SPACE USE BY ROE DEER IN A FRAGMENTED LANDSCAPE SOME PRELIMINARY RESULTS

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RÉSUMÉ

Les patrons d'utilisation de l'espace par le chevreuil sont bien connus, à la fois dans l'habitat forestier et dans la plaine agricole. Mais les stratégies d'utilisation de l'espace dans des paysages fragmentés sont à peu près inconnues. Dans cet article nous présentons les premiers résultats sur les domaines vitaux de neuf chevreuils suivis par radiotracking dans un paysage de coteaux agricoles où les bois représentent un habitat fragmenté. Capturés sur le même site, ces animaux ont présenté deux modes différents d'occupation de l'espace en fonction de l'ambiance plus ou moins forestière du lieu. Les domaines vitaux les plus forestiers étaient de petite dimension et l'écart entre leurs barycentres successifs montrait une forte stabilité spatiale. Les deux chevreuils installés en milieu agricole avaient des domaines très vastes et mobiles dans le temps, dont la superficie dépendait de la fréquence et de la dispersion des bosquets. La surface absolue d'habitat boisé incluse dans un domaine ne différait pas entre les animaux forestiers et ceux de la matrice agricole. Nos résultats suggèrent que le chevreuil a besoin d'une certaine surface d'habitat boisé pour l'alimentation, le repos et des activités sociales. Ainsi la fragmentation de la forêt aurait des conséquences marquées sur le patron d'utilisation de l'espace par les individus et probablement sur la dynamique de la population à l'échelle du paysage.

SUMMARY

Patterns of space use for roe deer have been extensively described, both in its traditional forest habitat and in the recently colonized agricultural plain. Much less is known about space use strategies in fragmented landscapes. Here we present the first results on home range characteristics of radio-collared deer inhabiting a landscape of small woodland fragments disseminated within a matrix of agricultural activity (mostly pastoral). We compare patterns of space use of individuals inhabiting one of only two woods of notable size (600 ha) with those inhabiting the copses (average size 3 ha), hedgerows and open fields of this fragmented landscape. The two deer living in the copses and open fields had significantly larger home range sizes than the seven forest deer, particularly outside the period of territoriality. Home range size and stability were similar to that reported in the literature for true field roe deer and true forest roe deer respectively. Roe deer living in the copses and fields retained strong ties with the woodland structures of the landscape. Indeed, home ranges of both copse-living and forest deer included approximately the same surface area (27 ha) of wooded habitat. Home range size of the copse-living deer increased with increasing distance between remnant

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patches of woodland. We interpret our results to suggest that roe deer require a certain base area of woodland habitat for food, shelter and social functions and that fragmentation of woodland habitat will have marked consequences on the patterns of space use of individuals and probably on the dynamics of the population at the landscape level.

INTRODUCTION

Over the last twenty years roe deer populations have developed considerably across Europe, both in terms of numbers and geographic range (Danilkin & Hewison, 1996; Andersen et al., 1998; Boisaubert et al., 1999). As a corollary to this expansion, this species of essentially forest origins has colonized a variety of new habitats (Gaudin et al., 1997), notably the open agricultural plain (Zejda & Bauerova, 1985; Maublanc, 1986; Cibien et al., 1989). Despite this ecological and behavioural plasticity (sensu Komers, 1997; for roe deer see Maublanc et al., 1987; Hewison et al., 1998), several authors have underlined the importance of the availability and distribution of resources for determining patterns of space occupation by roe deer (Zejda & Bauerova, 1985; Cibien & Sempéré, 1989; Tufto et al., 1996; Maillard et al., 1999). Indeed, whether in forest or open field habitats, the roe deer generally retains a strong tie with the remnant woodland structures for the purposes of feeding, shelter and possibly social functions such as territoriality among males (Maublanc, 1986; Aulak & Babinska-Werka, 1990; Tufto et al., 1996; Hewison et al., 1998; San José & Lovari, 1998; Vincent et al., 1998). However, at extreme levels of landscape openness, the roe deer may adopt a completely open field habit, actually remaining at a distance from any woodland patches (Hewison et al., 2001).

Although patterns of space use are thus well documented for roe deer occupying forest habitat and the agricultural plain, much less is known about space use strategies in fragmented landscapes where woodland habitat remains a prominent feature (but see Lovari & San José, 1997). The aim of the work presented here was to provide an initial description of space use at the individual level by roe deer in a landscape where forest habitat is widely present, but is disseminated over the landscape in small patches of wood and hedgerows of varying size. In such a landscape, we made the following predictions: 1. Because roe deer retain strong ties with woodland in almost all landscapes, we predicted a strong spatial association of roe deer with the woodland structures present in this landscape, 2. Because field roe deer have much larger home ranges than forest living animals, we predicted a home range of intermediate size between open field roe deer populations and forest populations, dependent on the spatial distribution of woodland habitat, 3. Because roe deer seem to have a minimum requirement for a certain surface area of woodland, we predicted a constant surface area of this habitat within the home ranges of individual deer.

METHODS

STUDY SITE

The study site is a landscape of roughly 10 000 ha situated in the Midi-Pyrénées region (Bas Comminges), in the southern part of the Haute-

Garonne département, France. The climate is oceanic with an average annual temperature of 11-12 °C and around 800 mm of precipitation. It is a hilly region at an average altitude of 350 m with a mixture of clay and calcareous soils. Land use is primarily pastoral, with sheep and cattle grazing and some agricultural crops. About 25 % of the surface area is forested (Fig. 1), mostly comprising small wood lots or copses predominantly of oak coppice (*Quercus* sp.) averaging 3 ha (Guyon *et al.*, 1996; Vincent *et al.*, 1996), but with 2 larger woodland blocks. The first, to the north of the study site, is a 600 ha private plantation mainly of Douglas fir (*Pseudotsuga menziesii*) planted in the 1970's (Reby *et al.*, 2000), and a second



Figure 1. — Map of the study site showing wood habitat (black) and the point of capture © for the radio-tracked deer.

4 km to the south, consisting of 450 ha of deciduous forest. We estimated woodland dispersion in a given area (*e.g.* an individual's home range) as the average distance between the centre of gravity of each pair of woodland copses (minimum size of $\frac{1}{4}$ ha). The area is inhabited, with a large number of farms and small holdings, mostly along the extensive road network.

A large population of roe deer has been established in the area for some time and is hunted regularly by stalking from June onwards and by drive hunts from September. An estimation of deer density from capture-mark-recapture was possible in the private plantation to the north and indicated about 20 deer/100 ha (Reby *et al.*, 1998; Reby *et al.*, 2000). No notable fluctuations of roe deer abundance were discerned between 1992 and 2000 in the open agricultural areas of the landscape using standardized car transects in winter (unpubl. data).

DATA COLLECTION AND ANALYSIS

We captured 15 roe deer over 2 winters (February 1996 and February 1997) using standard net capture methods in the private plantation to the north (Fig. 1) of which we were able to track 9 for at least 18 months. These animals were equipped with radio collars. Ages were estimated from tooth emergence and wear using 4 age classes (fawn, yearling, sub-adult [2-3 years], adult [4 years or more]) as more precise estimates are not possible using this method (Van Laere *et al.*, 1989; Hewison *et al.*, 1999). Information on the marked animals is given in table I. All males were considered to be territorial as defined by Johansson (1996) and Liberg *et al.* (1998); females are not generally territorial in this species (Hewison *et al.*, 1998). In the days following capture, two deer (1 male and 1 female) left the forest. Therefore, in this paper, we distinguish two types of habitat use strategies among adults: "forest deer" (1-7, Table I) which, although sometimes located at the forest edge, did not use the open agricultural habitat, and "copse-living deer" (8 & 9, Table I) which spent most of their time in the small copses, hedges and the open agricultural plain.

TABLE I

Number	Age-sex class	Habitat	Date of capture	Tracked until	Average home range	Notes
1 2 3 4 5 6 7 8	Adult male Adult male Adult male Adult male Adult male Adult male Adult female Adult male	Forest Forest Forest Forest Forest Forest Plain	February 1996 February 1996 February 1997 February 1997 February 1997 February 1997 February 1997 February 1996	September 1998 October 1998 February 2000 November 1999 February 2000 July 1999 February 2000 February 2000	32.5 28.5 23.3 17.8 17.4 32.2 28.0 204.3	Shot during hunt Shot during hunt Transmitter failure Shot during hunt Transmitter failure Shot during hunt Shot during hunt Transmitter failure
9	Adult female	Plain	February 1996	July 1997	81.2	Transmitter fa

Characteristics of the 9 radio-tracked roe deer, the average seasonal home range size (ha) and the duration of the tracking period.

The deer were tracked intensively from February 1996 to February 1999 and then in a less systematic way until the transmitters failed to function. During tracking sessions (two or three per week), each individual was located to the nearest hectare, covering both periods of activity (dawn, dusk, night) and rest (day). Only tracking points that were at least 2 hours 30 minutes apart were included for analysis. Home ranges were calculated using the Minimum Convex Polygon (MCP) method (95 %) and the centre of gravity determined from the Kernel method (Kenward & Hodder, 1996). Although the MCP method may introduce bias due to the inclusion of areas which were not used by the animal (Harris *et al.*, 1990), home ranges of roe deer are sufficiently compact so as to minimize this problem. Home range overlap was calculated for two consecutive seasons for the same individual from the following formula:

 $[A \cap B/((A \cup B) - A \cap B)]*100$

where A and B are the home ranges to be tested for overlap expressed in hectares. This describes the area of overlap (common range) as a percentage of the total surface area of the two home ranges.

For analysis, we considered two periods for which the roe deer exhibits contrasting patterns of space use (Hewison *et al.*, 1998): the period of non-territoriality (also referred to as the winter home range) from September through to the end of February, and the period of territoriality (also referred to as the summer home range and including the rut) from March through to the end of August. We estimated the beginning of male territoriality for our study site from occasional observations of territorial behaviour (rubbing, aggressiveness) and spatial behaviour (separate and distinct home ranges).

We tested for differences in 1. average home range size, and 2. woodland surface area within the average home range, between the forest deer and the copse-living deer for the territorial and non-territorial periods using standard analysis of variance (ANOVA). We looked for a relationship between seasonal home range size and wood dispersion of the copse-living deer using regression analysis. All analysis was carried out using the Ranges V programme for calculating home ranges and SPSS for statistical testing.

RESULTS

Home range size was greatest outside the period of territoriality for both forest and copse-living deer ($F_{1,7} = 23.7$, P = 0.002). In both seasons, copse-living deer had larger home ranges than forest deer ($F_{1,7} = 16.5$, P = 0.005), but this was particularly the case during the winter period ($F_{1,7} = 18.8$, P = 0.003). Home ranges contained a larger surface area of woodland during the winter period (average = 31.3 ha, SE = 5.0) compared to the period of territoriality (average = 23.2 ha, SE = 1.6, N = 9) ($F_{1,7} = 5.70$, P = 0.048) and this difference was similar for both types of deer ($F_{1,7} = 1.63$, P = 0.242). However, there was no difference between forest deer and copse-living deer in the absolute surface area of woodland habitat included within their home ranges ($F_{1,7} = 0.79$, P = 0.403).

i) Forest roe deer: the 95 % MCP annual home ranges were relatively small (average 26 ha, min. 8 ha, max. 55 ha, N = 7), particularly during the period of

territoriality (23.1 ha, SE = 1.5) compared to the rest of the year (28.5 ha, SE = 3.5). These forest deer were extremely sedentary, with the distance between the centre of gravity of successive seasonal ranges never exceeding 400 metres (average 104 m, SE = 19.8, N = 25). The distance between the centre of gravity of the first and last available home range of an individual was of a similar magnitude (164 m, SE = 38.2, N = 7). Successive home ranges of an individual overlapped by up to 88 % of their surface with an average of 57.5 % (SE = 3.3, N = 24). The summer territory of a male always fell within his winter home range.

ii) Copse-living deer: deer in the more open areas of the landscape exhibited a less stable pattern of space occupation. Home ranges were much larger (territorial period: average 108 ha, SE = 51; outside period of territoriality: average = 200 ha, SE = 95, N = 2), variable between seasons and therefore overlapped little from one season to the next (31.8 %, SE = 8.1, N = 7). Each seasonal home range contained a variable number of copses (maximum 12) and home range size increased as the average distance between these copses in the home range increased (Fig. 2, R² = 0.80, P = 0.001). The male was observed to exhibit territorial behaviour in the copses included within his home range that he used in succession. More tracking locations were situated within the copses during the day (96 %) and in the open agricultural plain during the night (39 %) than would be expected by chance ($\chi^2 = 125.5$, df = 3, P < 0.001).



Figure 2. — Relationship between the size of successive seasonal ranges (hectares) of the two deer living in the copses of the fragmented landscape and the degree of woodland dispersion within the home ranges, estimated as the average distance between centres of gravity for each pair of copses (metres). A value of woodland dispersion of zero occurs when the range includes only a single copse.

DISCUSSION

From the literature on roe deer, we can identify two principal modes of space occupation and social behaviour, with no significant differences between the sexes (Hewison et al., 1998), the first, essentially confined to forest habitat, where roe deer use small home ranges which are spatially stable over time (Bramley, 1970; Standgaard, 1972; Pielowski & Bresinski, 1982; Bideau et al., 1983; Vincent et al., 1983: Bideau et al., 1993: Johansson, 1996: Liberg et al., 1998) and the second, in the open plain, where roe deer roam over much larger areas and use home ranges which may differ between seasons (Zejda & Bauerova, 1985; Maublanc et al., 1987: Cibien et al., 1989: Jeppesen, 1990: Gerard et al., 1995). In our study of roe deer in a fragmented landscape, we expected to identify a strategy of space use somewhat intermediate between these two modes. In fact, our results revealed plasticity of response of roe deer to their environment within a single population. We observed individuals living within the largest wood patch whose pattern of space use resembled closely that described for classical forest populations (e.g. Bideau et al., 1983; Vincent et al., 1983) and other individuals in the more open areas with a space use strategy very similar to that of field roe deer (e.g. Maublanc, 1986). Indeed, we even observed a single individual who adapted his space use in consecutive seasons in relation to the landscape features of his home range, from a "field type" strategy, using several copses disseminated across the landscape, to a "forest type" strategy, resulting in a six fold decrease in home range size and concentration of all his activity within a single large wood (see also Cibien & Aîne, 1990). This illustrates well the high level of behavioural and ecological plasticity of this species (see Hewison et al., 1998).

The deer living in the more open areas of the landscape had home range sizes typical of true field roe deer (Hewison et al., 1998) and were much larger than those of the forest deer, particularly during winter when the home ranges were in general at their biggest. Winter ranges of roe deer are indeed typically larger than summer ranges in open habitats (Zejda & Bauerova, 1985; Maublanc, 1986). Despite this, the deer in the more open areas of the landscape retained a strong spatial attachment to the woodland structures available (copses, hedges, etc.) as has been described in all but the most open landscapes (Hewison *et al.*, 2001). Several authors have noted that spatial behaviour of roe deer can be interpreted as a response to the availability and distribution of resources (including food and mates) (Zeida & Bauerova, 1985; Cibien & Sempéré, 1989; Tufto et al., 1996; Maillard et al., 1999). In this context, we found that the absolute surface area of woodland habitat included within the home range was roughly equivalent for individuals living entirely within the forest and those in the more open landscape using copses and hedgerows. We interpret this to indicate that these roe deer have a minimum base requirement of woodland habitat (around 27 ha in this case) for purposes of feeding, shelter and possibly social functions such as territoriality for males and birth sites for females (Hewison et al., 1998). Indeed, our data indicated that the size of the seasonal home range of deer living in the more open areas of the landscape was larger when the remnant woodland patches were more spatially dispersed (Fig. 2). Similarly, other authors have also suggested that home range size is partly determined by the spatial distribution of copses across the landscape in open field habitats (Maublanc, 1986; Lovari & San José, 1997; Marchal, 1998). In this fragmented landscape, woodland structures such as hedges and copses are rather fragile and prone to deterioration or removal (Guyon et al., 1996). Such

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modifications of the landscape are therefore likely to provoke marked perturbations in the pattern of space use of individual roe deer (*cf.* Smith *et al.*, 2000) and, as a consequence, may well have an impact on the local dynamics of the roe deer population.

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