in large groups and fast paces, even when using the familiar trails. These trends could also be observed in this study, but could not be statistically verified (small sample). Kucera (1976) observed shorter flushing distances of white-tailed deer towards equestrianscompared with persons on foot. Depending on circumstances roe deer can show very different reactions towards equestrians. In regions with frequently used riding trails roe deer often only stand alert when encountering riders without fleeing and it is possible to pass the animals much nearer than on foot, sometimes by only a few meters. In areas, where equestrians are a rare occasion and other disturbance factors such as free-roaming dogs are present, roe deer may panic when confronted with horses (personal observations). Color did not seem to play a major role. In this study it was irrelevant for the reactions if the horse was of white or brown color. Likewise chamois approached by persons in differently colored jackets (bright yellow, red or dark blue) showed similar flush distances (Raveh, 2004, cited in Ingold, 2005).

The reactions towards tractors were minimal. This is in contrast to Mrlik (1987), who observed high flight distances of roe deer when confronted with tractors and other motor vehicles. Yet most studies show that wild ungulates reacted less toward vehicles than toward humans on foot (Schultz and Bailey, 1978; MacArthur, 1979; Ward and Cupal, 1979; Kucera, 1979; Stankovich, 2008). Only if a vehicle stopped nearby the animals, they were alerted (Ward and Cupal, 1979). Elk displayed strong reactions (movement rates and probability of flight) towards all-terrain vehicles traveling off-roads, followed by mountain biking, and least reactions towards hiking and horseback riding (Wisdom et al., 2005; Naylor, 2009).

In contrast to the roe deer, red deer were barely disturbed by the hang-glider. Once by chance a hot air balloon crossed the enclosure very low and the red deer reacted merely with alertly watching it while lying. Also Delap (cit. Heidemann, 1973) mentions the total indifference of red deer towards objects above them. The reason seems to be, that birds of prey do not present a threat for red deer. Roe deer showed increased heart rate reactions after disturbance trials with the hang-glider, even though only the fawns are vulnerable for birds of prey (Raesfeld et al., 1985). Chamois, however, which can be prey to eagles, are very disturbed by hang-gliders, sailplanes and mock eagles (Hamr, 1988).

The high heart rate reactions of the red deer calf during feeding were surprising. This was probably caused by restlessness at the feeding site when the beets thrown in lay near to each other. The male deer chased the calf away which trotted to and fro before it dared to approach the beets again. In practice it is important when feeding red deer to have sufficient feeding sites with ample space between them to avoid social conflicts. Animals low in social rank that must wait at too small feeding stations until the other animals clear the site are also more inclined to bark peeling (Onderscheka, 1986).

In one case the male red deer spike at first fled from the group of people during a disturbance trial but then lay down in a corner of the enclosure and laid its head flat on the ground. As the group drew nearer it got up and continued its flight. Müller-Using and Schloeth (1967) describe adult cervids that are not integrated in a herd going in a prone position when alarmed. Walther (1969) observed two cases where adult Thomson's gazelles chased by dogs abruptly lay down, but he adds that this behavior is an exception. Also Kurt (1991) and Danilkin (1996) mention that adult roe deer can show prone responses towards very strong disturbance stimuli. According to Stöhr (1982) bradycardia combined with passive behavior is an indication for indecisiveness towards an overpowering stimulus.

4.3.2. Influence of Season and Time of Day

Both roe and red deer were more easily activated and stayed longer active in the morning and evening hours. Roe deer showed a strong endogenic activity pattern in early autumn that was barely influenced by disturbance trials, even when frequently carried out. In this time period the roe deer had an intense want for resting at daytime and could hardly be activated through optical or acoustical stimuli. If they had to escape, they were active for only a short time span and the animals mostly lay down again within a couple of minutes. Such short interruptions could split a resting bout, increasing the number of resting bouts per day and shortening the mean duration of the bouts, yet the total activity budget remained uninfluenced by the disturbances. Analysis of their behavior showed that the investigated roe deer mostly stood alert or showed locomotion during the short active phase, thus they could be considered as disturbed until they lay down again.

In late autumn roe deer reacted stronger towards disturbances, yet this should not necessarily be interpreted as sensitization towards disturbances, since the roe deer generally tended to be much more active in this time of season, also when not disturbed. If a lying deer was activated in late autumn it stayed longer active before lying down again, sometimes even for hours. However they did not show disturbed behavior during the whole active time period. The disturbance seemed to be more a stimulus for changing their activity, as Heidemann (1973) already stated.

Red deer were investigated in disturbance trials only in winter, so that no explicit statements about seasonal variation in disturbance effects can be made.

4.3.3. Compensation Strategies

Roe and red deer showed different strategies of compensating after being disturbed. Both in early and late autumn roe deer did not change the amount of total activity in the daytime as well as for 24 hours when disturbed. The lengths of resting bouts of roe deer were shortened on days with disturbance trials. At the same time the number of resting bouts per day increased, so that the total activity budgets for daytime as well as for 24 hours were not influenced by disturbance trials.

The red deer, when activated, stayed in average nearly 40 minutes active before lying down again. As a consequence of the activations red deer shortened their resting bouts, but instead of compensating the loss of resting time by increasing the number of resting bouts such as roe deer did, they increased the daily amount of time active. Thus their activity budget was modified by disturbances, on days with disturbance trials they rested half an hour less in the daytime and did not compensate this in the night.

In spite of the very short and strong heart rate reactions after disturbances, roe deer did not show any long-term changes in resting heart rate. Red deer in contrast had decreased resting heart rates on days on which disturbance trials were carried out. Possibly the animals compensate the increased proportion of activity on days in which they are often disturbed with subsequent deeper resting phases. Another explanation would be in raised attentiveness on restless days which is accompanied by bradycardia.

4.3.4. Habituation

Towards the end of the test period red deer showed a decreased duration of disturbed behavior and less heart rate reactions, which suggest a certain habituation towards optical and acoustical stimuli (but not significant). Yet solely with horse riding trials a significant reduction of heart rate reaction with proceeding disturbance trials could be observed. These findings correspond with Naylor et al. (2009), where elk showed no habituation towards all-terrain vehicles, mountain biking and hiking, but possibly towards horseback riding.

The responsiveness of roe deer towards disturbances seems to be strongly dependent on the season. In the second half of the test period (late autumn) roe deer were much more susceptible to disturbances as in the first half of the test period (early autumn). Therefore no habituation could be determined for the investigated time period.

In the mountain bike trial series it first seemed that the red deer habituated to the mountain biker with continuously lower heart rate peaks and no noticeable heart rate increase in the 7th trial. But from the 8th trial on heart rate increased again. In the behavioral analysis there were no signs of habituation.

4.3.5. Synchronization of Behavior

Between both red deer stronger synchronization of activity in the disturbances trials could be found than between the roe deer. One explanation could be the strong social structure of red deer that may lead to more uniform reactions. However, it must be pointed out that both deer species were investigated in disturbance trials in different seasons, therefore a direct comparison is not possible. Several investigations showed stronger synchronization of behavior during the winter months for roe deer (Ellenberg, 1978; Mertens, 1984; Jeppesen, 1989) and red deer (Georgii and

Schröder, 1981). Jeppesen (1989) attributes this to the stronger photoperiodic influence of behavior in winter. Thus synchronization of behavior is also much stronger during twilight than at daylight time (Turner, 1980). According to Bützler (1974) specific behavioral types, such as flight or standing alert, are stronger synchronized than others (e.g. comfort behavior).

4.3.6. Bedding Sites

Roe Deer

The sudden change of bedding site of the roe deer on October 24th was probably caused by spanning the rope for the hang-glider across the small grass patch where they usually had lain. The weather change and the change in activity pattern already took place beforehand on October 21st, and the third roe deer was introduced to the enclosure later on. The roe deer mostly chose bedding sites in which they were partly sheltered by high grasses or shrubs. According to Mysterud and Østbye (1995) winter bedding sites of roe deer in open habitat required ground cover for protection against the wind and no beds exposed to direct sunlight were recorded in the "summer" study of Mysterud (1996).

Red Deer

It was noticeable that the red deer investigated often chose the same bedding site again on one day, even when disturbed, but selected a different bedding site on the next day. Possibly weather conditions influenced their choice. According to Heidemann (1973) shelter from wind was crucial for fallow deer in selecting the bedding site and the red deer investigated by Fischer and Gossow (1985) preferred bedding sites under cover of trees. These tendencies could not be perceived with the red deer investigated in the trials, after all in almost half of all bedding cases they lay on the open grass field, partly even on the small, sun exposed mound with good overview. This was in accordance with the red deer Zhang and Xiao (1990) studied, which selected bedding areas exposed to the sun during late winter. Jiang et al. (2007) frequently found red deer bedded in shrub stands near sunny ridge tops and stated that human disturbances had only little discernible effect on bedding site selection. Also Millspaugh et al. (1998) found that wapitis were not influenced by predictable human disturbances in choosing their bed sites, but rather sought places with adequate thermal cover in summer.

4.3.7. Methodological Aspects

Activation and length of active bouts after being activated could easily be identified from the offline-data (based on minutes). Activation appears to be a better indicator for the influence of anthropogenic disturbances than the duration. With roe deer it was insignificant for the length of the following active bout by which type of disturbance it was induced.

Rather than comparing the active behavior after disturbance with the resting behavior before, it made sense to compare the behavior of activated animals with undisturbed active behavior and measure how long it takes until normal active behavior occurs again. In doing so food intake and standing alert should particularly be taken in account, since food intake is important for the energy budget of the animal and standing alert is an indication of disturbance. The share of time standing alert is a better criterion for disturbance than the frequency of lifting the head.

According to these criteria roe deer showed normal behavior within seven minutes after optical disturbances.

Heart rate is a good indicator for disturbance effects in animals and owing to its close coherence to energy budget and the relatively easy measurability it is a popular parameter for examining stress in animals. Thereby the number of additional heart beats proved to be a better measure for a disturbance effect than the maximal or mean increase in heart rate. Even so, heart rate, if used by itself, is not always conclusive, since it is highly dependent on the respective activity of the animal. In some situations heart rate actually drops when the animal is disturbed, e.g. during standing alert (alarm bradycardia). Therefore it makes sense to combine measurements of heart rate with behavioral analysis.

The results of the disturbance trials show the effects of various disturbances on heart rate, activity and behavior of roe and red deer under controlled, experimental conditions. However, the results cannot be simply transferred to free-ranging animals. Following points should be considered:

- The animals were raised in captivity and were to some extent accustomed to humans, although they were not tame. Entirely new stimuli for the animals were horses and hang-gliders.
- The enclosure limited the possibility for the animals to escape from the source of disturbance, so that the reaction provoked by the stimulus was possibly prolonged.
- The hang-glider always “flew” the same stretch. After a few trials the surprise effect of an object suddenly appearing in the sky from any direction is reduced (spatially specific habituation).
- The population was non-hunted (except single days per year for regulation culling). Experimental gunshots did not have a negative outcome for the animals. Bützler (2001) indicates that red deer integrated in a herd link the sound of gunshots with a culled animal and maybe even pass on this experience to the next generation. Hunted roe deer also had greater flight distances than non-hunted animals (de Boer, 2004).
- It should also be mentioned that the tractor was driven outside of the enclosure, whereas the disturbance trials with persons or horses took place inside the fenced area. The separating fence may have an influence on the flight reactions of the animals.
- The animals were fed ad libitum. This has an influence on the physical condition of the animals and the resultant behavior, for instance reindeer in bad physical condition reacted differently towards hunters than well-fed animals (Skogland and Grøvan, 1988). Undernourished and well-fed white-tailed deer had similar seasonal and circadian activity patterns, yet the undernourished animals showed much stronger flight reactions (Ozoga and Verme, 1970).
- Only two young red deer were tested in the trials. According to Petrak (1988) red deer groups including older and experienced animals often reacted only with standing alert when disturbed, whereas groups with young, inexperienced animals fled in the same situation.

Disturbance trials in enclosures also have many advantages. The good observability facilitates the interpretation of the biotelemetrically transmitted data, since it could repeatedly be compared with video recordings. Above all in the wild there are frequently uncontrolled disturbances, which hinder the interpretation of activity and heart rate.

5. CONCLUSION

Disturbances by humans can cause changes in behavior, activity pattern and heart rate of deer. Optical stimuli generally caused high short-time heart rate reactions, whereas acoustic stimuli evoked only mild heart rate reactions, except for gunshots, which elicited strong heart rate reactions both in red deer and especially in roe deer. Altogether the reactions of roe deer towards stimuli were short and strong, whereas red deer tended to show less obvious but persisting reactions.

Roe deer were much more susceptible to disturbances in times when they showed more activity (twilight, late autumn). It can be assumed, that in the rest of the year the animals are also more easily disturbed by human activities at times when they themselves are more active. Disturbances in winter are in double sense a concern. First, deer react more sensitive towards disturbance stimuli in this time of the year, and secondly the impact on their energy budget is of greater consequence in winter with food shortage. This should be specifically considered with human winter recreation activities, particularly at dawn and dusk.

Hunting also has a great influence on the reaction of deer towards disturbances. Non-hunted populations have less flight responses than hunted populations (Schultz and Bailey, 1978; de Boer et al., 2004; Stankowich, 2008). Deer shift their home range during hunting season and increase nocturnal activity (Kilgo et al., 1998). Burghardt et al. (2012) observed that intensively hunted red deer reacted with withdrawal in dense forest stands and reduction of locomotive activity, whereas deer in a non-hunted population in the Bavarian Forest National Park reacted with increased mobility when disturbed. They explain these diverging behaviors with differing adaptation towards human hunters dependant on eyesight, and natural predators, e.g. wolves. Elk were more likely to be harvested if they selected open areas and their movement rate increased (Ciuti et al. 2012b). With progressing hunting season deer changed behavior and visibility of deer decreased (Bonnot et al., 2012) making hunting effort more difficult (Grau and Grau, 1980). Thus hunting seasons should be kept short, if disturbances of deer are to be minimized. This can be realized by interval hunting (Reimoser, 1991). Focus hunting (Reimoser, 1991) on the other hand can be targeted to keep deer out of areas susceptible to game damage, by culling higher numbers and deliberately creating disturbance to drive the animals in other less sensitive areas. Continous selection of “bold runners” over “shy hiders” by hunting (Ciuti et al. 2012b) may lead to a genetic change in the behavioral traits of deer populations.

Especially red deer are less disturbed by equestrians than by persons walking alone or in groups. This may be that horses as herbivores are of no threat to deer and partly cover the scent of the rider or at least signalize that there is no threat of other predators nearby. This would not be the case if deer were hunted from horseback. Also wild animals tend to respond most to the human upright form (Taylor and Knight, 2003), which is concealed on horseback. Wildlife biologists can even take advantage of this fact and benefit from a better viewpoint, and easier transport of equipment in areas inaccessible by vehicles (Kucera, 1976). Particularly since disturbance by horseback riding is minimal compared to all-terrain vehicles (Naylor et al., 2009). Dogs should stay directly nearby to persons (e.g. on leash), then they do not affect deer considerably more than persons without dogs, contrary to free-running dogs.

Response of mule deer to mountain bikers is similar to hikers. Although bikers at higher speeds are more unpredictable than hikers, this is compensated by the fact that the human form is not distinguishable (Taylor and Knight, 2003). Walking off trails leads to more disturbance of deer than staying on paths (Herbold, 1995; Miller et al., 2001; Taylor and Knight, 2003) and deer flee much more often when an observer stops, as opposed to walking continuously onward (Borkowski, 2001).

People are not always aware of how they affect wildlife and often underestimate their impact (Taylor and Knight, 2003; Sterl et al., 2008). This should be taken into account, as animals may lose large parts of their habitat due to frequent recreational activities (Gander and Ingold, 1997). To which extent is also dependent on the species, e.g. roe deer are behaviorally very flexible (Jepsen and Topping, 2004) and seem to cope with human disturbance near settlements better than red deer (Jiang et al., 2008). In critical habitat areas and wildlife sanctuaries recommendations for recreationists should be given to minimize disturbances (Figure 62), for example using paths instead of going off-trail, avoiding very attractive areas for deer such as forest-meadow boundaries (“edge effect”, Reimoser and Ellenberg, 1999) or breeding places (Knight and Cole, 1995a), especially at times when animals are more susceptible to disturbances, e.g. in winter, at dawn or dusk.

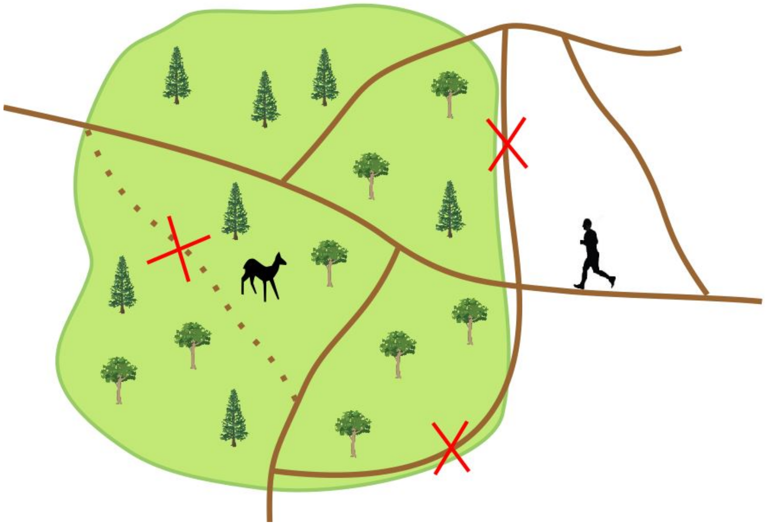


Figure 64. Example of recommendations for recreationists to minimize disturbances. Paths should be used instead of going off-trail. Very attractive areas such as forest-meadow boundaries (“edge effect”) or breeding places should be avoided especially in critical time periods.

In management plans it is also important to distinguish between local, short-term disturbances and regional, long-term disturbances, such as road constructions, and also take cumulative effects into account (Knight and Cole, 1995b; Vistnes and Nellemann, 2008).

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