HOW THE ESTIMATES OF HOME RANGE SIZE AND COMPOSITION ARE AFFECTED BY DIURNAL, NOCTURNAL AND 24-HOUR SAMPLING METHODS: EXAMPLE OF THE RED DEER (*Cervus elaphus*) IN SLOVENIA

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Abstract

Most of the previous research on the mammals' home range (HR) is based on diurnal sampling, while the results are often implicitly considered as representative for an entire 24-h period. However, there is a growing body of research on populations, whose habitat selection changes circadianly, which leads to the hypothesis that HR patterns may vary at different periods of the day. This study used 24-h data from 15 red deer equipped with GPS collars to explore differences in the size and composition of their HRs, estimated on diurnal, nocturnal and 24-h samplings. The differences in composition were shown on the forest/non-forest variable. We established that nocturnal, and in particular the 24-h HRs, largely overlapped with the diurnal HRs (64% and 76%, respectively) and that parts of the HRs that are used exclusively nocturnally are contiguous or adjacent to diurnal HRs. The differences in HR sizes were significant only between diurnal and 24-h HRs. However, the HR composition varied substantially: the average proportion of non-forest areas was 15% in diurnal, 26% in 24-h and 31% in nocturnal HRs. This study demonstrated that with diurnal sampling it is impossible to assess accurately the size and composition of 24-h HRs of red deer in Slovenia. There are several indices that the same is true of several other populations/species. It is therefore important to be aware that HR patterns estimated on the basis of diurnal sampling may be incomplete or even wrong if generalised across the 24-h period.

Key words: *Cervus elaphus*, home range size, home range composition, GPS telemetry, diurnal, nocturnal, 24-hour location sampling, Slovenia

VPLIVI DNEVNE, NOČNE IN 24-URNE SHEME SNEMANJA LOKACIJ NA OCENE VELIKOSTI IN ZGRADBE INDIVIDUALNIH OBMOČIJ AKTIVNOSTI NA PRIMERU JELENJADI (Cervus elaphus) V SLOVENIJI

Izvleček

Večina raziskav območij aktivnosti (v nadaljevanju HR) sesalcev temelji na dnevnem vzorčenju lokacij, pri čemer rezultate implicitno pogosto privzemamo kot reprezentativne za celotno 24-urno obdobje. Vendar je raziskanih vse več populacij, pri katerih se habitatni izbor cirkadiano spreminja, kar navaja k hipotezi, da se med deli dneva lahko razlikujejo tudi značilnosti HR. V raziskavi smo na osnovi 24-urne GPS telemetrije 15 osebkov analizirali razlike v velikosti in zgradbi dnevnih, nočnih in 24-urnih HR jelenjadi. Razlike v zgradbi smo prikazali na primeru binarne spremenljivke gozd-negozd. Ugotovili smo, da se nočni in zlasti 24-urni HR pretežno prekrivajo z dnevnimi (64 % oz. 76 % prekrivanje) in da se deli HR, ki jih jelenjad uporablja izključno ponoči, praviloma stikajo z njenimi dnevnimi HR ali pa so v njihovi neposredni okolici (mediana oddaljenosti 125 m). Razlike v velikostih HR so statistično značilne le med dnevnimi in 24-urnimi HR. Močno pa se razlikujejo zgradbe HR: delež negozdnih površin v dnevnih HR znaša 15 %, v 24-urnih 26 % in nočnih HR 31 %, zlasti velik (56 %) pa je v delih HR, ki jih jelenjad uporablja izključno ponoči. Pričujoča raziskava je pokazala, da v Sloveniji z dnevnim spremljanjem ni mogoče točno ugotoviti velikosti, še manj pa zgradbe 24-urnih HR jelenjadi. Več indicev kaže, da je podobno tudi pri mnogih drugih populacijah/vrstah. Zato se je pomembno zavedati, da so lahko značilnosti HR, ki so ugotovljene na osnovi dnevnih spremljav, pomanjkljive ali celo napačne, če jih generaliziramo na 24-urno obdobje.

Ključne besede: Cervus elaphus, velikost območij aktivnosti, zgradba območij aktivnosti, GPS telemetrija, dnevno, nočno, 24-urno vzorčenje lokacij, Slovenija

INTRODUCTION
UVOD

Home range (HR) is an area traversed by the individual in its normal activities of food gathering, mating, and caring for young (BURT 1943). HR size is therefore an important ecological parameter affected by body mass, nutrition, spatial distribution and abundance of resources, as well as gender, reproductive status and mating system (DAHLE / SWENSON 2003; FISHER / LARA 1999; HARESTAD /BUNNELL 1979; LITVAITIS / SHERBURNE / BISSONETTE 1986; MASSEI *et al*. 1997; TUFTO / ANDERSEN / LINNELL 1996). HR is typically estimated from a sample of observations, used to establish the probability that an animal was in a certain area during the specified period of time. It is important to know, therefore, how HR (and HR patterns) depends on the methodology (e.g. HR estimator, sampling scheme, location errors) with which it is established.

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The greater part of the previous HR research is based on animal locations sampled only in a part of the day, typically in the diurnal period. Considering its financial and logistical limitations, VHF telemetry – until just a few years ago the most frequent monitoring method – typically rendered 24-h sampling impossible in practice (e.g. PRIEDE 1992; RODGERS 2001). Knowledge of nocturnal and 24-h HRs, and the differences in HR size and composition between parts of the day, is therefore lacking. Nevertheless, the results of diurnal sampling are often implicitly considered as representative of the entire 24-h cycle. For example, BEYER and HUFLER (1994) reviewed 56 habitat selection studies of mammals thought to be active throughout 24-h periods, and determined that 39.3% of investigators only sampled habitat use during diurnal hours and 21% did not even report when the sampling occurred.

The diurnal and nocturnal habitat selection and activity of animals may differ due to several factors, such as predator activity, circadian oscillation of air temperature and other abiotic factors (AGER *et al.* 2003; LOE *et al.* 2007; MILLSPAUGH *et al.* 1998; MOEN 1976). Remarkable differences have been estimated for populations in areas with frequent anthropogenic disturbance. Red deer in Michigan and east Kentucky, for example, avoid open areas in diurnal hours, when people are active, but use them extensively during the night (BEYER / HAUFLER 1994). Similar adaptations to human disturbances – which can be manifested externally in the diurnal avoidance of roads and settlements, a pronounced diurnal use of security cover and nocturnal use of feeding habitats, and a shift to nocturnal activity – have also been reported for other ungulate species (HAYES / KRAUSMAN 1993; KILPATRICK / SPOHR 2000; WICHROWSKI et al. 2005) as well as large predators (KUSAK / MAJIĆ-SKRBINŠEK / HUBER 2005; KACZENSKY *et al.* 2006; MOE *et al.* 2007). Therefore, one would expect that HR size may also be different at different parts of the day. However, for the ungulates, for example, which are a well studied animal group, we have found only two published papers, comparing the size of diurnal and nocturnal HRs (HAYES / KRAUSMAN 1993; PERELBERG *et al.* 2003). They did not establish significant differences in HR size, but these were not expected, as there was no difference between the diurnal and nocturnal habitat selection. Similarly, there are surprisingly few studies that analysed the differences in HR composition between parts of the day (BORKOWSKI / PUDELKO 2007; HAYES / KRAUSMAN 1993; KERNOHAN *et al.* 1996).

The purpose of this study was to determine the size and spatial overlap of diurnal, nocturnal and 24-h HRs of red deer in Slovenia, where this species is regularly exposed to anthropogenic disturbances affecting its year-round, seasonal and diurnal-nocturnal habitat selection (DEBELJAK *et al.* 2001; JERINA 2006; JERINA *et al.* 2002). Furthermore, using the binary forest – non-forest variable, which in a preliminary study (JERINA 2006) explained most of the variance between the diurnal and nocturnal spatial distribution of red deer locations, we analysed the differences in HR composition.

Forest is the primary habitat of red deer in Slovenia, as it provides cover from extreme abiotic factors, predators, and humans, and satisfies a large part of the species' nutritional demands. Yet local density, body mass and population dynamics of the red deer are also strongly affected by accessibility of meadows and other non-forest areas (JERINA 2006; JERINA 2007; JERINA *et al.* 2002), which are a key feeding habitat for red deer, providing approximately a half of its annual food (ADAMIČ 1990). In all previously analysed areas, red deer move on a daily basis from the forest, where they stay during the day, to open areas, where they spend parts of the evening until the morning period (JERINA 2006). During the daytime, they typically use parts of forest farther from the forest edge, but otherwise they select forests of similar composition in both parts of the day. Ungulates use different functional groups of habitats over the 24-h cycle: diurnal and nocturnal resting places and diurnal and nocturnal feeding habitats (FORESTER *et al.* 2007; GREEN / BEAR 1990; MYSTERUD / OSTBYE 1995; TENG et al. 2004). The important trade off criterion in the selection of these groups of habitats is distance between them, which should be minimised, to lower the energy costs and time needed for travelling between them (MYSTERUD / IMS 1998; MYSTERUD / LIAN / HJERMANN 1999; MYSTERUD / OSTBY 1995). It can, therefore, be expected that red deer diurnal HR is adjacent to non-forest areas that they use nocturnally and that their diurnal and nocturnal HRs largely overlap.

This study tested the following hypotheses: a) the proportion of non-forest in the nocturnal HR is larger than in the 24-h HR, which in turn is larger than in the diurnal HR; b) diurnal and nocturnal HRs of red deer overlap at least partially; in parts of the HR, used exclusively nocturnally (i.e. the part of nocturnal HR located outside diurnal HR), the proportion of non-forest areas is larger than in diurnal or nocturnal HRs and grows with regard to the distance from the border of diurnal HR.

METHODS
METODE

STUDY AREA
RAZISKOVALNO OBMOČJE

The study was carried out in several parts of Slovenia (for details see JERINA 2006), from the north-westernmost area bordering Hungary to southern and central areas and the western edge along the border with Italy (45°33′–46°51′ N, 13°24′–16°20′ W; Figure 1). The study areas cover a broad gradient of ecological factors, which is important in terms of general validity of the results. From the east towards the west, the climate shifts from sub-continental with great seasonal and diurnal-nocturnal temperature variations and little precipitation to a sub-Mediterranean with mild winters and hot summers. The high Dinaric plateaus in the south have a mountain climate with high precipitation and long periods of snow coverage. The average annual temperatures range from 5.1 °C to 8.5 °C and annual precipitation from 700 to 1,900 mm. The vegetation is diverse: over 70 different forest associations and sub-associations have been described in the study areas. The most common tree species are the silver fir (*Abi-es alba*), European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), pedunculate and sessile oaks (*Quercus petrea* and *Q. robur*), and Scots pine (*Pinus sylvestris*). The average forest cover ranges from 55% to 90%, the rest being mostly meadows, arable land, and early succession stages of forest. The red deer population density is relatively high, from 1.7 to 5.0 animals / km², except along the border with Italy, an area that is still colonized by the species. In all the study areas, red deer have to cope with anthropogenic disturbances, be it due to logging, hunting, recreation, traffic or settlements. For example, the average distances to the nearest main road in study areas are only 1,000 – 1,900 m, to a forest road 130–250 m, and to settlements 1,000 – 2,200 m. The cumulative size of the study areas is 1,820 km².

RED DEER CAPTURE AND TELEMETRY
ODLOV IN TELEMETRIJA JELENJADI

In the 2004–2007 period, we captured 15 animals of both sexes and equipped them with GPS-UHF PLUS 3 collars (Vectronic Aerospace GmbH). The collars were set up to record locations every full hour, 24 hours a day for one year, and then fall off. The monitoring of two animals ended

Fig. 1: Study areas and capture locations of 15 red deer, which were monitored every hour, 24-hours per day up to one year with GPS telemetry, Slovenia.

Slika 1: Območje raziskave in mesta lokacij odlova 15 osebkov jelenjadi, ki smo jih z GPS telemetrijo spremljali vsako uro, 24 ur na dan v obdobju do enega leta.
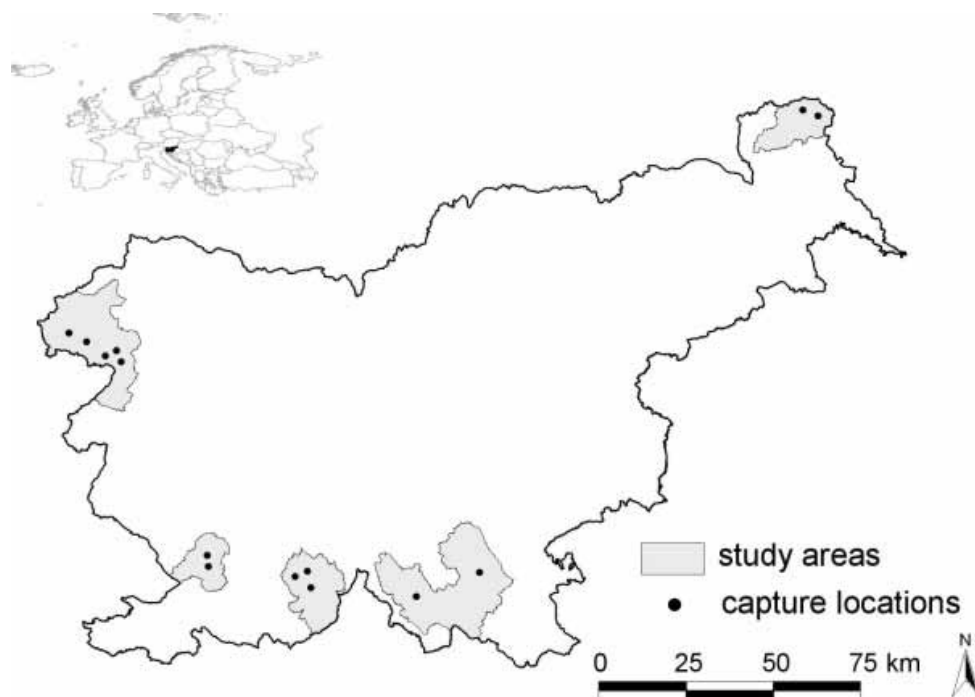
prematurely (after 3 and 11 months) due to poaching and a fatal car accident, while on two collars the power supply failed prematurely (both 11 months). The average location sampling success rate (i.e. the number of recorded locations / the total number of attempted recordings) was 71.2%.

SELECTION OF LOCATIONS FOR ANALYSIS OF HR SIZE AND COMPOSITION
IZBOR TELEMETRIJSKIH LOKACIJ JELENJADI ZA ANALIZE VELIKOSTI IN ZGRADBE HR

All existing HR models assume that recorded locations are an unbiased sample of the spatial distribution of the monitored animal (HORNE *et al*. 2007). Yet the sampling methods typically fail to meet this assumption (GRAVES / WALLER 2006), sometimes resulting in significant bias in the established HR size and composition (HORNE *et al*. 2007). Several researchers tried to control for the sampling bias by assessing the impact of presumably important environmental variables on the probability of location recording and giving each location a weight depending on the local values of these variables (D'EON *et al*. 2002; FRAIR *et al*. 2004; JOHNSON *et al*. 1998). HORNE *et al*. (2007) showed that such an approach provides better results (smaller bias in data) than uncorrected data.

The GPS locations used in this study are clearly biased, as the success of recording in the diurnal period, when the red deer are less active and stay almost exclusively in the forest,

is smaller than in the nocturnal period (see figure 2). The average hourly success of location recording and the proportion of non-forest on locations are, for example, almost functionally related (r = 0.99; p < 0.001; n = 24). Therefore we used the above mentioned correction procedure and, in accordance with objectives of the present study, tried to diminish the sampling bias by controlling for the influences of vegetation composition (forest, non-forest) and the time (diurnal, nocturnal period) on probability of successful location recording. Using the procedure described below, we filtered (selected) the locations to obtain samples with balanced diurnal and nocturnal temporal density of locations and with a forest–non-forest proportional to their actual use. These samples of locations (on average 72% of all recorded locations) were used to estimate HRs.

In a previous study (ŽNIDARŠIČ 2005), a subsample of the animals included in the present study were monitored simultaneously with GPS and VHF telemetry. A comparison of the results showed that the probability of successful location recording with GPS telemetry was 0.57 in the forest and 0.92 (unpublished data) in the non-forest, which is within the interval reported for ungulates by other researchers (MOEN *et al.* 1996). The inverse values of these probabilities (e.g. 1.77 and 1.08) were used as weights to the locations. Subsequently, a weighed sum of locations and the frequency of attempted recordings were calculated for each animal for the diurnal and nocturnal period. These two values provided

Fig. 2:   Average hourly success rate of location recording (thick black line) and proportions of non-forest vegetation (thick grey line) at the recorded locations of the monitored red deer in Slovenia. Interrupted grey lines show the average yearly time of sunrise and sunset.

Slika 2:   Povprečna urna uspešnost snemanja lokacij (odebeljena črna črta) in povprečni deleži negozdnih površin (odebeljena siva črta) na posnetih lokacijah spremljane jelenjadi v Sloveniji. Prekinjene sive črte prikazujejo povprečen čas sončnega vzhoda in zahoda v letu.
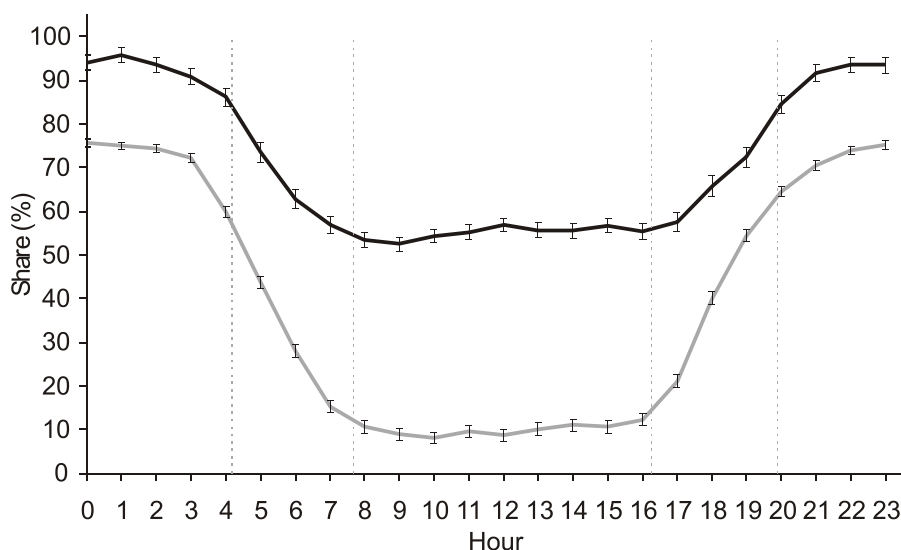
the basis for the calculation of diurnal and nocturnal weights, which made the weighed sum of locations in both parts of the day identical to the number of attempted recordings. A cross-multiplication of both pairs of weights (forest – non-forest, diurnal – nocturnal) produced 4 weights for 4 groups of locations for each animal (diurnal – forest, diurnal – non-forest, nocturnal – forest, nocturnal – non-forest). Finally, in each of the four groups we randomly selected a number of locations whose frequency was proportional to the corresponding weight; all locations were selected in the group of locations with the greatest weight and proportionally fewer were selected in the other groups.

ESTABLISHING HR SIZE AND COMPOSITION
UGOTAVLJANJE VELIKOSTI IN ZGRADBE HR

GPS telemetry data were analysed with the GIS application Arcview 3.2 (Environmental Systems Research Institute Inc., Readlans, USA) and the Animal Movement extension (HOOGE / EICHENLAUB 1997). HR areas were estimated using the 95% fixed kernel estimator (WORTON 1989) with least squares cross validating smoothing parameter, which gives the best estimate of HR size (SEAMAN / POWELL 1996). Diurnal, nocturnal and 24-h HRs were calculated for each animal based on locations selected with the method described above, whereby diurnal HR is based on locations recorded between sunrise and sunset and nocturnal HR vice versa. In dividing the locations in these two groups, we used the time of sunrise and sunset, as the activity of ungulates is tightly synchronized with the photoperiod (BERGER *et al*. 2002; GREEN / BEAR 1990). In all HRs, the frequency of locations was higher than the minimal required (30-100), below which estimated HR can be biased (Girard *et al*. 2002).

The analyses of HR composition was based on land use vector maps of the Slovenian Ministry of Agriculture, Forestry and Food, which are made under standardized protocols using digitized aerial orthophotographs on a 1:5,000 scale and distinguish 42 land use types. The map was re-categorised to forest and non-forest. In red deer HRs, the latter comprise predominantly meadows and arable land: the total proportion of other types of land use (e.g. water, rocks, urban areas) is less than 1%.

We also analysed variation in the composition of parts of the HR that red deer use only nocturnally with regard to the distance to diurnal HR. Data for this analysis were prepared by overlaying parts of the HR used only in nocturnal period

with a grid of points 25 x 25 m, determining the vegetation type for each point (forest, non-forest), and calculating their distance from the nearest boundary of the given animal's diurnal HR.

STATISTICAL ANALYSIS
STATISTIČNE ANALIZE

Data on HR size and composition were tested for the assumptions of normality and homogeneity of variances. One-way ANOVA were used to analyse effects of sex and the sampling duration (full year or part of the year) on HR size and composition. Since none of the tests showed significant differences (minimal p = 0.24), the data from all animals were used, variables were not transformed, and parametric tests were used in the analyses.

Differences in the size and composition of diurnal, nocturnal and 24-h HRs were analysed with one way ANOVA for dependent (within ID of an animal) and once for independent samples. The latter analysis has been performed to determine whether the differences were also significant in general, when individual effects are not controlled for. The differences in pairs of groups of data were examined with the post-hoc Tukey HSD test.

Differences in variability of HR size and composition of the same animal over different periods (hereinafter: variance between periods) and of different animals over the same period (hereinafter: variance between animals) were analysed with the F test. The former was calculated as variance of dependent samples and the latter as pooled variance of both compared periods between animals. For example, in analysing the diurnal – nocturnal variability of HR size, we calculated the variance of HR size between nocturnal and diurnal period within animals and compared it to the pooled variance of HR between animals for the diurnal and nocturnal period.

RESULTS
REZULTATI

HR SIZE
VELIKOST HR

The size of diurnal HRs is on average 424±93 ha, nocturnal 453±139 ha, and 24-h HRs 525±124 ha (Table 1). Significant differences between them were found with the ANOVA for dependent (p = 0.004), but not for independent samples

Table 1:   Comparison of size and composition (proportion of non-forest areas) in diurnal, nocturnal and 24-h HRs of red deer, Slovenia.

Preglednica 1: Primerjava velikosti in zgradbe (delež negozdnih površin) v dnevnih, nočnih in 24-urnih HR jelenjadi v Sloveniji.

		Mean ± conf. int. *Aritmetična sredina ± interval zaupanja*	Min.	Max.
HR size (ha) Velikost HR (ha)	Diurnal / *Dnevni*	424 ± 93	243	845
	Nocturnal / *Nočni*	453 ± 139	178	964
	24-h / *24-urni*	525 ± 124	277	1038
Proportion of non-forests in HR (%) Delež negozdnih površin v HR (%)	Diurnal / *Dnevni*	15.0 ± 5.1	1.2	30.8
	Nocturnal / *Nočni*	31.1 ± 8.0	8.0	50.5
	24-h / *24-urni*	25.5 ± 7.0	5.3	43.6

Table 2:   Spatial overlap of diurnal, nocturnal and 24-h HRs: characteristics of parts of HRs that the red deer use exclusively in the nocturnal period.

Preglednica 2: Prostorsko prekrivanje dnevnih, nočnih in 24-urnih HR: značilnosti delov HR, ki jih jelenjad uporablja izključno ponoči.

	Nocturnal HR (min., max.) *Nočni HR (min, maks)*	24-h HR (min., max.) *24-urni HR (min., maks.)*
Proportion of HR outside diurnal HR (%) *Delež HR zunaj dnevnega HR (%)*	36.0 ± 7.4 (8.6–52.4)	24.5 ± 6.2 (0–40.5)
Proportion of non-forest areas in part of HR outside diurnal HR (%) *Delež negozdnih površin v delu HR zunaj dnevnega HR (%)*	56.0 ± 12.6 (18.5–88.0)	52.4 ± 14.9 (16.4–87.3)
Average, median and 95 percentile distance to the diurnal HR (m) *Povprečje, mediana in 95-percentil oddaljenosti od meje dnevnega HR (m)*	311 ± 165; 191; 523	241 ± 93; 125; 416

($p = 0.43$). Using the post-hoc test, we established significant differences only between diurnal and 24-h HRs (Tukey HSD, $p = 0.008$), which are on average 25±15% larger than diurnal HRs. The size of diurnal, nocturnal and 24-h HRs are correlated (maximum $p = 0.02$; $0.61 < r < 0.89$) (Table 4, see also Figure 4). The variability of HR size between periods was also significantly smaller (F test; maximum $p = 0.004$) than between animals. The variances of size of HRs between animals were 4.3- to 11.3-fold larger than variances between periods (Table 3).

HR COMPOSITION
ZGRADBA HR

The proportion of non-forest areas was 15±5% in diurnal HRs, 25±7% in 24-h HRs, and 31±8% in nocturnal HRs

Table 3:   Comparison of variances of size and composition (proportion of non-forest) of red deer HRs for the same animals at different times of day and between animals at the same time of day.

Preglednica 3: Primerjava varianc velikosti in zgradbe (deleža negozdnih površin) HR jelenjadi za iste osebke med različnimi deli dneva in med osebki za iste dele dneva.

Comparison *Primerjava*	Variance in groups for different individuals *Varianca v skupinah med osebki*	Variance between groups for the same individual *Varianca med skupinama za iste osebke*	F	df1	df2	p
Size of diurnal and 24-h HR *Velikost dnevnega in 24 urnega HR*	34760.7	6046.6	5.7	29	14	0.001
Size of diurnal and nocturnal HR *Velikost dnevnega in nočnega HR*	40443.7	9376.2	4.3	29	14	0.004
Size of 24-h and nocturnal HR *Velikost 24-urnega in nočnega HR*	50370.8	4446.0	11.3	29	14	0.000
Proportion of non-forests in diurnal and 24-h HR *Delež negozdnih površin v dnevnih in 24-urnih HR*	0.0107	0.0038	2.8	29	14	0.027
Proportion of non-forests in diurnal and nocturnal HR *Delež negozdnih površin v dnevnih in nočnih HR*	0.0129	0.0111	1.2	29	14	0.405
Proportion of non-forests in 24-h and nocturnal HR *Delež negozdnih površin v 24 urnih in nočnih HR*	0.0162	0.0027	6.0	29	14	0.001

Table 4: Size and composition (proportion of non-forest) of red deer HRs: correlations between diurnal, 24-h and nocturnal HRs. Correlations for HR size are shown above the diagonal on the upper right side of the table and correlations between proportions of non-forest areas in HRs below the diagonal.

Preglednica 4: Velikost in zgradba (deleži negozdnih površin) HR jelenjadi: korelacije med dnevnimi, nočnimi in 24-urnimi HR. Korelacije velikosti HR so prikazane nad diagonalo na zgornji desni strani preglednice, korelacije med deleži negozdnih površin v HR pa pod diagonalo.

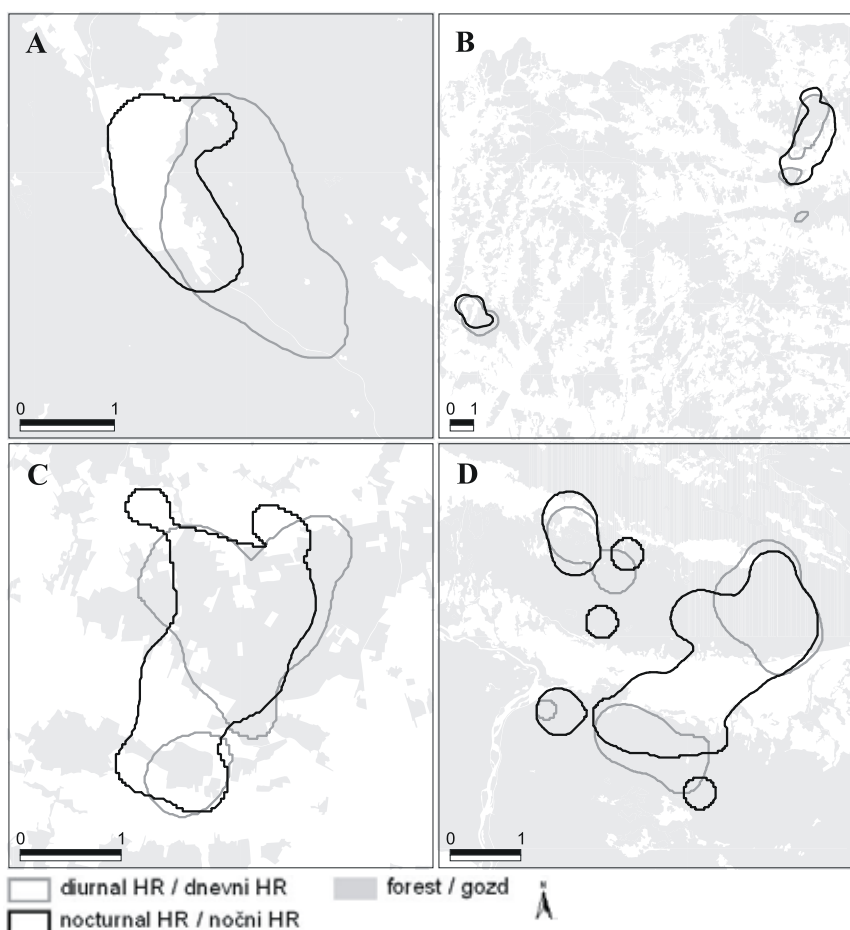|	Diurnal HR *Dnevni HR*		24-hour HR *24-urni HR*		Nocturnal HR *Nočni HR*		HR size *velikost HR*
	r	P	r	p	r	p	
Diurnal HR *Dnevni HR*			0.851	0.000	0.611	0.015	
24-hour HR *24-urni HR*	0.896	0.000			0.889	0.000	
Nocturnal HR *Nočni HR*	0.941	0.001	0.967	0.000			
HR composition (proportion of non-forest areas) *Zgradba HR (delež negozdnih površin)*							

Fig. 3: Diurnal and nocturnal red deer HRs, and forest and non-forest areas. The figure shows four animals (A: Gotenica, hind; B: Goričko, hind; C: Goričko, hind; D: Kobarid, stag) from extremely contrasting environments (highest and lowest forest density) having different life strategies (two residents and two seasonally migrating). Note that diurnal and nocturnal HRs always largely overlap and that parts of nocturnal HRs outside diurnal HRs contain a large proportion of non-forest areas, which are for the greatest part of the year the most important feeding habitats of red deer in Slovenia.

Slika 3: Dnevni in nočni HR jelenjadi in razporeditev gozdnih ter negozdnih površin. Slika prikazuje 4 osebke (A: Gotenica, košuta B: Goričko, košuta; C: Goričko, košuta; D: Kobarid, jelen) iz kontrastnih okolij (največja in najmanjša gozdnatost) z različnimi življenjskimi strategijami (dva osebka sta izrazito sezonsko migratorna, dva pa rezidentna). Iz slike je razvidno, da se dnevni in nočni HR jelenjadi vedno v veliki meri prekrivajo in da deli nočnega HR zunaj dnevnega HR vsebujejo velik delež negozdnih površin.
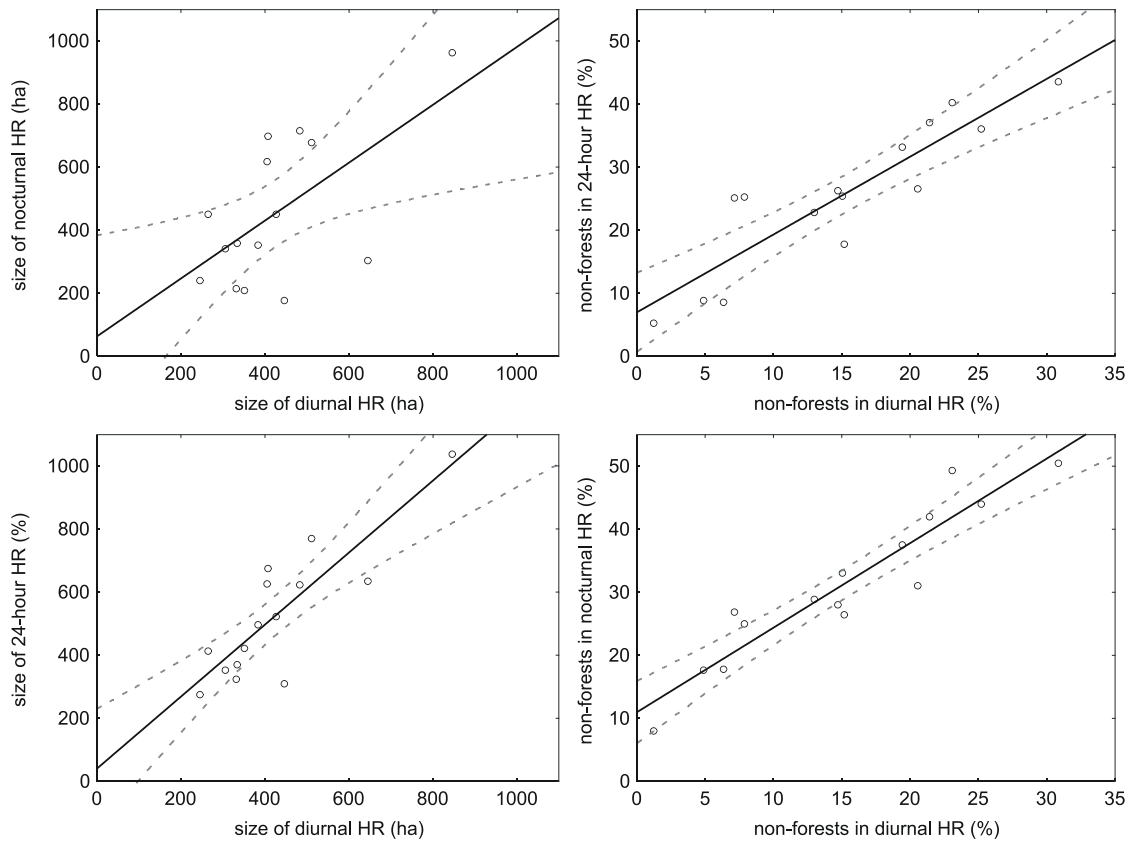
Fig. 4: Linear regression functions between diurnal, nocturnal and 24-h red deer HRs for HR size and composition (proportion of non-forest).

Slika 4: Linearne regresijske funkcije med dnevnimi, nočnimi in 24-urnimi HR jelenjadi za velikosti in zgradbo (deleže negozdnih površin) HR.

(Table 1). HR composition differed significantly with regard to sampling scheme whether the effects of an individual animal's variability were controlled for or not (maximum $p = 0.001$). The post-hoc analysis showed differences between all pairs of comparisons (Tukey's HSD, maximum $p = 0.003$). The proportion of non-forest in nocturnal HRs was on average $190 \pm 104\%$ larger than in diurnal HRs, while in 24-h HRs it was $103 \pm 57\%$ larger. The diurnal – nocturnal change in use of non-forest is apparently very common, as for all monitored animals the proportion of non-forest was largest in the nocturnal HRs, smaller in 24-h HRs, and the smallest in diurnal HRs. The proportion of non-forest areas in diurnal, nocturnal and 24-h HRs were tightly correlated (maximum $p = 0.001$; $0.90 < r < 0.97$) (Table 4, see also Figure 4). Yet due to large nocturnal – diurnal differences in the use of non-forest areas, individual effects were – compared to magnitude of their effects in HR sizes – less influential than the effects of sampling scheme. Variances in the proportion of non-forest between animals were 15% to six-fold larger than between periods (Table 3). The variances of proportions were significantly different in comparisons of diurnal – 24-h period (F test, $p =$ 0.03) and nocturnal – 24-h period (F test, $p = 0.001$), but not in comparison of diurnal – nocturnal period (F test, $p = 0.40$).

HR OVERLAP
PREKRIVANJE HR

HR overlap was analysed only for the pairs 24 h – diurnal and diurnal – nocturnal periods. Previous research typically analysed only diurnal HRs, so these two comparisons are of greatest interest. The areas used by red deer nocturnally, but in particular over the entire 24-h period, largely overlapped with diurnal HRs (Table 2, see also Figure 3); the proportion of 24-h HRs outside diurnal HRs was between 0% and 31% ($24 \pm 6\%$) and the proportion of nocturnal HRs outside diurnal HRs between 9% and 52% (36 ± 7 %). In the part of nocturnal HRs outside the diurnal HRs, the proportion of non-forest was especially high ($56 \pm 13\%$). The same was true of the part of 24-h HRs outside diurnal HRs, where the proportion of non-forest areas averaged $52 \pm 33\%$. Both proportions were significantly larger than the proportion of non-forest in the entire 24-h or nocturnal HRs (paired t-test; maximum $p < 0.001$).
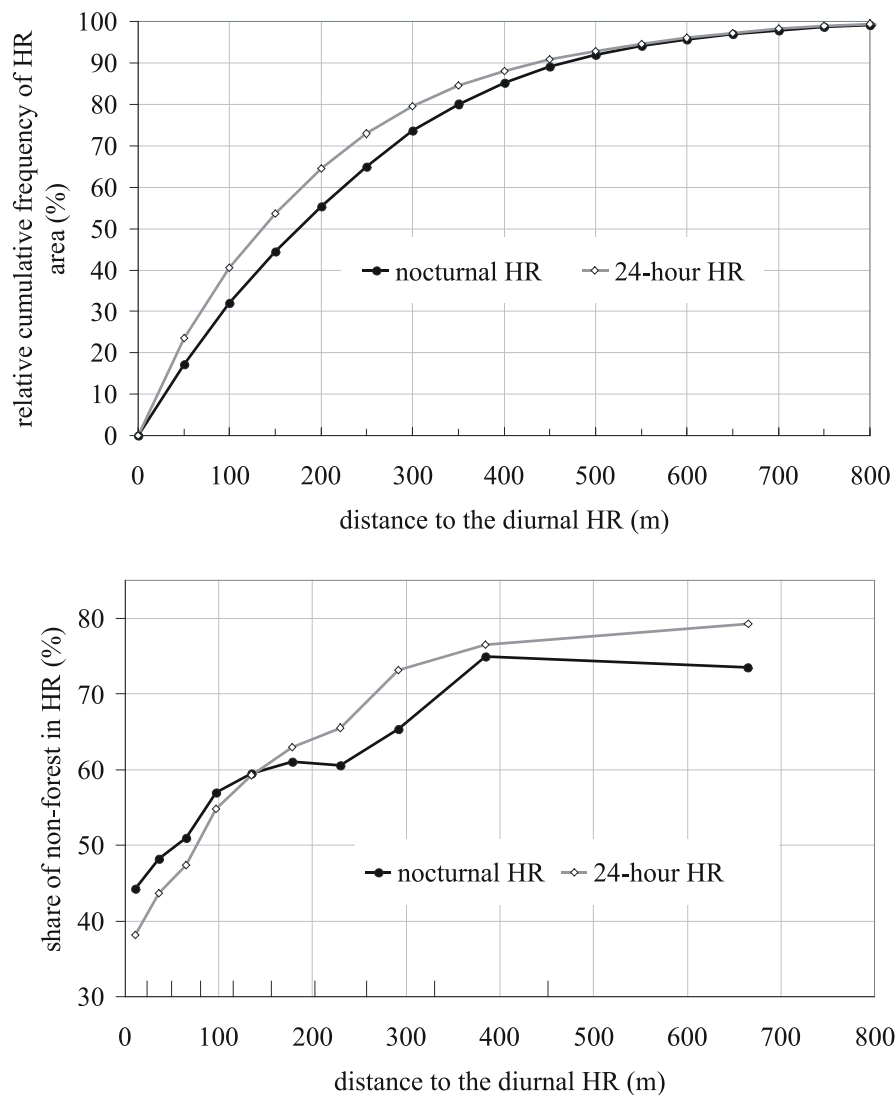
Fig. 5:   In the nocturnal period, the monitored red deer typically used the same areas as in the diurnal period, or areas that im-
mediately surround its diurnal HR. The upper figure shows the relative cumulative frequency of parts of nocturnal and
24-h HRs, which lie outside diurnal HRs with respect to the distance from the diurnal HR boundary; the lower figure
shows the proportion of non-forest in the part of nocturnal and 24-h HRs outside the diurnal HR with respect to the
distance from the diurnal HR.

*Slika 5:   Ponoči je spremljana jelenjad praviloma uporabljala ista območja kot podnevi, ali pa območja, ki se stikajo in so blizu
dnevnim HR. Zgornja slika prikazuje relativno kumulativno frekvenco delov nočnih in 24-urnih HR, ki ležijo zunaj
dnevnih HR, glede na oddaljenost od meje HR, spodnja slika pa deleže negozdnih površin v teh območjih glede na
oddaljenost od meje dnevnih HR.*

The areas that red deer use nocturnally and as a rule over-
lap with the daily HR are contiguous to them or located in their
immediate vicinity. The average distance of parts of nocturnal
and 24-h HRs outside the diurnal HR was only 311±165 m
and 214±93 m, respectively, from the boundary of the diurnal
HR. Due to asymmetrically distributed distances, the medians
were even smaller, at 191 m and 125 m, respectively, and the
last decile 523 m and 416 m, respectively. The proportion of
non-forest areas in parts of nocturnal and 24-h HRs, which
lie outside diurnal HRs, increased with the distance from the
boundary of diurnal HRs (Spearman r = 0.98 and 0.95; maxi-

mum p < 0.001). The remotest parts of the nocturnal HRs thus
comprised as much as 80% of non-forest (figure 5).

DISCUSSION
RAZPRAVA

The study is based on GPS telemetry, which does not pro-
vide an unbiased sample of the spatial distribution of animals,
as the probability of successful location recording may vary
due to multiple factors such as vegetation, topography, and
activity of the animal (CAIN *et al.* 2005; GRAVES /WAL-

LER 2006; MOEN *et al.* 1996). While controlling for the observation bias, we accounted for the influences of vegetation type (forest – non-forest) and time (diurnal, nocturnal period). Other potentially important environmental variables (e.g. growing stock, variables describing terrain characteristics) were either insignificant or were so largely interdependent with the monitored animals that the extrapolation would be unreasonable (JERINA 2006; ŽNIDARŠIČ 2005; unpublished data). Nevertheless, the accounted variables very likely explain a large proportion of the variability of location recording success. After controlling for their effects, the variance of average location recording success, calculated between all hours in 24-h cycle, was reduced 37-fold compared to the raw data (from 0.0290 to 0.0007) and the standard deviation from 17% to less than 3%. The selected locations can, however, still contain some observation bias. As a result, the size and composition of the estimated HRs may be somewhat different than the true HRs, but it seems highly unlikely that the differences would be large and systematic enough to make the results of the study – in which we are interested in comparisons, not absolute values of parameters – an artefact of a residual bias in the data. We therefore considered our data as appropriate for the addressing the posed questions.

Several studies have shown that the circadian habitat selection of animals can be affected by human disturbances. For example, KERNOHAN *et al.* (1996) reported that in areas with infrequent disturbances, daily sampling satisfactory describes the 24-h habitat selection patterns of white tailed deer (*Odocoileus virginianus*). Similarly, HAYES / KRAUSMAN (1993) concluded that nocturnal sampling of habitat selection of desert mule deer (*O. hemionus*) in Arizona is representative of the diurnal period as well. In contrast, studies of ungulates in areas with frequent anthropogenic disturbances established that their diurnal and nocturnal habitat selection were remarkably different (see references in introduction). In Slovenia, for example, red deer spend diurnal hours farther away from roads and settlements, deeper in the forest; they use non-forest areas less frequently, but when they do they keep closer to the forest edge than in the nocturnal period (JERINA 2006). The use/impact of these variables also changes during the week in accordance with the dynamics of human activities, which provide for further evidence of human influences. Most of the listed studies compared the habitat composition of recorded locations of the monitored animals. Moreover, our study showed that diurnal – nocturnal habitat selection changes unduly, which is also reflected in the estimated HR

composition, more specifically in the proportion of non-forest areas in HR. We believe that differences between composition of HRs could probably be estimated also for the other previously mentioned variables from the study of red deer, whose diurnal and nocturnal use/impacts were different, as they all vary on a greater spatial scale.

This study demonstrates that the location sampling scheme does affect the established HR size of red deer, but the differences were smaller and less consistent among individuals than in HR composition. The HRs of the majority of the monitored animals (12 out of 15) had multiple centres of activity; for one-third of the animals (5 out of 15) that migrated seasonally, the centres were as far apart as 10 km to 20 km. In the multiple-centres use of space, the kernel method typically provides small estimates of HR size compared to circular, bivariate normal HR models (JENNRICH / TURNER 1969) and the minimum convex polygon method (HAYNE 1949), frequently used in the past. Unlike the kernel method, these methods always produce convex and continuous HRs that may therefore include areas that the animals do not use. With the minimum convex polygon method, for example, the HRs of the monitored red deer are on average almost 5-fold larger than the kernel method estimates (JERINA, unpublished data). Since the diurnal – nocturnal movements of red deer are commonly small compared to seasonal migrations (GEORGII / SCHRODER 1983; KAMLER / JEDRZEJEWSKA / JEDRZEJEWSKI 2007), we infer that the relative differences in HR size would be even smaller if HRs were determined with one of the above mentioned estimators. The same is true of HR composition, but just the opposite the correlations between HR size as well as composition would probably be larger.

HRs of the red deer, estimated for different temporal sampling schemes, largely overlapped. The proportion of nocturnal HRs outside the daily HRs e.g. averaged 36%, whereby they typically surrounded the daily HRs or were in their immediate vicinity: the medians of distances from the boundaries of the diurnal HRs were only 191 m. Considering the maximum diameter of the HRs of the monitored red deer of up to 22 km and an average of 7.6 km, this is a very short distance. The established patterns of use of space are in agreement with expectations. Exclusive diurnal or nocturnal use of certain areas necessarily enlarges the expenditure of time and energy to get to and from those areas. The areas that are used only nocturnally are therefore typically not far from the other parts of HR and their proportion is small. On the other hand, the proportion of non-forest areas in nocturnal HRs is

large and increases with the distance from the boundary of the diurnal HRs. For most of the year, non-forest areas have a much larger food carrying capacity than forests, which is reflected in the red deer's body mass and population density (ADAMIČ 1990; JERINA 2006; JERINA 2007). By feeding in non-forest areas, red deer can thus compensate for the increased expenses of prolonged daily migration.

The present study has thus shown that the size of 24-h HRs of red deer in Slovenia and, to an even greater extent, their composition cannot be accurately accessed by diurnal sampling. There are several indices that the same is true of several other populations/species, in particular in areas with frequent anthropogenic disturbances. Sampling in studies which set out to determine the general characteristics of HR should therefore be designed to cover the entire 24-h period. Research, which analyses HR based on incomplete sampling (e.g. diurnal), should meanwhile equalise location sampling procedures to the greatest possible extent so that all HRs cover the same part of the day, as the established HR characteristics may otherwise also differ due to the sampling differences between animals. For the monitored red deer, for example, even a smaller change in the beginning or end of sampling in the diurnal or nocturnal periods could generate great differences in the established average diurnal or nocturnal use of forest and non-forest areas (see Figure 2) and, consequently, their proportion in the HR.

As already mentioned, most previous studies of HR are based on diurnal sampling, with the results often implicitly taken as being representative of the entire 24-h cycle. Considering the results of this study, this raises doubts as to the accuracy and conclusions of the previous research. In interpreting the studies, which are based on incomplete sampling, it needs to be kept in mind that the HR size, shape and composition may be different if they were established on the basis of 24-h sampling. Consequently, the results of HR-based analyses (e.g. analyses of first- and second-order habitat selection, HR overlap within and between species) may be incomplete or even wrong if generalised across the 24-h period. MOE *et al.* (2007), for example, report that in Scandinavia the brown bear prefers thick tall conifer stands during the day, when it mostly rests, but avoids them in the evening to morning period, when it forages for food, whereas across the entire 24-h period the use of this vegetation type does not differ from what would be randomly expected. Similarly, red deer in Slovenia avoids open areas during daytime, but selects them during night time, as determined by second order habitat selection analysis (JERINA 2006).

On the other hand, it should be also emphasized that our study shows the size and composition of diurnal, nocturnal and 24-h HRs to be highly positively correlated. Furthermore, the established differences in HR size are relatively small, several folds smaller than differences between individual animals or HR estimators. If the same is true of other species, many general HR patterns (e.g. relationship between body mass and HR size, trophic level and HR size, HR size and composition) established on the basis of diurnal monitoring are also valid for the 24-h period, and vice versa. For example, HR sizes are allometrically dependent on the body mass of an animal (DAMUTH 1981; HARESTAD / BUNNELL 1979; OTTAVIANI *et al.* 2006), which is varying in orders of magnitudes among species. Small differences between diurnal and 24-h HRs are therefore probably unimportant in inter-species comparison. The brown bear in Scandinavia spends most of the diurnal period resting (MOE *et al.* 2007). Nevertheless, studies based exclusively on diurnal monitoring have shown that the size of its HRs depends on the food carrying capacity (DAHLE / SWENSON 2003). Similarly, red deer are less active in the diurnal period; they stay and feed at supplemental feeding places and in non-forest areas almost exclusively during the evening-morning period (JERINA 2006). However, the size of their diurnal HRs are inversely dependent on the proportion of non-forest areas, the density of the forest edge, and the intensity of supplemental feeding (JERINA 2007a), which in both species is probably a consequence of the interdependence of the composition of diurnal and 24-h HRs.

POVZETEK
SUMMARY

Večina dosedanjih raziskav območij aktivnosti (home ranges: HR) sesalcev temelji na dnevnem vzorčenju lokacij, pri čemer so rezultati implicitno pogosto privzeti kot reprezentativni za celotno 24-urno obdobje. Vendar je raziskanih vse več populacij, pri katerih se habitatni izbor cirkadiano spreminja, kar navaja k hipotezi, da se med deli dneva lahko razlikujejo tudi velikosti in zgradbe HR.

V raziskavi smo na osnovi 24-urne GPS telemetrije 15 osebkov jelenjadi obeh spolov iz različnih delov Slovenije, ki so bili spremljani v obdobju do enega leta, analizirali razlike v velikosti in zgradbi njihovih dnevnih, nočnih in 24-urnih HR. Razlike v zgradbi smo prikazali na primeru binarne spremenljivke gozd-negozd. Negozdne površine so eden ključnih prehranskih habitatov jelenjadi v Sloveniji, vendar jih ta upo-

rablja skoraj izključno ponoči, saj ne dajejo kritja. Pri razvrščanju lokacij v dnevno in nočno obdobje smo upoštevali čas sončnega vzhoda in zahoda na dan, ko so bile lokacije posnete. HR smo ugotavljali s fiksno kernelsko metodo. Podatke o deležu negozdnih in gozdnih površin v HR smo pridobili iz vektorske karte rabe kmetijskih zemljišč Ministrstva za kmetijstvo, gozdarstvo in prehrano. Razlike v velikosti in zgradbi HR med različnimi deli dneva smo analizirali z analizo variance in post-hoc Tukeyevim HSD testom.

Velikosti dnevnih HR spremljane jelenjadi znašajo 424±93 ha, nočnih 453±139 ha in 24-urnih 525±124 ha. S post-hoc testom smo odkrili značilne razlike med dnevnimi in 24-urnimi HR (Tukey HSD, p = 0.008), ki so od dnevnih v povprečju večji za 25 %. Velikosti dnevnih, 24-urnih in nočnih HR dokaj tesno korelirajo (0.61 < r < 0.89). V dnevnih HR znaša delež negozdnih površin 15±5 %, v 24-urnih 25±7 % in v nočnih 31±8 %, zlasti velik je v delu HR, ki ga jelenjad uporablja izključno ponoči (56 %). Razlike v deležih negozdnih površin v HR so značilne pri vseh treh parih primerjav (Tukey HSD, maksimalni p = 0.003). Deleži negozdnih površin med različnimi deli dneva korelirajo še tesneje (0.90 < r < 0.97) kot površine HR. HR se med različnimi deli dneva v veliki meri prekrivajo (dan – noč: 64 %; dan-24-ur: 75 %).

Pričujoča raziskava kaže, da pri jelenjadi v Sloveniji z dnevnim vzorčenjem ni mogoče nepristransko oceniti velikosti 24-urnih HR, še manj pa njihovo zgradbo. Več indicev (npr. evidentirane razlike v rabi prostora in aktivnosti) kaže, da podobno velja tudi za mnoge druge populacije in vrste. Zato se je pomembno zavedati, da so lahko značilnosti HR, ki so ugotovljene na osnovi dnevnih spremljav, pomanjkljive ali celo napačne, če jih generaliziramo za celotno 24-urno obdobje. Raziskave, katerih namen je ugotoviti splošne značilnosti HR, je torej smotrno zasnovati tako, da pokrivajo celotno 24-urno obdobje. Pri raziskavah, ki zaradi takšnega ali drugačnega razloga analizirajo HR, ugotovljene na osnovi nepopolnega vzorčenja (npr. dnevnega spremljanja), pa je treba postopke vzorčenja lokacij čim bolj poenotiti, tako da vsi HR pokrivajo isti del dneva, sicer se lahko ugotovljene značilnosti HR razlikujejo tudi zaradi razlik v vzorčenju.

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