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## The diurnal habitat used by red deer (*Cervus elaphus L.*) in the Haute Ardenne

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**Abstract** We describe diurnal habitat used by red deer (*Cervus elaphus L.*) in two representative forests of Haute Ardenne. We captured 17 calves and 13 adults and fitted them with VHF transmitters (ear tags or collars). Each animal was radio-tracked at least once per week during the daylight hours and relocated by triangulation. To determine habitat use, we used compositional analysis. We defined use for each animal as the proportion of relocations in each vegetation association. Each relocation was weighed according to its accuracy (i.e., based on the confidence ellipse computation). We defined availability as the proportion in the area of each vegetation association within its home range (i.e., minimum convex polygon). Red deer calves preferred edges in open areas (e.g., clear-cuts) during their first 3 months of life. Adults used open coniferous [e.g., natural regeneration of spruce (*Picea abies*)] stands and edges between coniferous stands and other vegetation associations. Closed coniferous stands were preferred during winter and deer usually used the edges of habitat patches rather than the core areas, except in winter for coniferous stands. The deciduous stands [e.g., old growth stands of beech (*Fagus sylvatica*)] were usually avoided, except in winter when the edges of deciduous stands were used. The availability of coniferous stands and edges partly determined the size of the diurnal home ranges.

**Keywords** Bedding site · Belgium · Confidence ellipse · Habitat selection · Home range · Radio-tracking

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### Introduction

Red deer (*Cervus elaphus elaphus*) is the largest wild herbivore in Belgium and population densities have increased dramatically in recent years ( $3.3/\text{km}^2$  in 2003 vs  $1.5/\text{km}^2$  in 1983). Its habitat is mainly the forested areas in Ardenne. Without natural predation, hunting is the main mortality factor and tool to manage this population. This increased population density was apparently accompanied by a lower carrying capacity of the forest. During the last decades, coppices have been progressively replaced by timber production and endemic deciduous stands by exotic coniferous forests, thereby reducing availability of herbs and forbs. Concurrently, urban development in the countryside and pressure due to recreational uses in the forest has increased. Red deer are sensitive to anthropogenic disturbance (Boyle and Samson 1985; Jeppesen 1987) and they escaped from open landscapes to hide deep into the forest where they found cover but only limited food resources. Reduced accessibility of food resources may therefore result in damage to forest stands (e.g., bark peeling). In this study, we investigated diurnal habitat use by deer. We first determined the home range of radio-tagged individuals and then analyzed the use they made of various vegetation associations within their home range: we performed second- and third-order selections defined by Johnson (1980). The identification of preferred bedding sites may provide guidelines for improved forest management.

### Study areas

This study was conducted on the Royal Hunts (Hertogenwald and St Michel - Freyr) in Southern Belgium (Wallonia). Both sites were dedicated in 1982 to model game management, science, recreation, and education by King Baudouin. The Royal Hunts are managed by the General Direction for Natural Resources and the Environment of the Walloon Region. Both sites are subdivided into lower (240–350 m), middle (350–500 m), and upper Ardenne (>500 m). Mean temperature

and precipitation range from 8°C and 900 mm (lower) to 6°C and 1,400 mm (upper Ardenne). Snow cover is concentrated approximately from November 15 to April 15.

The West Hertogenwald (6,350 ha, 50°35'N 6°05'E; forest district of Verviers) is located inside a forest of more than 50,000 ha in the Hautes-Fagnes region along the eastern border of Belgium. The study site is the northwest approach to the Hautes-Fagnes Nature Reserve. The altitude varies from 240 to 600 m. The ratio of deciduous to evergreen trees in West Hertogenwald is of 1 to 2. At a lower altitude, the *Luzulo-Fagetum* climax communities have given way to stands of sessile oak (*Quercus petraea*) and silver birch (*Betula pendula*), but beech (*Fagus sylvatica*) cover is increasing under the canopies of oaks. *Luzulo-Fagetum*-blueberry communities occur at higher altitudes on slopes. From 400 m, deciduous stands (exhausted coppices) are succeeding to spruce (*Picea abies*) stands. Spruce can be usually found on the plateaux accompanied by systematic draining of the ground with permanent or alternating high moisture contents (i.e., hydromorphic soils, peaty soils, and peat bogs). These spruce stands have replaced stands of downy birch (*Betula pubescens*), alder (*Alnus glutinosa*), and willow (*Salix* sp.). Twenty percent of the roughly 4,000 ha of land devoted to coniferous timber production is currently clear-cut or left-fallow. The main species in the area are moor grass (*Molinia caerulea*), wavy hair grass (*Deschampsia flexuosa*), and blueberry (*Vaccinium myrtillus*). In recent years, the forest was managed to increase game populations. A network of grassy food patches was established on firebreaks and in meadows established within forest stands. During winter, supplemental forage (silage, haylage, and alfalfa hay) is supplied at >20 feeding stations. Red deer densities on the Crown Hunt of West Hertogenwald are estimated at 5 deer/km<sup>2</sup> (April 2003) and has remained fairly stable since 1998. Red deer are harvested annually by stalking and still-hunting from high seats with takes of 1.9 animals/km<sup>2</sup>. Roe deer and wild boar (*Sus scrofa*) populations are also present in the forest.

St Michel - Freyr (50°04'N, 5°25'E; forest districts of St. Hubert and Nassogne) forest is located in the heart of the Saint Hubert forest (about 20,000 ha) in the central Ardenne. Total acreage is 4,000 ha but is split into two demographically independent blocks by a fenced motorway. The altitude ranges from 320 to 570 m.

The ratio of deciduous to evergreen species is 70 to 30%. The forest is dominated by beech communities with subassociations varying with elevation and slope. Some oaks are found mixed with beech, maples (*Acer pseudoplatanus*) subsist on some slopes, and alders along some rivers. Spruce trees were introduced on the hydromorphic soils. Primary groundcover is tufted hair grass (*Deschampsia cespitosa*) and blueberry under beech stands and moor grass, wavy hair grass and blueberry under spruce stands and in open areas.

Food patches that combine meadows with browsing resources were created in the forest since 1982. Overall, the proportion of hydromorphic soils is lower than in West

Hertogenwald. In winter, 17 feeding stations are supplied with bales of alfalfa hay. Red deer density (April 2003) on the part northwest of the motorway is estimated at 5/km<sup>2</sup> and on the part southeast of the motorway is 2.9/km<sup>2</sup>. Roe deer and wild boar also are found on the forest. The high proportion of deciduous trees apparently allows a higher carrying capacity for boars than in Hertogenwald. Three hunting methods are used on the Crown Hunts of St Michel - Freyr: stalking and still-hunting from high seats, traditional drives, and silent drives. Hunting is aimed primarily at red deer. Most of the wild boars and roe deer are shot by drives.

## Materials and methods

We used a sample of radio-tagged deer to determine home ranges and to describe habitat use of specific age classes of red deer at a patch (smallest area showing the same vegetation association) scale by comparing use (no relocations within each vegetation association) and availability (vegetation associations in hectares within each home range) using compositional analysis (Aebischer et al. 1993). Although use of telemetry data in habitat use studies may lead to an important bias if the relocation inaccuracy is higher than the habitat complexity (White and Garrott 1990), we evaluated telemetry errors as part of the statistical analyses of the data.

Calves were captured in the first days after birth (mid-May to the beginning of June). One or two groups of seven people walked around in places where calf bedding-sites were the most probable (e.g., open areas of moor grass along spruce saplings) and tried to detect their presence. Once detected, a 1.5-m high net was erected at a distance of 10 to 20 m from the bedded animal (Richard and Picars 1996). The calf was caught by hand within the net perimeter and tagged with a transmitter. We used transmitter ear tags in 1998 (PD-2, Holohil, Carp, Canada) and 1999 (TXH-1, Televilt, Lindesberg, Sweden) and expandable collars (Trans Red Deer, Advanced Telemetry System, Isanti, USA and MOD-310 on CB-4 expandable/break-away collar, Telonics, Mesa, USA) from 2000 to 2002.

Adults were captured during winter by teleanesthesia at supplemental feeding points where hides were established. We used rifles (MK24B.509, PAXARMS, Timaru, New Zealand) fitted with night vision riflescope (Pantera GEN II+, Hi-Tek, Redwood City, USA) to allow darting in the dark. The darts (Pneudart, Williamsport, USA) had a 3-cc capacity containing the anesthetic and a second compartment containing a small VHF-transmitter. A standardized solution of 1.5 cc of IMALGENE 1,000 (Ketamin, Merial, Lyon, France) and 1.5 cc of Zalopine ( $\alpha_2$  agonist, OrionPharma, Turku, Finland) was used to dart all animals. Animals typically traveled 100 to 700 m before becoming sedated. We used handheld receiver (STABO XR100, Gesellschaft für Telemetriesysteme mbH, Horst, Germany) with directional antenna to track darted animals. Once located, deer were radio-collared (TXE-3, Televilt) and an antidote (Antisedan, Atipamezol, Pfizer Inc, NY, USA)

was injected at a rate of approximately 1 cc every 10 min until arousal.

Each animal was monitored at least weekly on a random basis from June 1998 to September 2002. The radio-trackers located deer with VHF-receivers (RX900, Televilt), directional H-antennas, and compasses (with sighting scope) and receiving locations were plotted on 1:10,000 topographic maps (Belgian National Geographic Institute–IGN). We used triangulation from >2 receiving locations to relocate animals. Bearings were measured within 1°. One operator moved around the animal by car to perform sequential measurements of bearings. Mean time to relocate an animal ranged from 10 to 30 min. When visual contact occurred, the animal was located as accurately as possible on the map.

Telemetry error was evaluated by obtaining position estimates of radio-collars at known locations using a blind testing approach. The effects of the study area (Hertogenwald vs St Michel - Freyr) and transmitter type (ATS, Holohil, Televilt TXH1, and TXE3) were calculated by measuring the bearing error ( $\varepsilon_{ij}$ ) corresponding to the difference between the true ( $\alpha_i$ ) and the estimated bearing ( $\hat{\alpha}_{ij}$ ) for the  $i$ th location and  $j$ th replicate:

$$\varepsilon_{ij} = \alpha_i - \hat{\alpha}_{ij}$$

Precision is a measure of the variability of the estimated bearings and may be calculated by the standard deviation ( $s$ ). The precision of each telemetry system was then tested by comparing their corresponding  $s$  (White and Garrott 1990) by ANOVAs (StatView, Abacus Concepts, Berkeley, USA).

$$s = \left[ \frac{\sum_{i=1}^n \sum_{j=1}^r (\varepsilon_{ij} - \bar{\varepsilon})^2}{(nr - 1)} \right]^{0.5}$$

We used the M-estimator Andrews with a tuning parameter of 1.5 and 60 iterations (Lenth 1981) and a magnetic deviation of 3° on both sites (IGN) to estimate the relocations  $x_{\text{est}}$  and  $y_{\text{est}}$  [Location of a Signal software (LOAS), Ecological Software Solutions, Sacramento, USA].

## Habitat use analysis

### Availability

The habitat availability ( $A$ ) for each animal corresponded to the proportion in hectares of each habitat category within its Minimum Convex Polygon (MCP) home range. We created a Geographic Information System (GIS) database using ArcView (Environmental Systems Research Institute, Redlands, USA) that consisted of vegetation associations categories. Vegetation association was based on

interpretation of color aerial photographs (PPNC-DGRNE) presenting a mean resolution of 1 pixel:0.4 m. Information from forest stand maps of the Nature and Forest Division helped the photo interpretation. We established four vegetation associations to produce a standard map for both study sites: open area, open coniferous stands, closed coniferous stands, and deciduous stands (Table 1). Vegetation associations were handmade and digitized at a scale ranging from 1:2,000 to 1:3,000.

To evaluate the effect of vegetation association edges on habitat use, they were condensed into three categories (i.e., open area and coniferous and deciduous stands) and a 30 m internal buffer was generated (ArcView) creating six modified vegetation associations: open area edge, open area core, coniferous stand edge, coniferous stand core, deciduous stand edge, and deciduous stand core.

MCPs were drawn for each animal with Animal Movement Analysis ArcView extension (Hooge and Eichenlaub 1997) and these areas were overlain with vegetation associations and modified vegetation associations.

### Use

Habitat use ( $U$ ) was the proportion of relocations occurring in each vegetation association. We weighed each relocation according to its accuracy. We calculated the confidence ellipse based on a  $\chi^2$  distribution (2 df and 1- $\alpha$  probability level) for each relocation (White and Garrott 1990). We then used LOAS to calculate the shape parameters of the ellipse for each relocation: the ellipse center ( $x_{\text{est}}$  and  $y_{\text{est}}$ ), the size of the principal axes (var  $x_{\text{est}}$  and var  $y_{\text{est}}$ ), and the

**Table 1** Correspondence between vegetation associations (as detected on aerial photographs) and tree communities

Vegetation association	Tree community
Open area	Clear-cut Establishment stage Moor or peat bog Firebreak Pasture
Open coniferous stand	<i>Picea abies</i> prethicket stage <i>Picea abies</i> prefelling stage Mature <i>Pinus sylvestris</i> and <i>Larix decidua</i> stands <i>Pseudotsuga menziesii</i> , <i>Pinus sylvestris</i> , and <i>Larix decidua</i> prethicket stage
Closed coniferous stand	<i>Picea abies</i> thicket stage <i>Pseudotsuga menziesii</i> , <i>Pinus sylvestris</i> , <i>Larix decidua</i> , and <i>Abies</i> sp. thicket stage
Deciduous stand	Mixed <i>Quercus</i> sp.— <i>Betula pendula</i> stands Mixed <i>Quercus</i> sp.— <i>Betula pubescens</i> stands Mature <i>Fagus sylvatica</i> stands Mixed <i>Fagus sylvatica</i> — <i>Quercus</i> sp. stands <i>Acer pseudoplatanus</i> stands

Tree communities are ranked according to their occurrence within each habitat category

ellipse orientation ( $\text{cov } x_{\text{est}}$  and  $y_{\text{est}}$ ). According to these shape parameters, we scattered 100 normally distributed points ( $x_1, y_1; \dots; x_{100}, y_{100}$ ) centered on  $x_{\text{est}}$  and  $y_{\text{est}}$  and showed the general shape and orientation of the confidence ellipse ( $x_{\text{ellipse}1}, y_{\text{ellipse}1}; \dots; x_{\text{ellipse}100}, y_{\text{ellipse}100}$ ) of each of the relocations. Once these point scatters were generated for each relocation of each animal, they were added to the GIS and crossed with vegetation associations.

### Analytical procedures

We used compositional analysis (Aebischer et al. 1993) to evaluate habitat use. Red deer calves were analyzed separately from birth to the 31st of August. Within the adult-class, we distinguished among and expressed results as all-year-long habitat use, summer (May to October), and winter data (November to April). When unused components were present, we replaced the zero values with a small nonzero value (0.0001) (Aebischer et al. 1993). Concerning the availability of data, MCP home ranges were calculated on the basis of the entire set of data of each animal, whatever the season was. We used RESOURCE SELECTION FOR WINDOWS software (Leban 1999) to test use-versus-availability with compositional analysis.

## Results

### Capture and telemetry

From 1998 to 2002, 25 red deer calves (13 females, 12 males) were fitted with transmitter ear tags (15) or expandable collars (10). Only 17 (nine females and eight males), providing >10 diurnal relocations and 3 months monitoring, were retained for habitat use analysis. Anticipated loss of transmitter (mainly ear tags), transmitter breakdown, and death are the main causes of the loss of sampling units. Three calves were radio-tracked long enough to provide data more than 6 months later. They were added to the adult class when 6-month-old because

they obviously should reflect preferences of their dam. We did not monitor dam–calf pairs in this study. Eleven adult females and five adult males were radio-tagged although three collars failed. In the analysis, the data used are from 13 adults plus three calves older than 6 months (10 females and six males).

We did not detect differences in telemetry systems related to transmitter type (ANOVA  $F_3=1.361, P=0.286$ ) or study site (ANOVA  $F_1=2.986, P=0.099$ ). The value of precision used in the calculation of confidence ellipses is:  $s=11.61^\circ$ .

We obtained 333 relocations of calves and 1,625 relocations of adults. The mean size of the confidence ellipse (95%) was  $60,099 \text{ m}^2 (\sigma=100,452 \text{ m}^2)$  for calves and  $111,995 \text{ m}^2 (\sigma=156,390 \text{ m}^2)$  for adults.

### Home range size and habitat availability

Based on the hypothesis that habitat availability corresponded to the area of each vegetation association within an animal's home range, we calculated the MCPs based on the scattered points of each relocation and summed the area of each habitat category according to their vegetation association (four categories) and modified vegetation association (six categories) characteristics (Table 2). Home range size varied greatly among the radio-tracked red deer calves (54 to 534 ha) from their birth to end of August. Adult home ranges also varied in size. Two yearlings in Hertogenwald had home ranges <200 ha from November 2001 to September 2002. During the same period, the home range of one female encompassed >2,000 ha in St Michel - Freyr.

### Habitat use and compositional analysis

The compositional analysis compared availability (Table 2) and use (Table 3). When considering vegetation associations, they appeared to be randomly selected by newborn calves ( $\chi^2_3 = 2.89, P = 0.409$ ). When adding the edge

**Table 2** Home range statistics of calves and adults, proportion of vegetation associations, and modified vegetation associations within home ranges

	MCP (ha)	Loc. (n)	Vegetation associations (%)				Modified vegetation associations (%)						
			OA	OCS	CCS	DS	OAE	OAC	CSE	CSC	DSE	DSC	
Calves	$\bar{x}$	160	19	31	7.6	36	25	20	11	29	14	11	15
	$\sigma$	118	6.0	19	4.9	15	30	11	11	10	8.0	12	22
	Min	54	11	1.9	0.3	9.0	0.0	1.8	0.1	5.3	1.7	0.0	0.0
	Max	534	32	59	16	59	89	38	32	42	28	37	78
Adults	$\bar{x}$	666	102	23	4.9	29	43	13	9.0	22	12	16	28
	$\sigma$	618	112	18	3.1	16	30	7.5	12	9.9	8.7	8.9	26.1
	Min	156	31	1.8	0.1	2.5	3.9	1.7	0.1	2.0	0.6	3.1	0.6
	Max	2664	480	69	11	57	96	23	4.9	36	29	34	86

OA Open area, OCS open coniferous stands, CCS closed coniferous stands, CDS closed deciduous stands, OAE open area edge, OAC open area core, CSE coniferous stand edge, CSC coniferous stand core, DES deciduous stand edge, and DSC deciduous stand core

**Table 3** Mean proportion of use (%) by calves and adults (according to the period of the year) of the different vegetation associations and modified vegetation associations within their home ranges

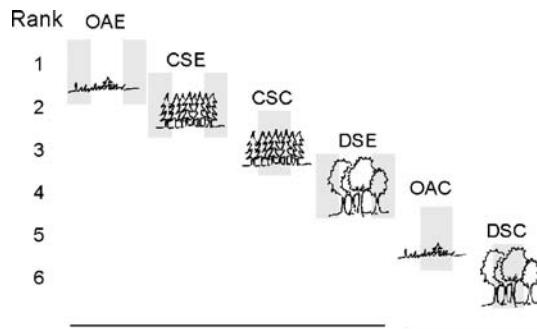
	Vegetation associations (%)				Modified vegetation associations (%)						
	OA	OCS	CCS	DS	OAE	OAC	CSE	CSC	DSE	DSC	
Calves from birth to Aug. 31	$\bar{x}$	31.2	9.6	36.2	23.2	24.4	6.7	30.0	15.7	11.6	11.6
	$\sigma$	15.9	6.1	16.4	26.9	12.2	5.6	9.6	8.6	12.2	18.4
Adults all year-long	$\bar{x}$	22.2	10.1	34.6	33.0	17.5	4.7	26.8	18.0	13.4	19.7
	$\sigma$	12.0	5.3	15.9	29.4	10.0	3.0	9.2	11.6	10.1	24.7
Adults in summer	$\bar{x}$	24.8	12.1	36.0	27.1	19.1	5.5	29.4	18.6	12.5	14.9
	$\sigma$	10.0	5.0	15.7	25.0	8.7	3.3	7.4	11.2	10.2	19.7
Adults in winter	$\bar{x}$	19.9	7.5	35.5	37.0	15.6	4.3	24.7	18.5	15.5	21.4
	$\sigma$	13.2	6.4	16.9	31.1	10.7	3.4	10.2	12.3	10.8	24.6

OA Open area, OCS open coniferous stands, CCS closed coniferous stands, CDS closed deciduous stands, OAE open area edge, OAC open area core, CSE coniferous stand edge, CSC coniferous stand core, DSE deciduous stand edge, and DSC deciduous stand core

effect to the vegetation associations, a nonrandom use is highlighted ( $\chi^2_5 = 18.39, P < 0.05$ ). Edges are first preferred by calves and cores of deciduous and open areas are avoided (Fig. 1).

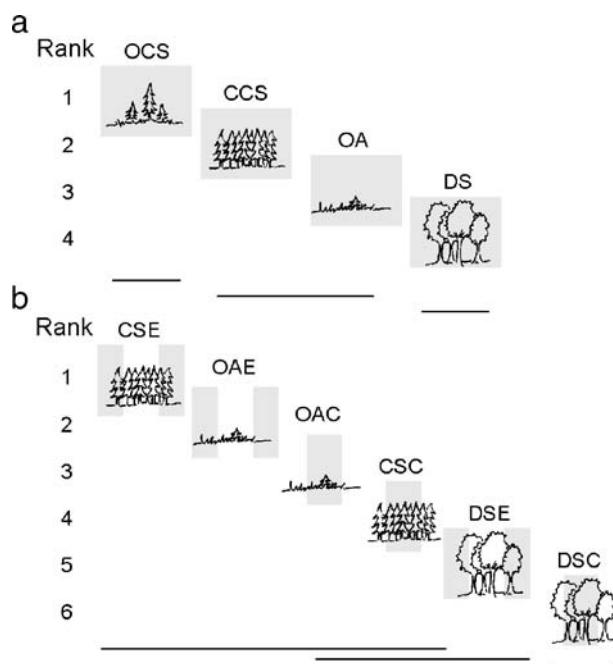
Year-round habitat use of adult red deer was nonrandom ( $\chi^2_3 = 23.1, P < 0.0001$ ). Open coniferous stands were preferred and deciduous stands were avoided (Fig. 2a). When adding the edge component to the vegetation associations, a nonrandom use of categories can also be highlighted ( $\chi^2=16.7, 5 \text{ df}, P<0.05$ ). The most preferred category consisted in the edge of coniferous stands. Both edge and core of deciduous stands were avoided (Fig. 2b).

Differential use of vegetation associations by adults during summer was significant ( $\chi^2_5 = 16.5, P < 0.001$ ) as was the use of modified vegetation associations ( $\chi^2_5 = 18.0, P < 0.05$ ). The summer rankings followed almost the same trends as all-year-long use of vegetation associations. Pair wise comparisons between modified vegetation associations indicated preferences for open coniferous stands, edges of coniferous stands, and avoidance for cores of deciduous stands.

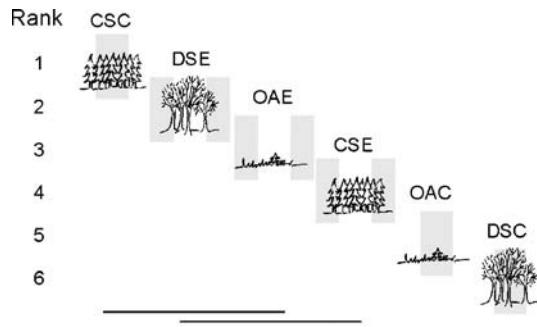


**Fig. 1** Preferences by red deer calves ( $n=17$ ) during the first 3 months of life. Vegetation associations that share a common underscore have preference rankings that are not significantly different ( $P<0.05$ ). OAE Open area edge, OAC open area core, CSE coniferous stand edge, CSC coniferous stand core, DSE deciduous stand edge, and DSC deciduous stand core

Habitat use by adults during winter did not differ among vegetation associations ( $\chi^2_3 = 0.829, P = 0.843$ ), although selection among edge types was observed ( $\chi^2_5 = 14.9, P < 0.05$ ). Core areas of coniferous stands, edges of deciduous stands, and open areas are preferred while core areas of deciduous stands are avoided (Fig. 3).



**Fig. 2** All-year-long preferences by red deer adults ( $n=16$ ). Vegetation associations that share a common underscore have preference rankings that are not significantly different ( $P<0.05$ ). **a** OA Open area, OCS open coniferous stands, CCS closed coniferous stands, and CDS closed deciduous stands. **b** OAE Open area edge, OAC open area core, CSE coniferous stand edge, CSC coniferous stand core, DES deciduous stand edge, and DSC deciduous stand core



**Fig. 3** Preferences by red deer adults ( $n=16$ ) during winter (November to April). Vegetation associations that share a common underscore have preference rankings that are not significantly different ( $P<0.05$ ). *OAE* Open area edge, *OAC* open area core, *CSE* coniferous stand edge, *CSC* coniferous stand core, *DSE* deciduous stand edge, and *DSC* deciduous stand core

## Discussion

### Home range and habitat availability

The largest calf home ranges were mainly made of mature beech stands (up to 89% of home range area) or wide moor grass open areas (up to 55%) with poor cover and low edge resources, which were not intensively used by animals. Home ranges, <100 ha (corresponding to six of the 17 calf home ranges), were primarily spruce stands (46%) interspersed with small clear-cuts (37.5%) and only some small deciduous stands (16.5%). The small home ranges showed a high edge effect while the larger home ranges showed a low proportion of edges. For animals with home ranges <100 ha, habitat availability corresponded to habitat use.

Variation in adult home range size was likely due to the spatial organization of the home range rather than differences in sex or age classes. One female often moved across its home range from its usual activity center to a more secured area 6 km away when disturbed by human activities (e.g., drives and holiday) (Licoppe et al. 2005). Both activity centers (around 300 ha each) were composed of spruce cover and separated by a mature beech forest where this animal rarely stopped. Notwithstanding these extreme cases, the mean adult home range was around 665 ha, which is relatively small compared to other European studies (Georgii 1980; Jeppesen 1987; Hamann et al. 1997; Szemethy et al. 1998). Smaller home ranges in this population likely reflected important land fragmentation due to human pressure, even in the Ardenne. In St Michel - Freyr, a fenced motorway and a fenced estate prevent animals to range to east and north. In both territories, artificial feeding during winter holds the animals in the core of the forest. Deer move out of the forest to graze in the pastures only at night. This is not highlighted in this study which uses only diurnal data.

### Habitat use

During the first 3 months of their life, red deer calves appeared to select open areas situated at a small distance (<30 m) from forest cover. When capturing calves, most of them were found lying alone in sunny places (79%) next to spruce prethicket where their mother was detected (45%). Sunny exposure and heterogeneous ground conditions (moor grasses, brackens, or branches on the ground), which are preferred by calves, are more often available in clear-cuts, young seedlings or plantations, and edges than in mature stands. Moreover, occasional human incursions can be monitored by the hinds in open grounds (Birtles et al. 1998). When using deciduous stands, calves were usually found next to small coniferous stands or small clear-cuts.

Deer changed use of vegetation associations between summer and winter. During summer, animals chose open coniferous stands and open areas rather than closed coniferous or deciduous stands. When vegetation was still high and abundant, they were able to find adequate hiding places together with food resources. Moreover, the use of edges of coniferous stands or clear-cuts allows the animals to lie hidden behind young spruce seedlings or high moor grasses, yet, providing a good visibility. Animals spent significantly less time in core deciduous stands, although some animals almost exclusively used mature deciduous stands. Animals using deciduous stands appeared to take advantage of topographic components such as steep slopes and small enclaves of coniferous stands or adapt their home range size according to coniferous cover resources.

Spruce stands that suffered from wind storms created natural edges and habitat complexity and seemed to be particularly attractive for red deer as a diurnal bedding place and as a breeding place. These stands mainly corresponded to the open coniferous stand category and were preferred during summer. As they were generally located on grounds with high moisture contents; but these patches were avoided during winter.

During winter, there was no evidence for a preferred vegetation association, although the effect of edges appeared to be more relevant to explain red deer space use. The core area of coniferous patches was preferred from November to April. The dense cover of the center of these patches likely provided thermal cover and a more secured shelter against human activities. From October to December, both study areas are heavily hunted and from January to March, they are heavily used for snow tourism. The dense coniferous stands provided the only high-quality shelter when herbs and shrubs are dead and down. During this period, animals used the edges of beech and oak stands along spruce cover, foraging on acorns and beechnuts, when available, and on blueberry. Disturbance from snow tourism should be evaluated as a cause of the use of these vegetation associations in winter.

Whatever the age class (calf vs adult) or the season (summer vs winter), the diurnal habitat use of red deer in

Hertogenwald and St Michel - Freyr was determined by the presence of coniferous stands, likely because of their capability to provide a natural shelter against hunters and weather (Staines 1974; Mysterud and Ostbye 1999). This attraction was enhanced when coniferous covers were interspersed with open areas or deciduous stands creating edge effects. These edges were intensively used because they offered hiding and escaping possibilities into the forest cover and foraging on low vegetation. Creation or restoration of edges should be part of forest management guidelines to increase bedding site availability of the forest.

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