

Habitat use by female western roe deer (*Capreolus capreolus*): influence of resource availability on habitat selection in two contrasting years

M. Pellerin, C. Calenge, S. Saïd, J.-M. Gaillard, H. Fritz, P. Duncan, and G. Van Laere

Abstract: In most previous studies of habitat selection, the use of a given habitat type is assumed to be directly proportional to its availability. However, the use and (or) the selection of a given habitat may be conditional on the availability of that habitat. We aim here to (i) identify the environmental variables involved in habitat selection, (ii) identify classes of individuals with similar patterns of habitat selection, and (iii) assess whether habitat use changes with changing availability of habitat types, within monthly home ranges of female western roe deer (*Capreolus capreolus* (L., 1758)). We found that some females adjust their habitat use according to the distribution of resources within habitats. Females with similar home ranges in terms of resource quantity and quality showed similar patterns of habitat selection. Differences in habitat use between 2 years with contrasting resource availability showed that temporal changes of environmental conditions influenced the pattern of habitat selection by female roe deer. Habitat selection also differed between periods of the life cycle likely because of contrasted energy requirements. This study shows that the relationship between habitat use by herbivores and habitat availability is nonproportional, and that the availability of resources influences use mostly at intermediate values.

Résumé : Dans la plupart des études antérieures sur la sélection de l'habitat, l'utilisation d'un habitat donné est supposée être directement proportionnelle à sa disponibilité. Cependant, l'utilisation et (ou) la sélection d'un habitat donné peut être conditionnelle à la disponibilité de cet habitat. Le but de cette étude est (i) d'identifier les variables environnementales impliquées dans la sélection de l'habitat, (ii) d'identifier les classes d'individus avec des patrons similaires de sélection de l'habitat et (iii) de tester si l'utilisation d'habitat change avec une disponibilité changeante des types d'habitat, dans les domaines vitaux mensuels des femelles chevreuils d'Europe (*Capreolus capreolus* (L., 1758)). Nous trouvons que certaines femelles ajustent leur utilisation d'habitat en fonction de la distribution des ressources dans les habitats. Les femelles avec des domaines vitaux similaires en termes de quantité et qualité de ressources montrent des patrons de sélection de l'habitat similaires. Les différences dans l'utilisation d'habitat entre deux années avec des disponibilités de ressources contrastées montrent que les variations dans le temps des conditions environnementales influencent le patron de sélection de l'habitat chez les femelles de chevreuil. La sélection de l'habitat diffère aussi entre les périodes du cycle de vie à cause de besoins en énergie bien différenciés. Cette étude montre que la relation entre l'utilisation et la disponibilité des habitats est non-proportionnelle, et que la disponibilité des ressources influence l'utilisation, surtout aux valeurs intermédiaires.

Introduction

Habitat selection is a hierarchical process involving behavioural decisions at different spatial scales (Hutto 1985). These decisions may result in disproportional use of some habitats and may lead to marked differences in individual

fitness (McLoughlin et al. 2005, 2007; for a review see Gaillard et al. 2010). Habitat selection studies generally aim to determine how animals use habitats relative to their availability (Aebischer et al. 1993; Manly et al. 2002) and typically depends on the variability of resources in space (e.g., Mysterud and Ims 1998; Gillies et al. 2006) and time (e.g.,

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Mauritzen et al. 2003; Mosnier et al. 2003) and on variations in the metabolic needs of the animals (Mauritzen et al. 2003; Dussault et al. 2005).

Previous assessments of habitat selection have often consisted of testing the hypothesis that use of a given habitat type is directly proportional to its availability. However, it has been argued that the relative use of a given habitat type may exceed its relative availability when the habitat type is scarce and may be less than its relative availability when the habitat type is common (Mauritzen et al. 2003). Thus the variation of observed use of a given habitat type with its availability can be expected to be nonproportional if use is influenced by two resources, yielding changes of selection for a given habitat type in relation to its availability (Mysterud and Ims 1998). Some previous studies have raised the issue of changing use in a nonproportional way in response to variation in availability (Gillies et al. 2006; Hebblewhite and Merrill 2008; Godvik et al. 2009; Hansen et al. 2009a). In herbivores feeding in patches where plants are concentrated in space, habitat use may well not be directly proportional to habitat availability.

This study focused on western roe deer (*Capreolus capreolus* (L., 1758)), a selective feeder (Duncan et al. 1998) living within relatively small home range (about 25 ha in forest; Saïd et al. 2005a, 2009) and showing high site fidelity (Strandgaard 1972). By monitoring female roe deer using GPS, we measured the selection of food or rest sites within the home ranges (i.e., the third-order selection, Johnson 1980) and measured the habitats available at the scale of monthly home ranges.

We tested whether habitat selection was influenced by spatial variation in habitat availability and by temporal variation in climatic conditions. Because of their relatively small body size (20–30 kg), roe deer should be influenced by the quality of resources to a greater extent than larger animals (Demment and Van Soest 1985). We expect that (i) female roe deer should select habitats with high plant biomass and a high proportion of the preferred and principal plants in their diets (Tixier and Duncan 1996; Saïd et al. 2005a) and (ii) female roe deer should vary their selectivity for a given habitat depending on both the quality and the availability of that habitat (i.e., they should select for high-quality habitats when these habitats are not common and they should be less selective when habitats become more common) (Mauritzen et al. 2003). We thus expected roe deer to be more selective in 2003 (a poor year when a severe drought in summer led to a marked decrease in available resources; Van Laere et al. 2006) than in 2004 (a year when climatic conditions were close to average). However, when a given high-quality habitat type becomes very scarce, the use of this habitat should decrease owing to forage depletion (i.e., there is no time for rapid enough recovery of vegetation) (van Beest et al. 2010). Moreover, the searching time should increase as should the cost for selecting for it. We thus expect the highest selection to occur at intermediate availability, corresponding to a sigmoidal pattern when plotting habitat use versus availability.

We also tested whether habitat selection was influenced by between-individual variation in metabolic needs. Female roe deer are close to the income end of the “capital–income” continuum (sensu Jönsson 1997) and they allocate

to reproduction more resources than most other species of large herbivores (Andersen et al. 2000). A small income breeder that allocates high energy expenditures to reproduction each year like the roe deer thus needs a large amount of highly digestible and rich food. We thus expect that (iii) habitat selection should differ between periods of the life cycle because of contrasted energy requirements. Females should be more selective towards high-quality resources during fawning and rearing periods (May–June) when energetic demands peak (Sadleir 1969; Andersen et al. 2000). Moreover, females with offspring are spatially constrained so that they cannot wander over large areas (i.e., within a restricted home-range size in spring (Saïd et al. 2005a, 2009), females have to be highly selective).

Materials and methods

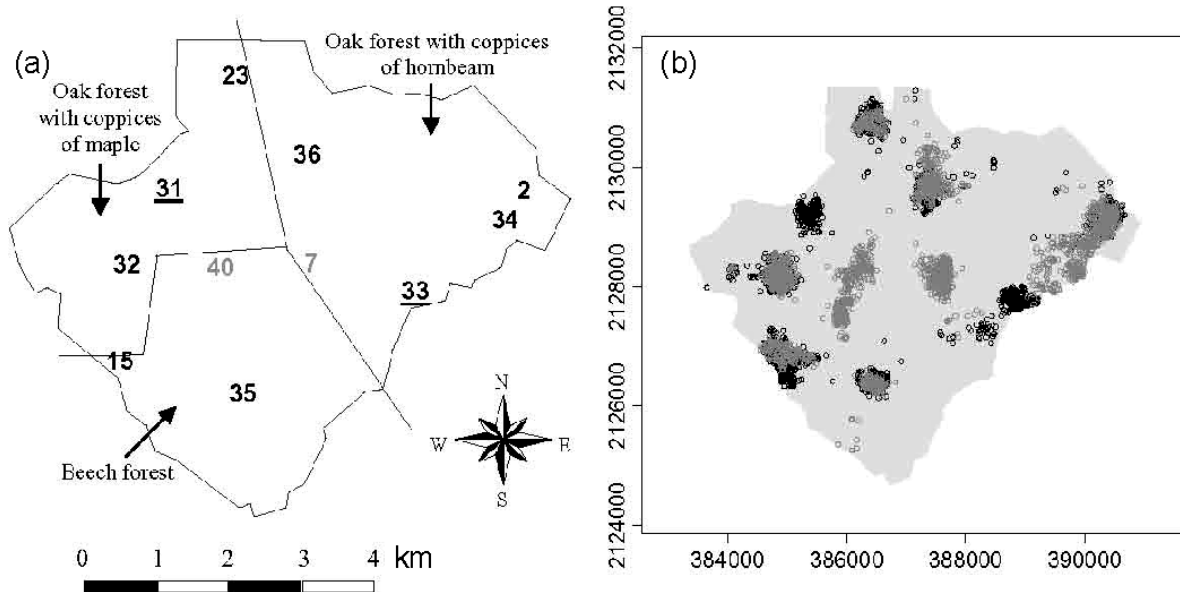
Study area

The study was carried out in the Chizé reserve, 2614 ha of fenced deciduous forest in western France (46°05'N, 0°25'W). The climate is oceanic with Mediterranean influences and is characterized by mild winters and hot, dry summers. The elevation varies between 47 and 101 m. The Chizé forest includes three habitats contrasting in quality for roe deer (Pettorelli et al. 2003; see Fig. 1a): an oak (genus *Quercus* L.) forest with resource-rich coppices dominated by European hornbeam (*Carpinus betulus* L.) in the north-eastern part, an oak forest with coppices of medium-quality dominated by Montpellier maple (*Acer monspessulanum* L.) in the northwestern part, and a poor European beech (*Fagus sylvatica* L.) forest in the south. The population size of the roe deer was estimated at about 400 individuals that were >1 year old in March 2003 and 450 in 2004 (using capture–mark–recapture methods; Gaillard et al. 2003; J.-M. Gaillard, F. Klein, and G. Van Laere, unpublished data).

Data collection: animals

Eleven different does were equipped with Lotek's GPS_3300 radio-collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) in January–February of both 2003 and 2004, allowing us to monitor 9 different females out of 11 equipped females in each of the study years (2 females out of 9 equipped females in 2003 died and were replaced with 2 other females in 2004). The collars provided information on GPS locations in differential mode (i.e., latitude, longitude, date, and time) at preprogrammed intervals, fix quality (DOP, dilution of precision), ambient temperature, and animal activity on two axes. We scheduled collars to provide one location every 4 h (at 0000, 0400, 0800, 1200, 1600, and 2000) from April to August in 2003 and 2004. Data on location and activity were recovered during the capture sessions in January–February 2004 and 2005. After removing poor-quality locations with high PDOP (positional dilution of precision values >10; D'Eon and Delporte 2005), from a monthly maximum of 180 locations per animal, we obtained a mean of 147 locations in 2003 (SD = 31.87, $n = 35$), i.e., a mean fix rate of 82%, and 110 locations in 2004 (SD = 21.62, $n = 39$), i.e., a mean fix rate of 61% (Fig. 1b). Because of some GPS (global positioning system) failures, we did not obtain the expected 45 monthly data (9 animals \times 5 months) per year. We did not account for

Fig. 1. (a) Distribution of female western roe deer (*Capreolus capreolus*) monitored at Chizé (France): females in black were monitored over 2 years (2003 and 2004), except underlined animals (dead) that were monitored in 2003 only, whereas those in grey were monitored only in 2004. (b) Maps of GPS locations of females in 2003 (black) and 2004 (grey).



temporal autocorrelation between locations because the time interval between locations was relatively long (White and Garrott 1990) and constant (Otis and White 1999) so that roe deer were potentially able to cross their home ranges several times within the 4 h period separating two consecutive locations. The location error estimated from GPS data was 25 m (mean = 25.6 m, SD = 34.0 m; Pellerin et al. 2008).

GIS (geographic information system) database

We used a vegetation map of the Chizé reserve generated by ArcView version 3.2 (Environmental Systems Research Institute, Redlands, California, USA; Saïd and Servanty 2005) showing the different landscape units of the forest: 6 categories of trees (*Carpinus betulus*, *Quercus* spp., maple (genus *Acer* L.), *Fagus sylvatica*, other broad-leaved trees, resinous trees) with 5 categories of forest openness (0%, 25%, 50%, 75%, >75%), grasses, roads, and ponds; these landscape units have led us to differentiate 30 unique landscape units (except for maple with 0% and 25% of forest openness). Maple was only present with 0% and 25% of forest openness, which explains why we only got 30 categories instead of the maximum potential number of 33.

We sampled plant biomass within each individual home range using a three-dimensional quadrat (Saïd et al. 2005b). The method is based on an index relating leaf biomass to a number of leaf contacts with a vertical, three-dimensional (25 cm × 25 cm × 165 cm) metallic quadrat with a central rod. During spring of 2001 and 2002, we clipped some vegetation plots and measured the biomass. Biomass was then estimated from the number of contacts using regression equations obtained for different types of plants (leaf shape, size, and thickness). We then used these regressions for estimating biomass in plots not clipped (for further details see Saïd et al. 2005b). We sampled biomass every 70 m using a grid that covered all the parts of the home ranges. For a

home range of 25 ha (the observed mean size for roe deer at Chizé; Saïd et al. 2005a), we sampled ~30 plots. Biomass was then interpolated using the inverse distance weighted method (Shepard 1968) under GIS ArcView version 3.2 to obtain, for each year and each month, the total biomass (0–165 cm), the biomass between 0 and 45 cm, between 45 and 85 cm, and between 85 and 165 cm. We estimated biomass for 11 species: the 9 most common species or genera of trees and shrubs (*Acer* spp. (field maple, *Acer campestre* L.; *Acer monspessulanum*); *Carpinus betulus*; *Cornus* spp. (Cornelian cherry, *Cornus mas* L.; bloodtwig dogwood, *Cornus sanguinea* L.); *Crataegus* spp. (smooth hawthorn, *Crataegus laevigata* (Poir.) DC.; singleseed hawthorn, *Crataegus monogyna* Jacq.); *Fagus sylvatica*; English ivy (*Hedera helix* L.); *Quercus* spp. (European turkey oak, *Quercus cerris* L.; holly oak, *Quercus ilex* L.; durmast oak, *Quercus petraea* (Mattuschka) Liebl.; downy oak, *Quercus pubescens* Willd.; English oak, *Quercus robur* L.); *Rubus* spp. (bramble blackberry, *Rubus fruticosus* L.; elmleaf blackberry, *Rubus ulmi-folius* Schott); butcher's broom (*Ruscus aculeatus* L.)) and two herbaceous species (English bluebell, *Hyacinthoides nonscripta* (L.) Chouard ex Rothm.; Pyrenees star of Bethlehem, *Ornithogalum pyrenaicum* L.) that are highly preferred by roe deer and positively associated with body mass of roe deer (Pettorelli et al. 2003) and fawn survival (Pettorelli et al. 2005b). During spring and summer, the diet of roe deer is essentially composed of tree species and shrubs (Tixier and Duncan 1996). Only some herbaceous plants belonging to genera *Hyacinthoides* and *Ornithogalum* are eaten by roe deer. The 11 species used in this study correspond to approximately two-thirds of the number of species eaten and are the most common species in the Chizé reserve (Pettorelli et al. 2005a). The other species of trees and shrubs that roe deer may eat are too scarce in the reserve to be taken into account in the analysis of habitat selection. Plant species were also grouped into 4 classes of decreasing importance for roe deer for each season (spring, April–May; summer,

June–August): preferred (*Carpinus betulus* (spring), *Cornus* spp. (spring–summer), *Crataegus* spp. (spring), *Hyacinthoides nonscripta* (spring), *Ornithogalum pyrenaicum* (spring)); principal (*Carpinus betulus* (summer), *Hedera helix* (spring–summer), *Quercus* spp. (spring–summer), *Rubus* spp. (spring–summer)); indifferent (*Acer* spp. (spring–summer), *Fagus sylvatica* (spring–summer), *Ruscus aculeatus* (spring)); and avoided (*Crataegus* spp. (summer), *Ruscus aculeatus* (summer)) (Tixier and Duncan 1996).

Only vegetation variables present in home ranges of females equipped with GPS collars in 2003 and 2004 were used, so we only used 16 landscape units (i.e., closed hornbeam stand; oak stand closed, open at 25%, 50%, 75%, and >75%; beech stand closed, open at 25%, 50%, 75%, and >75%; resinous stand closed, open at 25% and 75%; and grasses and roads; Fig. S1a²) out of 30. We defined 15 variables for plant biomass: the overall biomass (total and at height intervals of 0–45, 45–85, and 85–165 cm) and plant-specific biomass of 11 species (*Acer* spp., *Carpinus betulus*, *Cornus* spp., *Crataegus* spp., *Fagus sylvatica*, *Quercus* spp., *Hedera helix*, *Rubus* spp., *Ruscus aculeatus*, *Hyacinthoides nonscripta*, *Ornithogalum pyrenaicum*) (Figs. S1b, S1c).²

The biomass markedly differed between years. The severe drought in summer 2003 led to a lower biomass (total biomass = 64.56 ± 21.606 g/m²; mean \pm SD) than in 2004 (total biomass = 82.70 ± 38.264 g/m²). We therefore used different maps of plant biomass for the 2 years (Figs. S1b, S1c).²

We transformed vector maps representing habitat variables to raster maps under GIS ArcView version 3.2, with 30 m \times 30 m pixels, and then exported them in ASCII format.

Statistical analyses

We used the K-select analysis (Calenge et al. 2005) to identify categories of females with similar patterns of habitat selection (Calenge et al. 2005; Calenge 2007; Hansen et al. 2009a, 2009b). This analysis allowed us to include a large number of variables in the analysis of habitat selection and to take into account individual variation in habitat selection.

The K-select analysis is based on the concept of marginality. Each habitat variable defines a direction in a multi-dimensional space, i.e., the ecological space. Because any pixel of the map located in the field takes a value for all the variables, this pixel corresponds to a point in the multi-dimensional space. Consequently, for a given animal, the pixels in the home range define a cloud of “available” points in the ecological space. The pixels containing at least one location of roe deer define a subset of the available points, i.e., a cloud of “used” points in this space. The vector relating the barycentre of the cloud of available points to the barycentre of the cloud of used locations is called the marginality vector. The size of this marginality vector measures the intensity of habitat selection. The K-select analysis therefore provides a measure of habitat selection that allows availability to vary from one animal to another (design III studies according to the classification of Thomas and Taylor 1990). This factorial analysis focuses on the recentred marginality vectors (i.e., shifted in the ecological space so that

they share a common origin) and searches for a linear combination of the environmental variables so that the mean marginality is maximized on the first axis. This method therefore provides a way to define a classification of animal habitat selection by identifying categories of animals with similar patterns of habitat selection. We conducted separate analyses in 2003 and 2004 because the contrasting environmental conditions between years could have led to different habitat selection. To define the categories of animals displaying similar patterns of habitat selection, we used Ward’s algorithm for hierarchical clustering (Ward 1963). We computed a dendrogram linking the animals according to the coordinates of the marginality vectors on the axes of the K-select analysis (Legendre and Legendre 1998). This method allowed us to identify five categories of animals that showed similar patterns of habitat selection in a given year. The whole analysis was carried out using the “adehabitat” package (Calenge 2006) for the R software (R Development Core Team 2007) distributed under the GNU General Public License. Values of the availability and of the use of each habitat by each animal, as well as absolute and relative contributions of each habitat variable and each animal, on the two factorial axes of the K-select analysis are available upon request from the senior author.

Finally, we assessed the variations in habitat use according to habitat availability for female roe deer. The first axis of the K-select analysis corresponds to the linear combination of environmental variables for which selection by the roe deer is, on average, the highest. Each pixel of the map is characterized by a score on this direction. Pixels with a very high score on one of the first axis are strongly selected by the roe deer, whereas pixels with a very low score are strongly avoided. We transformed the first or the second axis of the K-select analysis into a categorical variable with two categories: highly selected habitat and weakly selected habitat. Selected (with respect to nonselected) habitats corresponded to the pixels with a score on the first or the second axis of the K-select greater (or lower with respect to nonselected) than 0.5 (= median value). Note that because there are only two broad habitat types, the study of the relationship between habitat use and habitat availability can be carried out on the selected habitat (results for the nonselected habitat would be exactly symmetrical as when performing demographic analyses based on survival or mortality). We computed the proportion of the home range of each animal-month covered by selected habitat (defining its availability), as well as the proportion of the relocations of each animal-month in the selected habitat (defining its use). We then examined the relationship between use and availability.

We assessed the influence of habitat availability on habitat use with linear mixed models. We first used an arcsine square-root transformation on the proportion of habitat use (p_{use}) and the proportion of availability (p_{av}) to normalize the distributions (Sokal and Rohlf 1981). We then fitted mixed models in which the individual roe deer (animal-month) were included as a random factor to account for pseudoreplication problems generated by repeated measures of individuals (Little et al. 1991). We fitted three models: a linear model (use $\sim b_1 + b_2 \cdot$ availability, where b_1 is a con-

²Supplementary figures for this article are available from <http://cjz.nrc.ca>.

stant and b_2 is a regression coefficient), which indicates that use is isometric with availability if the slope equal to 1, and two polynomial models (a quadratic with use $\sim b_1 + b_2 \cdot \text{availability} + b_3 \cdot \text{availability}^2$ and a cubic with use $\sim b_1 + b_2 \cdot \text{availability} + b_3 \cdot \text{availability}^2 + b_4 \cdot \text{availability}^3$), which indicate that use does not vary linearly with availability. These mixed-effect models were fitted using maximum likelihood to allow comparing with ANOVAs (Pinheiro and Bates 2000).

Results

Interannual variation in habitat selection

The results of the K-select analysis of habitat selection by the 11 females, by month, and by year are presented in Table 1. Data were available for 2–5 months per year for 2 years for seven females. Five females were not reported to show significant selection in any month, one was selective in 8 out of 9 months, and the other five were selective in 1–3 months; the patterns differed between years for the four selective females for which 2 years of data were available, supporting our second expectation that habitat selection varied between years in response to differences in available resources.

Habitat selection in 2003

The availability of habitats within a given home range is represented by the origin of the arrows and the intensity of the selection is indicated by the arrow's length. The first axis of the K-select analysis (Fig. 2a) indicated a selection of habitats with a high biomass of *Rubus* spp., a high proportion of oak stand open at 75%, a high overall biomass at 0–165 and 0–45 cm, and a high biomass of *Hyacinthoides nonscripta*. The second axis indicated a selection of habitats with a high proportion of oak stand open at 50% and a high biomass of *Carpinus betulus*. The selection of habitats with high overall biomass, high biomass of preferred plant species such as *Hyacinthoides nonscripta* and *Carpinus betulus* and high biomass of principal plant species such as *Rubus* spp., indicates that the roe deer selected habitats of high-quality plants, which supports our first expectation. Therefore, high-quality habitats are habitats identified as being the most selected, on average, from the K-select analysis.

We classified the females into categories of animals with similar patterns of habitat selection using Ward's algorithm for hierarchical clustering. A particular female could thus belong to different categories in different months. We identified 5 categories of animals with similar patterns of habitat selection (categories 1–5 in Fig. 2b). Females living in home ranges with either a high or a very low availability of high-quality habitat did not show evidence of habitat selection (indicated by short arrows in C, D, and G of Fig. 2b), supporting our second expectation that the highest selection occurs at intermediate availability of high-quality habitat. This lack of selection occurred during the whole study period or only during some months (mostly in April). Three females strongly selected high-quality habitat with low availability during the fawning period (May and June) only (E in Fig. 2b), supporting our third expectation. Finally one female consistently selected high-quality habitat with low availability (F in Fig. 2b; Fig. S2²).

Habitat selection in 2004

The first axis of the K-select analysis (Fig. 3a) opposed a selection of habitats with a high proportion of regeneration plots (>75% open in beech stands, i.e., very open) to a less pronounced selection of habitats with a high biomass of *Fagus sylvatica* and a high proportion of beech stand open at 75%. The second axis corresponded to a selection of habitats with a high proportion of oak stand open at 50% and a high biomass of *Rubus* spp. and *Fagus sylvatica*, as well as a counter-selection of habitats with a high proportion of closed oak forest. The selection of habitats with a high proportion of regeneration plots, which provide enhanced food availability for roe deer compared with more closed forest, and a high biomass of principal plant species such as *Rubus* spp. indicates that roe deer selected for habitats of high-quality plants, which supports our first expectation. As for 2003, high-quality habitats are selected habitats identified from the K-select analysis.

We also identified 5 categories of females with similar patterns of habitat selection in 2004 (categories 6–10 in Fig. 3b). Females living within home ranges with either a high or a very low availability of high-quality habitats were not selective (C and D in Fig. 3b) at least for some months, supporting our second expectation. Some females selected high-quality habitat with a low availability of high-quality habitats (E in Fig. 3b). One of these females strongly selected high-quality habitat with high availability in June (F in Fig. 3b). Female selection of sites of high-quality plants within oak forest during fawning time occurred in both years but was less marked in 2004 than in 2003, supporting our second expectation. On the other hand, one female counter-selected high-quality habitat (G in Fig. 3b).

Variation of habitat use with changing availability

We transformed the scores of the pixels on the first axis of the K-select analysis of 2003 data into a categorical variable with two categories (selected habitat and nonselected habitat). For each animal–month, we plotted the proportion of locations in selected habitat described by the first axis (corresponding to a habitat with a high proportion of open oak forest and a high plant biomass rich in *Rubus* spp. and in *Hyacinthoides nonscripta*) interpreted as a high-quality habitat, according to the proportion of the home range covered by this habitat type (Fig. 4a). For the 2004 data set, we used the second axis of the K-select analysis to define the selected and nonselected habitats instead of the first, which mainly depended on one female strongly selecting beech stands. Moreover, the second axis was determined by the same environmental variables as the first axis of the 2003 analysis, leading to a direct comparison between yearly relationships. We plotted the proportion of locations in the selected habitat described by the second axis (corresponding to a habitat with a high proportion of moderately open oak forest and a high biomass of *Rubus* spp.) interpreted as a high-quality habitat, according to the proportion of the home range covered by this habitat type (Fig. 4b).

In both years, the habitat use was not isometric with habitat availability (model 1) because the mixed model with a quadratic term for habitat availability (model 2) was the best among the three models (for 2003 — model 1 vs. model 2: $p = 0.067$; model 2 vs. model 3: $p = 0.497$; for

Table 1. Summary of habitat selection by female roe deer (*Capreolus capreolus*) at Chizé (France) from the results of the randomization test of the hypothesis that the observed marginality vectors of the females could have been generated by random habitat use, carried out at the α level of 5% (S, selection; NS, no selection; Calenge et al. 2005).

Female ID	Year	April		May		June		July		August		Forest type	Plant biomass at 0–45 cm (g/m ²)
		S vs. NS	Cat.	S vs. NS	Cat.	S vs. NS	Cat.	S vs. NS	Cat.	S vs. NS	Cat.		
2	2003	NS	3	S	4	S	4	—	—	—	—	OH	49
	2004	NS	7	NS	7	NS	7	NS	7	NS	7		61
7	2003	—	—	—	—	—	—	—	—	—	—	OH	—
	2004	NS	7	NS	7	NS	7	NS	7	NS	7		33
33	2003	NS	3	NS	3	S	4	—	—	—	—	OH	42
	2004	—	—	—	—	—	—	—	—	—	—		—
34	2003	NS	3	S	4	S	4	—	—	NS	3	OH	50
	2004	NS	7	S	8	NS	7	NS	7	NS	7		53
36	2003	NS	3	NS	3	NS	3	—	—	—	—	OH	35
	2004	NS	7	NS	7	NS	7	NS	7	NS	7		35
23	2003	S	5	S	5	S	5	S	5	S	5	OM	36
	2004	NS	7	S	8	S	8	S	8	—	—		56
31	2003	NS	3	NS	3	—	—	—	—	—	—	OM	35
	2004	—	—	—	—	—	—	—	—	—	—		—
32	2003	NS	3	NS	3	NS	3	NS	3	NS	3	OM	40
	2004	NS	7	NS	7	NS	7	NS	7	NS	7		77
15	2003	NS	1	NS	1	NS	1	NS	1	NS	1	B	77
	2004	NS	6	NS	6	—	—	—	—	—	—		110
35	2003	NS	2	NS	2	NS	2	NS	2	NS	1	B	85
	2004	S	10	S	10	S	10	—	—	—	—		106
40	2003	—	—	—	—	—	—	—	—	—	—	B	—
	2004	NS	7	NS	7	S	9	S	8	S	8		78

Note: The number under the Cat. column is the category to which each female is assigned. The results are presented by female, year, and month, with the location of the females in the forest (OH, oak forest with hornbeam coppices; OM, oak forest with maple coppices; B, beech forest) and the yearly mean of the overall plant biomass at 0–45 cm. The dashes indicate no available data.

2004 — model 1 vs. model 2: $p = 0.001$; model 2 vs. model 3: $p = 0.305$). The high-quality habitat was (i) less used than expected from the isometric relationship when occurring with low availability (i.e., <0.2), (ii) used more than expected from the isometric relationship when moderately abundant (i.e., between 0.2 and 0.6), and (iii) the use saturated above an availability of 0.6, suggesting a saturation of habitat selection when the high-quality habitat became very common (Figs. 4a, 4b). Therefore, female roe deer used a given habitat less than expected when the habitat was rare, more than expected when the habitat was moderately abundant, and showed a saturation when the habitat was very abundant. This fully supported our second prediction of a sigmoidal pattern of habitat use versus availability.

Discussion

This study demonstrates that female roe deer adjust their selection of habitat in relation to resource availability and that the intensity of selection varies among years likely as a response to changing resource availability. Females whose home ranges included similar habitats exhibited similar habitat use. When the availability of high-quality habitats is below a certain threshold, female roe deer use these less than expected, their use increases strongly with increasing availability for intermediate values of availability, and then habitat use saturates at high availability. Habitat use by roe deer is therefore strongly influenced by resource availability

within the home range. Mysterud and Ims (1998) were among the first to underline the importance of not considering use as directly proportional to availability in habitat selection studies. They applied their model, based on logistic regression, to gray squirrels (*Sciurus carolinensis* Gmelin, 1788) and Ring-necked Pheasants (*Phasianus colchicus* L., 1758), using two habitats at a larger scale than the present study of roe deer. Mauritzen et al. (2003) reported season- and population-specific variation of habitat use in two populations of polar bears (*Ursus maritimus* Phipps, 1774) in areas with different environmental conditions and prey availability by applying logistic and log-linear models. Some other studies have looked for variation in habitat use according to resource availability in Tawny Owls (*Strix aluco* L., 1758) (Sunde and Redpath 2006), grizzly bears (*Ursus arctos* L., 1758) (Gillies et al. 2006), gray wolves (*Canis lupus* L., 1758) (Hebblewhite and Merrill 2008), red deer (*Cervus elaphus* L., 1758) (Godvik et al. 2009), moose (*Alces alces* L., 1758) (Herfindal et al. 2009), and Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik, 1829) (Hansen et al. 2009a, 2009b). Gillies et al. (2006) demonstrated the crucial role of differences in availability on habitat selection by individuals. In our study, female roe deer selected a given habitat when the habitat occurred with an intermediate availability as compared with when the habitat was rare or very common in their home range (Fig. 4). The avoidance (i.e., used less than expected) of high-quality habitat at low availability should be due to forage depletion of

Fig. 2. Results of the K-select analysis carried out to measure habitat selection by female roe deer (*Capreolus capreolus*) at Chizé (France) from April to August 2003. (a) Main variable loadings on the first two factorial axes: landscape units (oak_50 and oak_75 correspond to oak stand open at 50% and 75%, respectively); plant biomass (*Carpinus b.*, *Carpinus betulus*; *Hyacinthoides n.s.*, *Hyacinthoides nonscripta*; *Rubus sp.*, *Rubus spp.*) and the overall biomass (total, 0–165 cm; total45, 0–45 cm). (b) Projection of the marginality vectors of all animals on the first factorial plane with non-recentered vectors (A); bar chart of the eigenvalues (B) measuring the mean marginality explained by each factorial axis; projections of the marginality vectors of the 5 categories of animals (C, D, E, F, and G) on the first factorial plane with non-recentered vectors. The origins of the arrows indicate habitat availability within the home range and the length of the arrows indicate the intensity of selection. The three colors of the arrows correspond to three periods of the life of a female roe deer: late gestation (April; light grey), birth and early lactation (May–June; dark grey), and lactation (July–August; black).

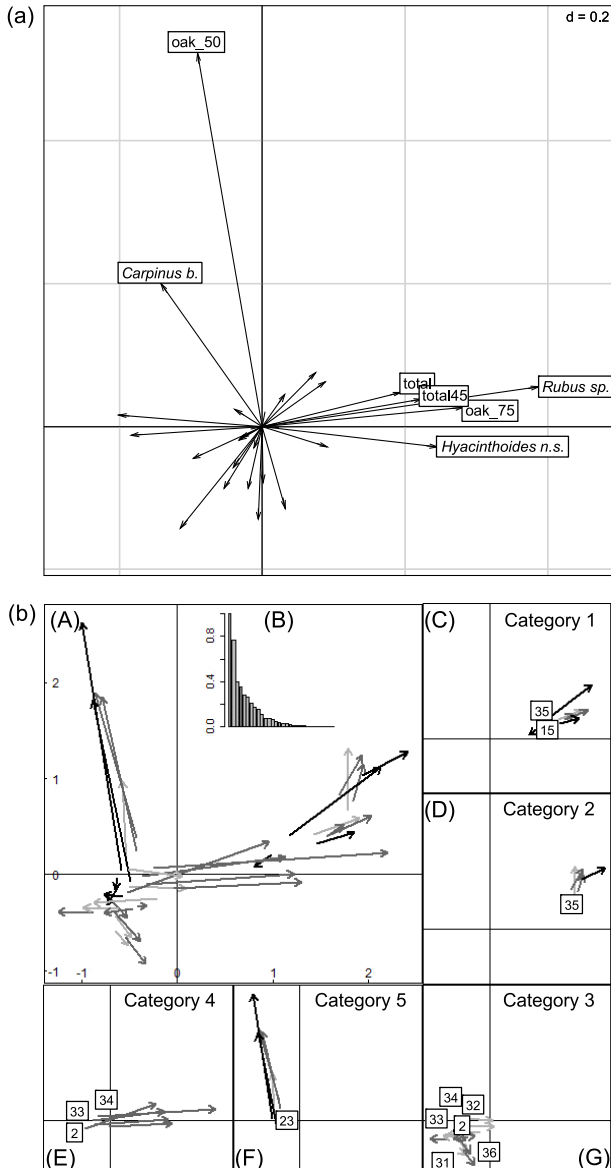


Fig. 3. Results of the K-select analysis carried out to measure habitat selection by female roe deer (*Capreolus capreolus*) at Chizé (France) from April to August 2004. (a) Main variable loadings on the first two factorial axes: landscape units (numbers 0, 50, 75, and more75 correspond to 0%, 50%, 75%, and >75% of forest openness, respectively; oak, oak stand; beech, beech stand) and plant biomass (*Fagus s.*, *Fagus sylvatica*; *Rubus sp.*, *Rubus spp.*). (b) Projection of the marginality vectors of all animals on the first factorial plane with non-recentered vectors (A); bar chart of the eigenvalues (B) measuring the mean marginality explained by each factorial axis; projections of the marginality vectors of the 5 categories of animals (C, D, E, F, and G) on the first factorial plane with non-recentered vectors. The origins of the arrows indicate habitat availability within the home range and the length of the arrows indicate the intensity of selection. The three colors of the arrows correspond to three periods of the life of a female roe deer: late gestation (April; light grey), birth and early lactation (May–June; dark grey), and lactation (July–August; black).

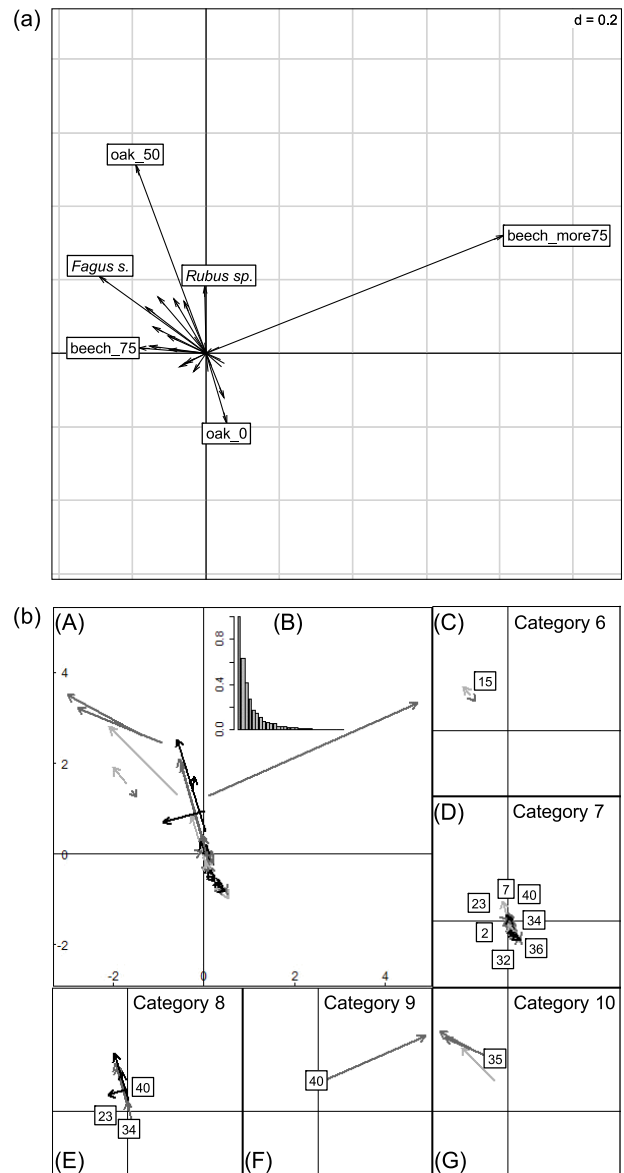
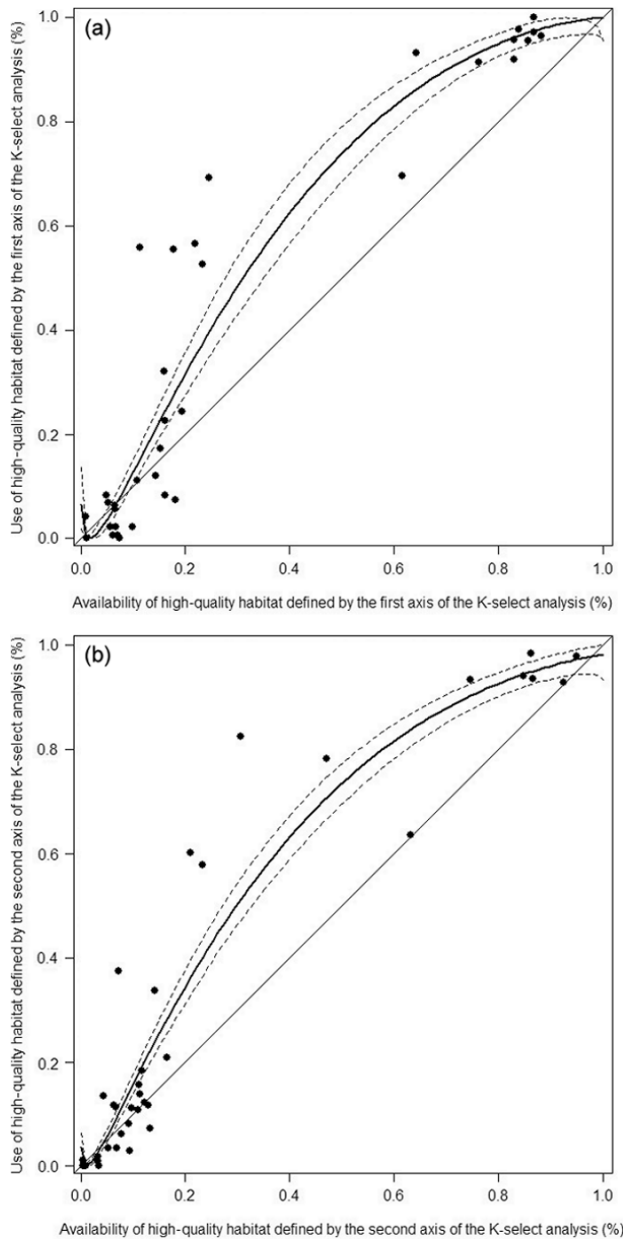


Fig. 4. Relationship between the use and availability of selected habitat (high-quality habitat; see text) by female roe deer (*Capreolus capreolus*) at Chizé (France) in 2003 (a) and 2004 (b). (a) In 2003, selected habitat corresponds to the pixels of the raster maps with a score >0.5 on the first axis of the K-select analysis (i.e., a high proportion of open oak forest and a high plant biomass rich in *Rubus* spp. and in *Hyacinthoides nonscripta*). (b) In 2004, selected habitat corresponds to the pixels of the raster maps with a score >0.5 on the second axis of the K-select analysis (i.e., with a high proportion of moderately open oak forest and a high biomass of *Rubus* spp.). For both plots, the proportion of locations of roe deer in the selected habitat is plotted according to the proportion of the home range covered by this habitat type (each animal-month is represented by a point). The mixed model relating use and availability, averaged over all the animals, is displayed (thick solid line) along with the standard error of the estimate (broken line). The thin solid line represents the 1:1 relationship between use and availability.



high-quality resources when they are scarce (van Beest et al. 2010). This avoidance may also be due to the cost of traveling between habitat patches: the use of high-quality habitats is not profitable below a minimum abundance; above this threshold, the animals strongly select these habitats; and when the abundance of high-quality habitats is very high (i.e., high-quality habitats cover the majority of the home range), animals do not need to select the habitat. This avoidance suggests that there should be a cost for using the habitat. The costs are currently unknown but could include spatial learning (e.g., how best to use resources like food).

The K-select analysis showed that for both years some female roe deer had marked habitat selection at particular periods and that some animals had similar patterns of habitat selection. In general, females selected for moderately open and heterogeneous sites, especially open oak forest, with large amounts of principal or preferred plant species of diet of roe deer in spring and summer, including *Hyacinthoides nonscripta*, *Carpinus betulus*, and *Rubus* spp., within moderately heterogeneous home ranges with intermediate availability of high-quality habitats. Some females living in oak forest with hornbeam coppices showed selection for high-quality habitats only in May and June, during the fawning period that is the most critical time for female roe deer (Gaillard et al. 1998). Thus, it seems that female roe deer living in oak forest with hornbeam coppices, a resource-rich area for roe deer (Pettorelli et al. 2001) associated with high fawn survival during harsh years compared with other forest stands (Pettorelli et al. 2005b), do not need selecting high-quality habitats within their home ranges except during May and June. The rearing period corresponds to the peak of energy requirements (Sadleir 1969), especially in income breeders like female roe deer (Andersen et al. 2000). Moreover, the large quantities of *Rubus* spp. within selected sites are likely to provide fawns a refuge from predators in spring, while the relatively open habitat offers to females good visibility, favouring predator detection around their fawns. This strong selection for high-quality habitats in May–June occurred mostly in 2003. In 2004, only one female of this category was selective during May. Our finding of marked between-year differences in habitat selection indicates that females living in the rich part of the reserve (i.e., oak forest with hornbeam coppices) did not generally need to select higher quality sites within their home ranges even during fawning and rearing period. However, these females were more selective during May–June 2003, apparently in response to the low levels of resource availability in that year. This result indicates that habitat selection should vary among years to track differences in available resources. Finally, the absence of selection for high-quality sites within the home ranges located in the rich part of the reserve revealed that the selection did not occur at the home-range level but rather at the landscape level. The choices of high-quality habitat were certainly already taken at the landscape scale when roe deer established the limits of their home ranges (for evidence of strong influence of home-range composition on individual fitness of roe deer see McLoughlin et al. 2007).

In the oak forest with maple coppices, some females selected moderately open oak forest and high biomass of *Carpinus betulus*. The home ranges of these females were

relatively homogeneous. The occurrence of saplings of *Carpinus betulus* in these open areas, a preferred species during spring and a principal species during summer, may account for that habitat selection patterns. Female selectivity increased from April to May–August when the metabolic needs of females peaked. In the poor beech forest, some females strongly selected for very open beech stand with high biomass of beech during June, perhaps for the same reasons as females living in oak forest with hornbeam coppices that selected for open oak stand during May and June. The high openness in beech stands provides enhanced food availability for roe deer compared with a more closed beech forest that represents poor-quality habitat (beech is an indifferent species in the spring and summer diets of roe deer). In August, these females showed a reverse selection by avoiding very open beech forest. This selection for more closed habitat in August may be antipredator behaviour for females with fawns at heel.

Our results are consistent with the argument that both cover and food resources are important in habitat selection by roe deer (Mysterud et al. 1999). Female roe deer select high-quality habitats (especially oak forest) containing principal and preferred species in large quantities, and in spite of relative openness of selected sites, they provide adequate plant cover because *Rubus* spp. are abundant. Our location data do not allow the differentiation of foraging areas from resting areas, but we show that selection of areas within the home ranges was correlated with the amount of food resources for the deer.

The understanding of changes in habitat use with habitat availability at the individual level, as analyzed in this paper, allows the large variability observed among individuals in resource selection to be understood. In many studies, individuals with very different patterns of resource selection are pooled to make generalizations about habitat use. From these results, habitat use in populations like this one will be better understood by analyzing the collective patterns of individual habitat selection rather than by averaging (see also Osko et al. 2004). Only when both the differences of habitat availability among individuals and the variations in their life cycle (e.g., in response to breeding) are taken into account will the spatial distribution of individuals over landscapes be predicted accurately. Finally, patterns of habitat use may change according to the scale used and the selection of an appropriate scale will vary depending on the research interest (Boyce et al. 2003). In our study, we analyzed habitat selection by female roe deer at the scale of patches within the home range (third order; Johnson 1980). More work will be required to assess the effects of individual variation and of the variation in habitat availability at larger (i.e., home ranges within the study area) and finer (i.e., food items within selected patches) scales.

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