

Research Article

The influence of landscape structure on female roe deer home-range size

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Received 26 August 2004; accepted in revised form 16 May 2005

Key words: *Capreolus capreolus*, Edge density, Generalized linear mixed model, Landscape structure

Abstract

Animal distribution and abundance are greatly affected by the availability of their food resources, which also depends on landscape structure. Lothar hurricane in 1999 had profoundly modified the structure of the forests in France, affecting the habitat quality of ungulates. We tested whether the variations in home-range size of 23 female roe deer were influenced by the fragmentation of the landscape caused by Lothar in the Chizé forest, namely by the increase in heterogeneity associated with the localized massive tree felling. Home-range size was studied in the summers of 2001 and 2002 and we found that variation in home-range size was mainly explained by only one landscape variable: edge density. Home-range size decreased as edge density increased, which is consistent with the fact that edges are good browsing habitats for roe deer. The result of this study suggests that, after 2 years, the hurricane had improved the quality of the home ranges by creating more forest heterogeneity and increasing the contacts between the different vegetation patches within the home range. These results highlight the fact that spatial heterogeneity is likely to be a key factor influencing the distribution and local population density.

Introduction

The distribution, abundance and diversity of animal species in an area are affected by the structural characteristics of a landscape such as habitat type, resource-patch size, edge length, configuration (Forman et al. 1976) and disturbance or man-made landscape structure (Fritz et al. 2003). Moreover, animal distribution and abundance are profoundly affected by the availability of their food resources, a process whereby a continuum of at least five spatial scales is involved: the geo-

graphic distribution of the species, the home range in which they choose to stay, the habitats selected within a home range, the feeding sites they selected, and the selection of bites within these sites (Johnson 1980; Manly et al. 2002). Interspecific variation in home ranges has been studied in some detail (Harestad and Bunnell 1979; Gittleman and Harvey 1982; Mysterud et al. 2001), but the causes of intraspecific size variation are poorly understood. According to the concept of the Ideal Free Distribution (IFD; Fretwell and Lucas 1970), the size of an animal home range within a population

should be related to the abundance of its resources in order to optimise fitness. In this context, animals should occupy the smallest area that contains the resources they require (Harestad and Bunnell 1979).

Home range size is also influenced by many different biotic factors such as body size (McNab 1963; Swihart et al. 1988), sex and age (Cederlund and Sand 1994; Relyea et al. 2000), reproductive status (Bertrand et al. 1996), social system (Hewison et al. 1998); and abiotic factors like season (Nicholson et al. 1997), water availability (Bowers et al. 1990) or population density (Kjellander et al. 2004). Among mammals, herbivores favour habitat heterogeneity (Kie et al. 2002), as it increases the amount of edges between plant communities and hence increases resources (Hunter 1990). The selection of different vegetation communities by a herbivore should reflect foraging and refuge-seeking strategies (Andersen et al. 1998). If an increase in the amount of edge is related to an increase in the availability of resources, then it should also result in a decrease in home range size. Also, if a greater resource availability is offered by habitat edges, then more time would also be spent near these edges.

Among the herbivores in continental Europe, the roe deer commonly live in deciduous woodlands, a vegetation type in which roe deer respond more to the abundance of resources than to the spatial variability in cover and resources (Andersen et al. 1998). Food abundance influenced the home ranges size of roe deer living in a heterogeneous landscape with woodland, heath and grassland (Tufto et al. 1996). Further, female summer habitat use is more sensitive to resource availability compared to males, which have to defend intrasexual territories (San José et al. 1998). In this species, variation in habitat quality seems to induce very strong spatial and temporal variations in the dynamic of the population (i.e. reproductive success; Pettorelli et al. 2001, 2002, 2003). Moreover, due to their small body size, roe deer may be more dependent on the quality than the quantity of resources (Demment and Van Soest 1985), hence resource heterogeneity could play a role at a very fine scale.

In France, in late December 1999, hurricane Lothar, which may have been a 1000-year storm event, caused widespread massive destruction of forest stands, but with a high heterogeneity in the

intensity of damage within and between forests. In fact, timber stands were more impacted than the shrub-coppice, since there are larger trees that were toppled by the storm (Widmer et al. 2004).

Our objective was to test how the summer home range size of female roe deer was influenced by landscape heterogeneity. In previous work on the same individuals, we have shown that variations in summer home-range size were not related to life-history parameters (such as body mass and reproductive success) but only by the amount and quality of biomass of the vegetation available within a home range (Saïd et al. in press). Prior to Lothar, the study site had been classified into two major cover types: high-forage-quality oak and low-forage-quality beech forests (Pettorelli et al. 2001). However, these two habitats were damaged in a differential way by Lothar, which resulted in increased habitat heterogeneity and more vegetation at the ground level in the southern beech forests (Fuller 2001). One possible results of the differential damages is that the habitat quality of the southern part of the reserve could have increased. Indeed, the consequence of a windstorm was that afterwards more light penetrated, which resulted in more vegetation on the ground level (Fuller 2001). We predict that home range size should vary with the distribution and cover of the different patches of vegetation within the home range, particularly the amount of edge. Home-range size should decrease with elevated resource availability associated high landscape heterogeneity. Consequently, the differences in home-range size between the two main habitats should not be pronounced due to the differential increase in heterogeneity in the beech forests following Lothar.

Material and methods

Study area

The study was conducted in the Chizé reserve (2614 ha), which is situated in western France (46°05' N, 0°25' W; Figure 1). The climate is oceanic with Mediterranean influences, characterized by mild winters and hot, dry summers. The dominant woody plant species include oak (*Quercus* spp.), pine (*Pinus* spp.), maple (*Acer* spp.), hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*),

plum (*Prunus avium*), hawthorn (*Crataegus monogyna*), dogwood (*Cornus* spp.), cedar (*Cedrus* sp.) and Douglas fir (*Abies douglasii*). In the Chizé reserve, 19% of the forest was destroyed by hurricane Lothar (Figure 1). Before Lothar, two major habitat types for roe deer could be distinguished (i) a rich quality of habitat with oak as the dominant species situated in the northern part of the reserve and, (ii) a poor quality of habitat situated in the southern part of the reserve where beech is dominant (Pettorelli et al. 2001).

Hurricane Lothar damaged 24.5% of the southern part of the reserve whereas only 4.6% of the northern oak forests was affected (Figure 1).

Roe deer population in Chizé has been monitored by mark and recapture studies since 1976 (Gaillard et al. 1993), and estimates obtained from this monitoring indicate that the population density did not vary during our study period (2001: mean = 11.1/km²; 2002: mean = 11.8/km²; Guy Van Laere and Jean-Michel Gaillard, Personal communication).

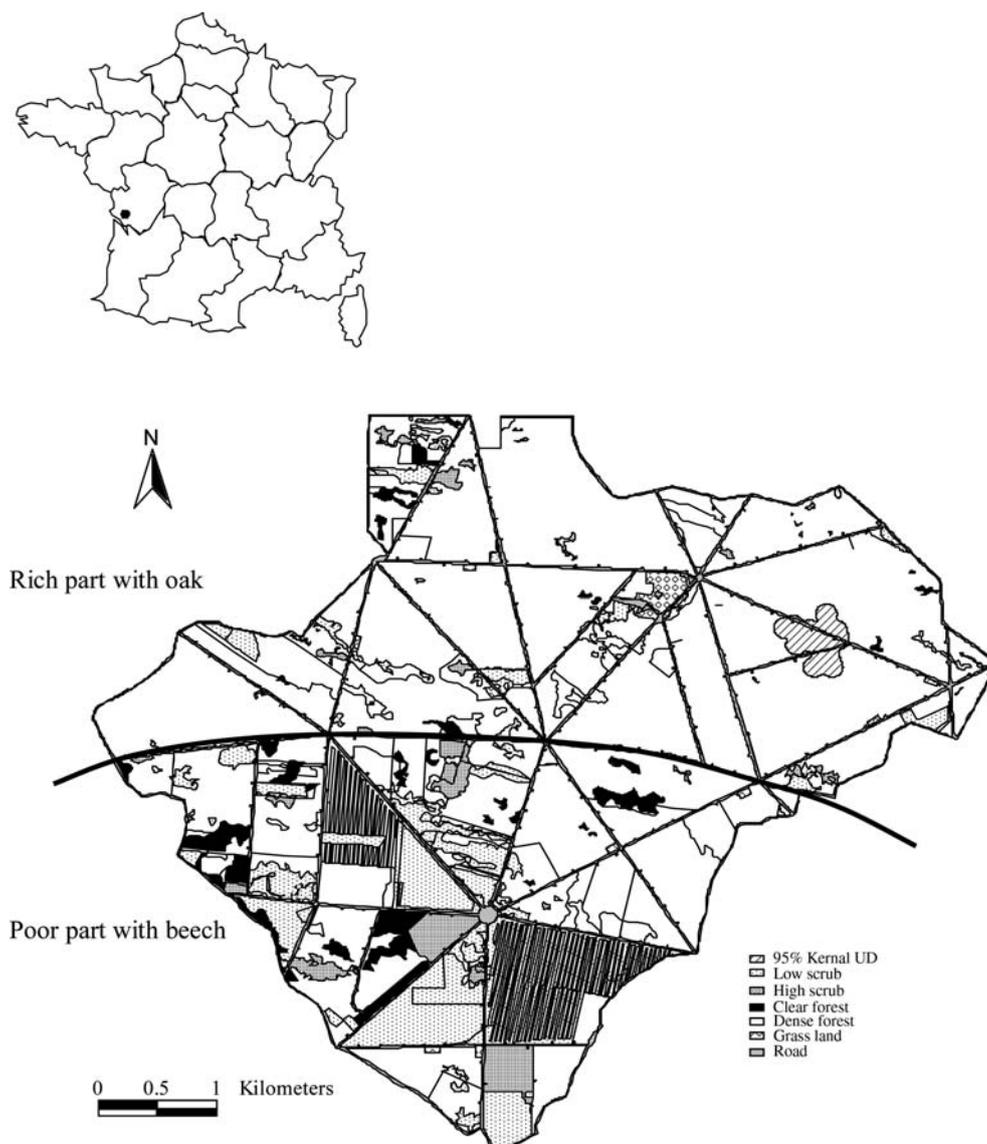


Figure 1. Location and spatial representation of the Chizé reserve (2614 ha), an enclosed forest in western France. One female home range in 2002 is also represented (95% kernel home-range size).

Model species

The roe deer is a generalist herbivore and a selective feeder (Andersen et al. 1998). In Western Europe, the principal food plants of this browser in summer are oak, hornbeam, maple, hawthorn and dogwood (Andersen et al. 1998). The availability of ligneous and semi-ligneous plants, which are preferentially eaten by roe deer, increased after the hurricane (Gill and Beardall 2001).

For this study, we monitored 15 female roe deer in 2001, 19 female roe deer in 2002, among which 11 were monitored during both years. In this paper, we only considered adult deer of known age (≥ 2 years).

Landscape sampling

In France, the forests managed by the Office National des Forêts (ONF) are generally divided up into parcels (plots). These forest plots are identified by a number, while the limits between them are demarcated by forest trails. In each plot, the dominant species for coppice wood (i.e. species with the maximum cover), and their cover (in %), were determined by aerial photographs and then corrected by foresters. These data have been collected by ONF since 1993. Using aerial photographs, we defined five landscape units based ligneous cover (Saïd and Gégout 2000) and the level of hurricane damage (Table 1). All aerial photographs of the study area taken during the most recent operation (2000) were classified by this method, after which all landscape units were numbered and incorporated into a Geographic Information Systems (GIS; Arc View 3.2;

Table 1). Roads were also integrated as one other landscape unit (Table 1).

Home-range sizes

Female roe deer fitted with Televilt TXH-3 radio collars were tracked in July and August in 2001 and 2002 (Table 2). The does were tracked by a TONNA five-element antenna attached to Televilt RX 900 or Yaesu FT-290R receivers, and located on average 17 occasions (range 16–18) per month. We determined the minimum number of fixes necessary to obtain an accurate estimate of home range size by conducting a bootstrap test and plotting the estimates of home-range size against sample size (Harris et al. 1990; Hansteen et al. 1997). This test was done with GPS locations in the same study area (M. Pellerin, S. Saïd, P. Duncan and J. M. Gaillard, unpubl. data). To reduce autocorrelation between two successive fixes, all points were taken with a minimum time interval of 15 h (Swihart and Slade 1985a, b, 1986; Hansteen et al. 1997). The fixes were determined by triangulation (White and Garrott 1990) and several bearings were taken with a compass to obtain locations with a high accuracy (mean = 100 m; SD = 19).

Radio-tracking data were analysed by GIS application Arcview 3.2 (Environmental Systems Research Institute Inc., Redlands, USA) and the Animal Movement extension (Hooze and Eichenlaub 1997). Home-range areas were estimated using fixed kernel estimator (Silverman 1986; Worton 1989; Table 2) with an optimum smoothing factor (H) calculated using least-squares cross validation, which gives the best

Table 1. Landscape units defined from the aerial photographs according to vegetation cover.

Photo interpretation	Vegetation cover	Consequences of Lothar	Percentage of hurricane damage
Homogeneous intermediate stage without high ligneous vegetation	Low scrub (LS)	Affected by hurricane Lothar	75%
Intermediate stage with high ligneous vegetation	High scrub (HS)	Affected by hurricane Lothar	50%
High heterogeneous stage	Clear forest (CF)	Affected by hurricane Lothar	25%
High homogeneous stage	Dense forest (DF)	Not affected by hurricane Lothar	0%
Homogeneous and linear surface	Road (R)	Not affected by hurricane Lothar	0%
Homogeneous low stage	Grassland (G)	Not affected by hurricane Lothar	0%

Table 2. Home-range size (ha) of female roe deer monitored during summers (i.e. in July and August) of 2001 and 2002.

Name	2001	2002
1		17.00
2	18.91	23.40
4		26.22
5	11.66	29.91
7	23.87	
8	25.72	21.42
9	35.00	25.57
10	21.58	21.51
11		23.22
12	21.76	22.25
13	39.63	31.83
14	15.33	
15	22.87	
16	19.87	14.37
17	26.11	28.36
18	25.38	
19	15.72	17.16
21	40.44	33.86
23		23.53
24		26.86
25		34.16
26		29.64
27		18.62
N		23
Mean		24.49
Standard deviation		6.93

estimate of the home range (Silverman 1986; Seaman and Powell 1996).

Spatial analyses

Thirteen spatial-pattern indices (Table 3) were calculated using FRAGSTATS (McGarigal and Marks 1995) in the Patch Analysis extension for ArcView (Elkie et al. 1999). Among all the metrics that can be calculated using FRAGSTATS, only those that were area insensitive were used in this study as we wanted to compare metrics among female roe deer home ranges. Furthermore, those spatial-pattern indices were selected to account for the fragmentation of the home range due to Lothar hurricane (Table 3).

We conducted the analysis for a 95% kernel home-range size (Worton 1989). We also conducted the same analyse at the 50% level. The latter led to the same results as those found for the 95% kernel so we only report the results obtained with the most-common estimate of home-range size (95% kernel).

Table 3. Definitions of spatial-pattern indices from Elkie et al. (1999).

Acronym	Fragstats metric	Description
NP	Number of patches	Total number of patches in the home range
RL	Proportion of road in landscape	Ratio (Area of road/Area of home range)
GL	Proportion of grassland in landscape	Ratio (Area of grazers/Area of home range)
MedPS	Median patch size (ha)	Median total landscape area divided by the total number of patches
SDPS	Patch size standard deviation	Standard deviation of patch areas
CoefVarPS	Patch Size coefficient of variation	Coefficient of variation of patch areas: patch-size standard deviation divided by mean patch size
ED	Edge density (m/ha)	Sum of length of all edge segments divided by total area. All edge segments are defined as contacts between different patches of landscape in the home range
MPE	Mean Patch Edge	Average amount of edge per patch (m/patch)
MSI	Mean shape index	Shape complexity. equals 1 when all patches are circular (polygons) or square (grids)
MPFD	Mean patch fractal dimension	Shape complexity. equals 1 for shapes with simple perimeters and approaches 2 for more complex shapes.
MPA	Mean Perimeter-Area ratio	Shape complexity
AWMPFD	Area-weighted mean patch fractal dimension	Patch shape complexity measure. weighted by patch area; AWMPFD approaches 1 for shapes with simple perimeters. and 2 for complex shapes
AWMSI	Area-weighted mean shape index	Mean patch shape complexity. weighted by patch area; equals 1 when all patches are circular and increases as patches become non-circular

For more information on each statistic. see McGarigal and Marks (1995). Statistics with units are reported in meters, hectares, meters per 100 ha. or percentage.

Statistical analysis

To select subsets of landscape variables among the spatial-pattern indices (13 variables; Table 3) and landscape units (five variables and roads; Table 1), we used a principal component analysis (PCA) as a variable selection technique (Jolliffe 1972, 1973). We retained the number of principal components (i.e. axes) with the 'Scree-test' (i.e. observation of the eigenvalues graph; Cattell 1966). Following Jolliffe's B4 method (Jolliffe 1972, 1973), we selected the landscape variable with the largest magnitude in the first loading vector and this process was repeated on all the remaining selected principal components. One disadvantage of this method is that only one principal component is examined when each variable is selected. Therefore, we selected the landscape variables based on an interpretation of the loading vector produced by the PCA on each selected principal components and that they were not correlated to each other. For this analysis ADE4 freeware was used (Thioulouse et al. 1997).

A generalized linear mixed model (GLMM) was applied with the 95% kernel home-range size as the dependent variable, and the independent variables were the year (2001 and 2002), forest cover types, and the variables selected by the PCA as covariates. Individual roe deer were included as a random factor, to take repeated measures of individuals and intra-individual variance into account (Little et al. 1991) and to avoid pseudo-replication (Hurlbert 1984). To validate the simple model corresponding to such restrictions, we calculated the proportion of variability among home-ranges that was accounted for by our different factors. We used the SPSS 10 software for statistical analysis (SPSS 1999). Before applying ANCOVA, the data were checked for normality (Kolmogorov-Smirnov test: $d = 0.0662$, p -value = 0.9517).

Results

Principal component analysis

The first two axes of PCA accounted for 38.93% of the total inertia (20.43% for the first axis, 18.51% for the second). The variable selection technique was performed based on these two axes

since less than 10% of the total inertia was further explained by the other axes. The first axis can be interpreted as a representation of the overall home-range structure (edge density, mean patch edge, proportion of road in home range and number of patches; Figure 2) and it describes the fragmentation of land cover types in the home range. Axis 1 is defined by two redundant groups of variables in opposite direction: one group is composed of variables that are quantifying edge (density and length) and the other group, is identified by number of patches (NP).

The second axis can be interpreted as a representation of patch-shape complexity of land cover in the home range: mean shape index (MSI) and mean patch fractal dimension (MPFD).

Impact of landscape structure on home-range size

Numerous indices of spatial-patterns were correlated with each other (Figure 2) and the correlation matrix confirmed the redundancy of the variables (Table 4). We fit the model with two orthogonal indices of landscape heterogeneity: ED (axis 1), MSI (axis 2) (Table 4).

The summer mean estimated home-range size was 24.5 ha (SD = 6.9). The fitted GLMM shows that there was no significant differences in female roe deer home-range size between the two different vegetation cover types in Chizé: Northern-oak forest = 23.8 ± 7.1 ha, Southern-beech forest = 25.3 ± 6.8 ha, ($F_{1,32} = 0.384$, $p = 0.540$). Furthermore, no difference in home range size was observed between years: 2001 = 24.26 ± 8.43 ha, 2002: 24.68 ± 5.72 ha ($F_{1,32} = 0.244$, $p = 0.637$), nor between individuals ($F_{22,32} = 0.959$, $p = 0.57$). Among the landscape variables edge density was significant ($F_{1,32} = 7.416$, $p = 0.030$) whereas mean shape index was not ($F_{1,32} = 0.107$, $p = 0.753$). Home-range size decreased with increasing edge density (Figure 3). We checked the validity of our selected model by plotting the observed values vs. the predicted ones ($r^2 = 0.68$; $p < 0.001$).

Discussion

Our results demonstrate that home-range size of the roe deer in the Chizé forest was primarily

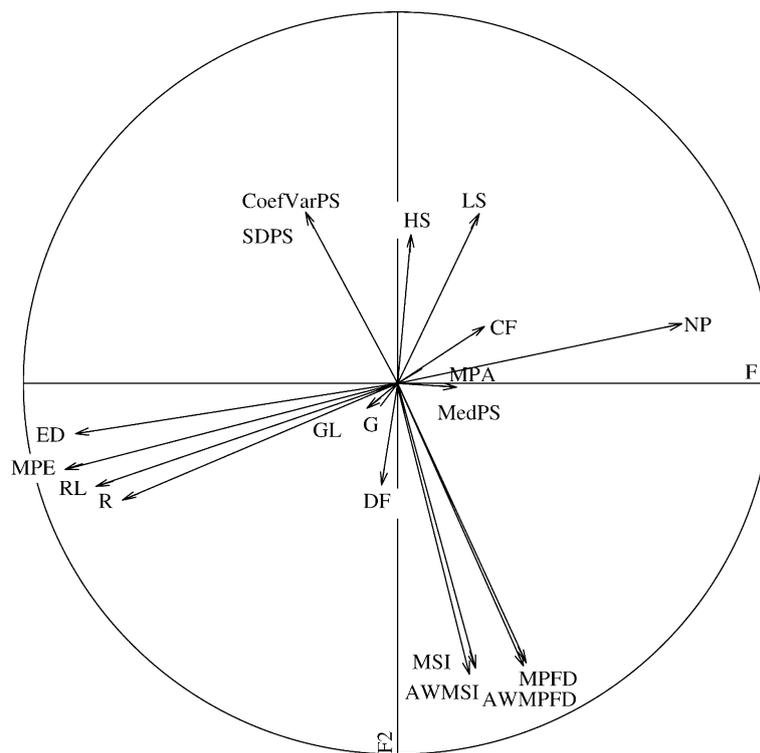


Figure 2. Correlation circle variables-axes (F1–F2 factorial plane). The variables are: number of patches (NP), median patch size (MedPS), coefficient of variation of patch size (CoefVarPS), edge density (ED), mean patch edge (MPE), mean shape index (MSI), area weighted mean shape index (AWMSI), mean perimeter-area ratio (MPA), mean patch fractal dimension (MPFD), area weighted mean patch fractal dimension (AWMPFD), low scrub (LS), high scrub (HS), clear forest (CF), dense forest (DF), grazers (G), road (R), ratio area of road-area of landscape (RL), ratio area of grazers-area of landscape (GL), patch size standard deviation (SDPS).

influenced by edge density. Following Lothar, variations in home-range size were not explained by the differences between the quality of the two

vegetation types that were identified inside the reserve before the hurricane (Pettorelli et al. 2001). Wahlström and Kjellander (1995) have observed

Table 4. Correlation matrix between eight variables selected by PCA.

	MPS	ED	SHDI	TE	CoefVarPS	MPE	Road	Grassland
MPS	1	-0.586	-0.651	-0.364	-0.41	0.769	0.137	-0.095
ED		1	0.609	0.624	0.113	-0.115	-0.049	-0.009
SHDI			1	0.604	0.028	-0.372	-0.218	0.031
TE				1	p = 0.0008	p = 0.0027	p = 0.0895	p = 0.8110
CoefVarPS					1	-0.536	0.036	0.124
MPE						1	p = 0.7845	p = 0.3367
Road							1	0.471
Grassland								1

Numbers in bold are significant at $\alpha = 0.01$. For descriptions and names of the abbreviated variables, see Table 3.

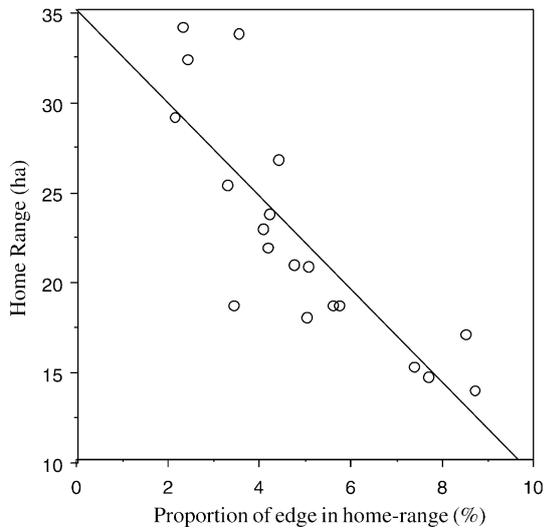


Figure 3. Relationship between home range size (95% adaptive-kernel analysis) in 2002 for female roe deer in the Chizé reserve and the proportion of edge in home range (%).

that in the poorer part (i.e. with a low resource availability) of their study site, female roe deer had larger home-range sizes. The lack of difference in home range size between the oak and beech forests indicates that the disproportionate damage from Lothar to the southern forest, and the subsequent increase in heterogeneity, has improved the environmental conditions from the perspective of the deer. The hurricane damage created pockets of preferred habitat in what was previously a relatively homogeneous beech forest (Fuller and Gill 2001). Differences observed between our results and those obtained by Pettorelli et al. (2001) prior to the hurricane may also be due to the use of different spatial scales: i.e. the type of habitat at the landscape level (Pettorelli et al. 2001) vs. the home range (our results), and/or by differences in local population density that could influence home-range size (i.e. as population density increased, female home range decreased; Kjellander et al. 2004). Indeed, the small body size of roe deer, compared to other European ungulates, means that they are more sensitive to variations in the quality of their food resources (abundance of preferred species) than in the quantity of available food (Demment and Van Soest 1985).

Observed variation in home-range size (24.5 ± 6.9 ha; $CV = 0.28$) could be explained by

differences in structure of habitat (e.g. edge density), insofar as variations in climate were constant for all individuals of the population. Among all the different types of landscape variables included in our models, only edge density was significant, accounting for 68% of the variability in roe deer home range size. The importance of this result was unexpected and emphasizes the potential interest of habitat heterogeneity in determining patterns of distributions for large herbivores (Kie et al. 2002).

We found that roe deer home-range size was negatively correlated with edge density (Figure 3). This can be related to the fact that roe deer is a browser (Andersen et al. 1998) and that its main food is located at the edge. However, the edge-density variable considered in this study included edge of all patches of vegetation cover within the home range and not only edge length created by forest trails or roads. More precisely, edge density is a function of the amount of border between patches of vegetation cover within the home range. Consequently, edges provide a good interspersed cover and forage. They make it easier for mammalian herbivores to penetrate farther into the forest where they may find many edible forest plant species (Alverson et al. 1988; Augustine and Frelich 1998).

Our results demonstrate that roe deer adjust home range size in response to landscape structure, but further research is warranted on how behaviour changes with land-management activities, climatic disturbance, or over time with plant community succession. In general, widespread agricultural and silvicultural activities have considerably improved deer habitat throughout the 20th century (Alverson et al. 1988; Fuller and Gill 2001). The early stage of forested landscape succession provide abundant, high-quality food that increase deer habitat carrying capacity (Sinclair 1997; Fuller and Gill 2001). Many openings are also intentionally managed to boost forage quality and population growth (Waller and Alverson 1997). In this context, deer impacts on vegetation are greater in fragmented landscapes (Reimoser 2003) or low-productivity habitats (Danell et al. 1991; see also Côté et al. 2004 for a review). Landscape structure influences patterns of deer movement in home ranges (Kie et al. 2002), which in turn may affect plant succession (Gill and Beardall 2001; Saïd 2001; Boucher et al. 2004).

Acknowledgements

This work was carried out thanks to the financial support by GIPECOFOR (France). We would like to thank Jean-Michel Gaillard, François Klein and Hervé Fritz for ideas, comments and suggestions on previous drafts of this work. Special thanks to Petter Kjellander, Dean Anderson and one anonymous reviewers for their critical and valuable comments. We are grateful to Guy Van Laere and Noël Guillon for their field assistance. We thank the 'Office National des Forêts' for their aerial photographs. Finally, we are grateful to Patrick Duncan, Antony Gill 'the friend of Oli' and Eveline Taran for helping us to improve the English.

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