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Spatial variation in springtime food resources influences the winter body mass of roe deer fawns

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Abstract It is well established that the dynamics of mammalian populations vary in time, in relation to density and weather, and often in interaction with phenotypic differences (sex, age and social status). Habitat quality has recently been identified as another significant source of individual variability in vital rates of deer, including roe deer where spatial variations in fawn body mass were found to be only about a tenth of temporal variations. The approach used was to classify the habitat into blocks a priori, and to analyse variation in animal performance among the predefined areas. In a fine-grained approach, here we use data collected over 24 years on 1,235 roe deer fawns captured at known locations and the plant species composition sampled in 2001 at 578 sites in the Chizé forest to determine the spatial structure at a fine scale of both vegetation and winter body mass of fawns, and then to determine links between the two. Space and time played a nearly equal role in determining fawn body masses of both sexes, each

accounting for about 20% of variance and without any interaction between them. The spatial distribution of fawn body mass was perennial over the 24 years considered and predicted values showed a 2 kg range according to location in the reserve, which is much greater than suggested in previous work and is enough to have strong effects on fawn survival. The spatial distribution and the range of predicted body masses were closely similar in males and females. The result of this study is therefore consistent with the view that the life history traits of roe deer are only weakly influenced by sexual selection. The occurrence of three plant species that are known to be important food items in spring/summer roe deer diets, hornbeam (*Carpinus betulus*), bluebell (*Hyacinthoides* sp.) and Star of Bethlehem (*Ornithogalum* sp.) was positively related to winter fawn body mass. The occurrence of species known to be avoided in spring/summer roe deer diets [e.g. butcher's broom (*Ruscus aculeatus*) and beech (*Fagus sylvatica*)], was negatively related to fawn body mass. We conclude that the spatial variation in the body mass of fawns in winter in this forest is as important as the temporal variation, and that the distribution of plant species that are actively selected during spring and summer is an important determinant of spatial variation in winter fawn body mass. The availability of these plants is therefore likely to be a key factor in the dynamics of roe deer populations.

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Introduction

Ecological factors such as density or weather generally account for most of the temporal variation in the dynamics of mammalian populations (Caughley 1977; Gilpin and Hanski 1991; Tilman and Kareiva 1997; Gaillard et al. 2000), often in interaction with phenotypic differences such as sex (Clutton-Brock et al. 1982), age (Charlesworth 1980) or social status (Lott 1991). Habitat

quality has recently been identified as a significant source of individual variability in ungulates (Coulson et al. 1997, 1999; Conradt et al. 1999), and it has been demonstrated that ignoring spatial variation in animal performance can lead to an inaccurate understanding of the dynamics of the populations, and to a significant loss of revenue from management, e.g. by harvesting two contrasting subpopulations at the same rate (Milner-Gulland et al. 2000).

Roe deer (*Capreolus capreolus*) are small and widespread cervids (20–30 kg; Andersen et al. 1998), the populations of which have recently increased strongly in western Europe (Andersen et al. 1998). They are highly sedentary ungulates with low levels of body reserves and show little within-year variation in body mass (income breeder strategy; Jönsson 1997; Andersen et al. 2000). The adults, and particularly the fawns, are thus very sensitive to variations in the availability of resources.

Fawn body mass can be considered as a reliable proxy for population condition (Hanks 1981). Moreover, the body mass of roe deer fawns in January–February is closely related to winter survival (Gaillard et al. 1993a), age at maturity (Gaillard et al. 1992) and subsequent adult body weight (Pettorelli et al. 2002). Understanding which factors influence this fundamental life history trait is thus of prime importance.

We aim here to determine the spatial structure of both vegetation and winter body mass of roe deer fawns, and then to test for links between the two. A common way of dealing with spatial data on individual performance involves classifying the population's habitat into a few blocks, generally based on vegetation analysis (Pettorelli et al. 2001) or on assumptions about plant quality such as phenology (Myrnerud et al. 2001) and then analysing variation in animal performance among the predefined areas. Previous work on this population has shown that spatial variation in habitat quality influenced the body mass of fawns (8-month-old fawns were on average 0.6 kg heavier in the rich oak stand than in the poor beech stand; Pettoelli et al. 2001) and adults (males and females were respectively 0.9 kg and 0.5 kg heavier in the oak stand; Pettoelli et al. 2002). We have also demonstrated that principal and preferred plant species in roe deer diet (Duncan et al. 1998) are more common in the oak stand than in the beech stand (Pettorelli et al. 2001).

The scale considered in the work described above was an a priori stratification of the reserve into major habitats. However, in ecology the scale may be a key determinant of the strength of patterns and processes observed (Levin 1992; Ray and Hastings 1996; Donaldson and Nisbet 1999). Changing the scale by analysing vegetation and life history traits separately could allow the identification of finer processes, and clarification of the importance of certain plant species for the phenotypic quality of fawns. We aim here to go beyond the habitat scale, and to test the hypothesis that the spatial distribution of preferred plant species induces a spatial structure in the distribution of fawn body mass.

Materials and methods

The study site

This study was carried out in the 2,614 ha fenced Chizé reserve situated in western France (46°05'N, 0°25'W), which has an oceanic climate with Mediterranean influences, characterised by mild winters and hot, dry summers. Mean monthly temperatures vary from 5.5°C (January) to 20.5°C (July) and precipitation from 49 mm (August) to 102 mm (December); summer droughts are common (Gaillard et al. 1996).

The forest is managed by the Office National des Forêts, and is divided by forest trails into plots of ca. 10 ha. The commonest trees are oak (*Quercus* sp.), beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), maple (*Acer campestre* and *A. monspessulanum*), dogwood (*Cornus mas* and *C. sanguinea*) and hawthorn (*Crataegus* sp.) (Cibien and Sempéré 1989).

At a coarse scale, the reserve contains contrasting habitats, according to the timber stand and the nature of the coppices (Pettorelli et al. 2001; Pettoelli, Dray, Maillard and Villarubias, unpublished data). The dominant tree of the northern part of the reserve (1,397 ha) is oak, while the southern plots (1,143 ha) are dominated by beech. The oak stands have contrasting shrub layers, with the eastern part dominated by hornbeam, the western part by maple.

Data collection

Fawn body mass

The roe deer population has been monitored intensively by capture-mark-recapture methods since 1978 (Gaillard et al. 1993a). 10 days of capture in January and February, with >100 people driving animals into 2–5 km of nets around a group of forestry plots, allow 150–350 roe deer to be caught each year, most of which are released with individual collars; the remainder are exported. All animals are weighed using an electronic balance.

A third to a half of the reserve is sampled each year, and capture areas are changed between years. A total of 1,235 fawns (639 males and 596 females) were captured between 1978 and 2001, and the site of capture and the sex noted. As female roe deer form small groups with their fawns and occupy overlapping home ranges (Hewison et al. 1998), we assume that the 8-month-old fawns were captured in their mothers' home ranges. We therefore attributed to each fawn the coordinates of the centroid of the capture area and stored the information in a GIS (Geographic Information System; Mitchell 1999).

The vegetation

Five hundred and seventy eight plots of 1 m² were sampled by one of us (N.P.) between 15 May and 15 June 2001, when all herbaceous and woody genera accessible to roe deer (<1.20 m tall) are recognisable. The plots were on average 200 m apart and were evenly distributed in the reserve [the L function (Besag 1977) is always negative for distances between 1 and 100 m]. The coordinates of all sampling plots were calculated using a Global Positioning System [Magellan GPS 315 (Magellan, Santa Clara, Calif.), 12 parallel channels, 15 m RMS accuracy], and were transferred to the GIS. To sample a particular plot, a quadrat was thrown at chance when approaching the defined average distance between two plots (indicated by the GPS); any herbaceous and woody plants were identified to the generic level (98 genera, without a pre-established list). For the analyses, rare genera with a <1% probability of occurrence were removed, 57 remained.

To check whether the plant distribution over the forest can be considered as perennial, we compared the distribution of plant species obtained from the intensive sampling of spring 2001 with that obtained from a survey performed in March 1993 by G.V.L. This survey was carried out according to the Aldous' method

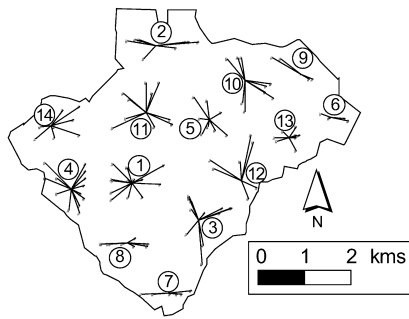


Fig. 1 The spatial distribution of the centroids of capture areas during the 24 years of monitoring. Each *dot* represents the centroid of a capture area, and their coordinates have been computed using GIS. A hierarchical cluster analysis was performed on these geographical coordinates and 14 clusters (numbered) defined. The coordinates of the cluster centres were calculated simply by averaging

(Aldous 1944) that is intended to assess both the coverage of woody plants and their use by deer (see further details in Morellet et al. 2001). Plant cover and their browsing intensity were recorded on circular plots of 40 m² (radius of 3.57 m). Cover of a given woody plant was ranked on a scale of increasing cover proportions according to Aldous' original procedure.

Statistical procedures

Centroids of capture areas have been computed with GIS. We first performed a hierarchical cluster analysis on the spatial coordinates of these centroids [Everitt 1974; see Coulson et al. (1997) for an application on red deer (*Cervus elaphus*)]. Fourteen clusters, which summarised the spatial distribution of captures, were considered in our analysis (Fig. 1): they provided a good compromise between the average number of individuals caught per year in the clusters, and the number of clusters.

Time is a major source of variation in fawn body mass, leading to a 5 kg range between extreme cohorts (Gaillard et al. 1996). As there is a strong auto-correlation in the effect of time on fawn body mass due to the effect of density dependence on this life history trait (Gaillard et al. 1996), we decided to model time using a five-degree polynomial [Diggle 1990; when more degrees were added, the Akaike Information Criterion (Sokal and Rohlf 1995) of the fit did not change by more than 5%].

Male fawns were consistently heavier than female fawns (Gaillard et al. 1996), so the analysis was replicated for each sex, running one model including only the temporal variation, and another including both temporal and spatial variations. We used the ANOVA procedure (Sokal and Rohlf 1995) to test the significance of the effects of these temporal and spatial variables and the interactions between them.

The relative importance of year and location in the among-individual variation in fawn body mass was determined using linear regression (Sokal and Rohlf 1995) between observed and predicted values from the interactive model.

As the linear model was not spatialised, it was necessary to look for autocorrelation among residuals. If the presence of autocorrelation was detected, it could imply the omission of regressor variables, the presence of non-linear relationships or that the regression model should have an autoregressive structure (Cliff and Ord 1981). To test the autocorrelation, we firstly established the neighbourhood of a capture area centroid with its two nearest neighbours. Then, we computed and tested spatial autocorrelation for original data and for residuals using a modified version of Moran's statistic (Cliff and Ord 1981 p203). This procedure, used recently by Michel et al. (2002) in the context of logistic regression,

allowed us to test the capacity of the model to take into account the spatial structure of data.

Finally, we analysed the spatial distribution of vegetation collected in May 2001 and in March 1993 using global PCA (Thioulouse et al. 1995), a spatially constrained multivariate analysis which allows spatial structure to be identified in a multivariate data set. The procedure of global PCA is very close to the standard PCA procedure, which allows the coefficients of variables (e.g. plant genera) to be determined in order to obtain scores for individuals (e.g. sites) which are calculated by using the linear combination of variables of maximal variance. The spatial structure of the data is taken into account in a global PCA which therefore allows a compromise between maximising the variance between the sites, and their spatial correlation.

To assess the links between spatial variation in the distribution of fawn body mass and plant species, we compared the patterns of distribution obtained from the two analyses graphically. The very different sampling schemes (14 clusters corresponding to the capture sites and 578 1 m² plots for plant distribution in spring 2001, and 150 40 m² plots for plant distribution in winter 1993) did not allow use of the usual measures of correlation.

Results

As expected, space was a major structuring factor of fawn body mass. Considering the same interactive model for both sexes, the integration of the spatial location of capture allowed us to account for 36.75% and 39.2% of variation in winter body mass of fawns at the individual level, for males and females respectively. Thus, nearly 40% of the variance in the body mass of male and female fawns was accounted for by cohort and the broad geographical location of the mothers' home range. Time alone accounted for about half of this (20.36% and 19.96% for males and females respectively).

No significant interaction was observed between temporal and spatial factors for male body mass ($F=1.27$, $df=65$, 555 , $P=0.08$), and the main effects were highly significant (space: $F=4.67$, $df=13$, 555 , $P<0.001$; time: $F=35.72$, $df=5$, 555 , $P<0.001$). A significant interaction between spatial and temporal factors was observed in females ($F=1.62$, $df=65$, 512 , $P=0.002$), contrary to what we found in males. However, when we repeated the analysis by removing three extreme individuals, the interaction between space and time was no longer significant ($F=1.25$, $df=65$, 509 , $P=0.097$), while the main effects were highly significant (space: $F=4.88$, $df=13$, 509 , $P<0.001$; time: $F=34.78$, $df=5$, 509 , $P<0.001$).

For both sexes, the same additive model considering the effects of space and time on fawn body mass was therefore retained. In both cases, space and time played a nearly equal role in determining fawn body mass, as time alone accounted for about 20% of variance, and the interaction between both temporal and spatial factors accounted for a negligible part of the variance. Under this additive model, we obtain the same perennial spatial distribution patterns in both sexes, as well as the same range of variation (Fig. 2). Estimated values from the additive model including space and time show a 2 kg range (from the poorest cluster to the best one) for males and females. There is thus spatial autocorrelation in fawn

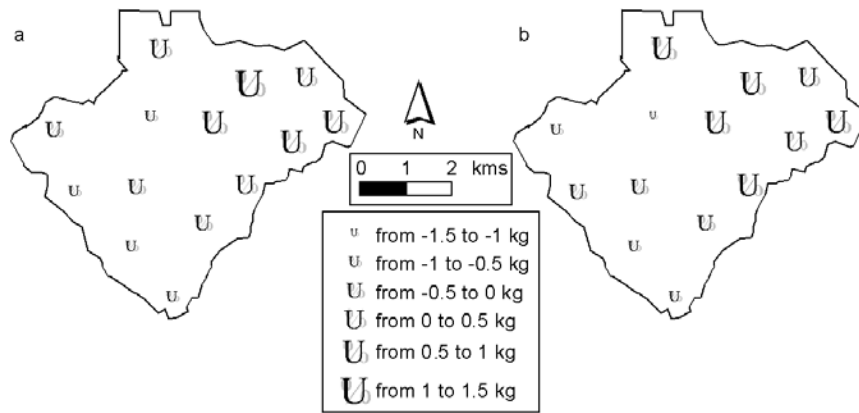


Fig. 2 The spatial distribution of the difference (in kg) between the average body mass and the male (a) and female (b) body masses calculated from the additive model considering a five-degree polynomial function of time (24 years) and clusters (14 clusters). The size of the symbol is proportional to the deviation from the

average body mass. *Small symbols* represent clusters where the predicted weight is less than the average body mass, while *large symbols* represent clusters where the predicted weight is greater than the average body mass

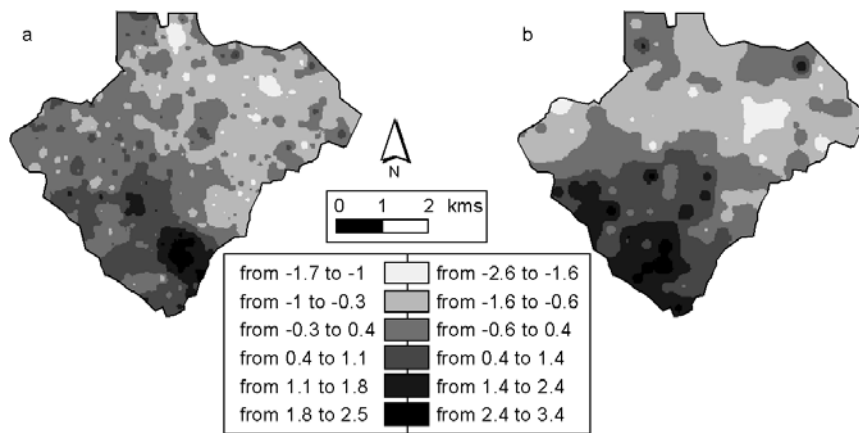


Fig. 3 Results for the first axis of global PCA for vegetation data collected in 2001 (a) and in 1993 (b). The data were smoothed by two-dimensional weighted local regression of the scores on the first axis of the global PCA for the stations sampled in May 2001 and in

March 1993. For the two analyses, high scores are found mainly in the South of the reserve, whereas low scores are found in the North East: this is the major spatial structure of plant communities in the Chizé forest

body masses in winter among clusters, and the pattern is a North East–South West gradient. Measures of spatial autocorrelation show that original data on weights are spatially correlated (males: $I=0.103$, $P<0.001$; females: $I=0.207$, $P<0.001$) while residuals of the additive models are uncorrelated (males: $I'=0.00003$, $P=0.194$; females: $I'=0.017$, $P=0.076$). This indicates that all the spatial structure contained in body weights is taken into account in the model by the 14 clusters.

The first axis of the global PCA performed on plant distribution observed in May 2001 was the major structuring axis of the plant data set, and its eigenvalue was twice that of the second one. Plotting the scores of the stations shows a pronounced spatial structure in the distribution of the plants. This axis opposed the scores of the stations sampled in the North East to the scores of the stations belonging to the South of the reserve (Fig. 3a). Results obtained from the global PCA of the Aldous

sampling of March 1993 (woody species only) provided very similar results (Fig. 3b). The distributions of butcher's broom (*Ruscus aculeatus*), beech, *Rubia peregrina* and brambles (*Rubus* sp.) were highly and positively related to the first axis of this PCA (Tables 1, 2), indicating that those species occur mainly in the South of the reserve. In contrast, the distributions of hornbeam (*Carpinus betulus*), bluebells (*Hyacinthoides* sp.) and star of Bethlehem (*Ornithogalum* sp.) were negatively related to this first axis (Tables 1, 2), indicating that these species occur mainly in the North East of the reserve. Pines (*Pinus* sp.), ivy (*Hedera helix*), ash (*Fraxinus excelsior*), hazel (*Corylus avellana*), dogwood (*Cornus* sp.) and true service tree (*Sorbus domestica*) were weakly related to this first axis (Table 1), so they occur throughout the reserve.

As can be seen clearly by comparing Fig. 2 and Fig. 3, the spatial distribution of fawn body mass closely

Table 1 Scores (ranging from -0.315 to 0.341) of the plant genera on the first axis of the global PCA of vegetation collected in May 2001. The genera presented are those highly correlated with the axis, and those described as important or avoided in roe deer diets (Duncan et al. 1998 and references therein)

| Species | coefficient |
|------------------------------|-------------|
| <i>Carpinus betulus</i> | -0.315 |
| <i>Ornithogalum</i> sp. | -0.243 |
| <i>Hyacinthoides</i> sp. | -0.185 |
| <i>Anemone nemorosa</i> | -0.140 |
| <i>Euonymus europaeus</i> | -0.097 |
| <i>Arum</i> sp. | -0.078 |
| <i>Crataegus</i> sp. | -0.077 |
| <i>Viola</i> sp. | -0.071 |
| <i>Ulmus</i> sp. | -0.042 |
| <i>Sorbus torminalis</i> | -0.025 |
| <i>Fraxinus excelsior</i> | -0.009 |
| <i>Hedera helix</i> | -0.003 |
| <i>Sorbus domestica</i> | -0.001 |
| <i>Pinus</i> sp. | 0.033 |
| <i>Corylus avellana</i> | 0.060 |
| <i>Cornus</i> sp. | 0.077 |
| <i>Prunus spinosa</i> | 0.121 |
| <i>Lonicera periclymenum</i> | 0.149 |
| <i>Acer</i> sp. | 0.153 |
| <i>Rosa</i> sp. | 0.170 |
| <i>Rubia peregrina</i> | 0.172 |
| <i>Euphorbia</i> sp. | 0.185 |
| <i>Quercus</i> sp. | 0.187 |
| <i>Ligustrum vulgare</i> | 0.214 |
| <i>Clematis vitalba</i> | 0.221 |
| <i>Fagus sylvatica</i> | 0.262 |
| <i>Ruscus aculeatus</i> | 0.328 |
| <i>Rubus</i> sp. | 0.341 |

Table 2 Scores of the species on the first axis of the global PCA of vegetation data collected in March 1993 (woody plants only)

| Species | coefficient |
|------------------------------|-------------|
| <i>Crataegus</i> sp. | -0.296 |
| <i>Cornus sanguinea</i> | -0.243 |
| <i>Carpinus betulus</i> | -0.227 |
| <i>Hedera helix</i> | -0.218 |
| <i>Cornus mas</i> | -0.177 |
| <i>Acer campestre</i> | -0.175 |
| <i>Ligustrum vulgare</i> | -0.107 |
| <i>Sorbus torminalis</i> | -0.093 |
| <i>Rosa</i> sp. | -0.076 |
| <i>Viburnum lantana</i> | -0.076 |
| <i>Prunus spinosa</i> | -0.052 |
| <i>Quercus</i> sp. | -0.043 |
| <i>Euonymus europaeus</i> | -0.042 |
| <i>Acer monspessulanum</i> | -0.040 |
| <i>Lonicera periclymenum</i> | -0.031 |
| <i>Prunus avium</i> | -0.014 |
| <i>Ulmus montana</i> | 0.019 |
| <i>Pinus laricio</i> | 0.030 |
| <i>Corylus avellana</i> | 0.050 |
| <i>Ilex aquifolium</i> | 0.088 |
| <i>Rubus</i> sp. | 0.088 |
| <i>Rubia peregrina</i> | 0.181 |
| <i>Fagus sylvatica</i> | 0.261 |
| <i>Ruscus aculeatus</i> | 0.729 |

matched the spatial distribution of plants in the Chizé forest. Thus, two main spatial structures occur in these data, along a gradient from the North East to the South: the first is characterised by a plant community with abundant hornbeam, star of Bethlehem and bluebells and occurs in the oak stand in the North East part of the reserve where fawns of both sexes are heaviest in winter. The other structure is characterised by butcher's broom, beech, *Rubia* and brambles, which occur principally in the beech stand in the southern part of the reserve where fawns of both sexes are lightest in winter. The spatial structures we report here for both plant distribution and fawn body mass in winter show that the presence of preferred plant species in the maternal home range covaries with body mass of fawns in winter.

Discussion

We have demonstrated here that the spatial component plays a fundamental role in explaining individual variability in the winter body mass of fawns, which is a reliable proxy of population condition (Maillard et al. 1989; Vincent et al. 1995; Gaillard et al. 1996), and affects the future performance of individuals (Pettorelli et al. 2002). By separating information on the vegetation and this important life history trait we have shown that spatial variation in the animals' resources appears to be a major factor shaping variation in the winter body mass of fawns in Chizé. We have previously found (Pettorelli et al. 2001) a 0.6 kg difference between male and female fawns raised in the oak stand or in the beech stand. Here, the estimated values show a 2 kg range in body mass, according to the location of the fawn's home range (about 15% of the average body mass of fawns in winter). The 2 kg difference between extreme locations is large enough to mean that, under harsh conditions, the fawns living in the poorest habitats may fall below the threshold body mass for surviving their first winter (Gaillard et al. 1993a). This analysis, where we first sought spatial variation in the two variables separately, has as expected shown that the effect of spatial variation in resources has a much more powerful effect on roe deer fawn phenotypic quality than has previously been thought.

The spatial structure in the distribution of fawn body mass is perennial over 24 years, which means that events like high population densities during the 1980s, summer droughts (in 1990 for example) and hurricane Lothar (in December 1999) had no strong interaction with this spatial pattern. The spatial constraints on body mass are thus robust, and are presumably linked to perennial spatial structures in the reserve. Predation on roe deer fawns is weak at Chizé (Gaillard et al. 1993a), so it is likely that the source of this perennial structure is in the soil, implying spatial variation in the distribution of plants, the animals' resources.

Under harsh conditions, male offspring generally suffer more than females in ungulates (Glucksman 1974), so the same range and spatial pattern of predicted

body masses should not be expected in the two sexes. However, the spatial distribution and the range of predicted body masses were closely similar in these male and female roe deer. Contrary to many other ungulates (see Clutton-Brock et al. 1982), male and female roe deer have similar birth weights, post-natal growth rates and juvenile survival rates (Gaillard et al. 1993a, 1993b, 1998). The result of this study is therefore consistent with the view that the life history traits of roe deer are only weakly influenced by sexual selection.

The striking result of this study is that the spatial pattern in fawn body mass (Fig. 2) was linked to the distribution of key plants (Fig. 3) in a manner which was consistent among years in spite of the fact that different timescales were used for measuring the variables. The body mass data were collected over 24 years, while the vegetation data were collected in only two sampling sessions (March 1993 and May 2001). However, the similarities between the information gathered on the spatial distribution of plant communities over the last 10 years indicates that the spatial distribution of the main plant communities is perennial. There is also a strong positive relationship between our vegetation data collected in 2001 after the 1999 storm and stand data collected in 1993 by foresters (Dray et al. 2002). Additional surveys made in 1995 and 1997 (Pettoirelli et al. 2001) also confirm the pattern, though they were performed by different observers and may therefore be less reliable (see Morellet 1998). Finally, bluebells and star of Bethlehem have bulbs (Rameau et al. 1989), which means that their distributions vary little between years. The different timescales used in this study should not therefore affect the main conclusions.

The spring and summer seasons are critical for roe deer populations as the nutritional plane of the females at this time appears to have profound effects on the survival of fawns (Gaillard et al. 1997, 1998). Roe deer are generalists, but highly selective feeders (Duncan et al. 1998): in this period of high energy requirements for lactation the animals select food items which are highly digestible and rich in soluble carbohydrates. Hornbeam and bluebells (Tixier et al. 1997; Maizeret and Tran Manh Sung 1984; Maizeret et al. 1991) and star of Bethlehem (G. Van Laere, personal observations) are among the principal and/or preferred species in these seasons. These species induced the major spatial structure observed in the floristic composition at Chizé because they occur principally in the North East part of the reserve, in contrast to other principal food resources of roe deer (like oak, dogwood, ivy, hawthorn or maple; Duncan et al. 1998), which are more broadly distributed. Since higher body masses were found in this particular part of the reserve, it is likely that the difference in the distribution of these particular plants affected the food supply of the breeding females, which in turn led to a high degree of spatial variation in fawn body mass.

Beech, butcher's broom and *Rubia* sp. are not preferred food plants of roe deer (Duncan et al. 1998 and references therein) and brambles, though one of the

most important foods of roe deer and consumed all year round, are avoided in spring (Tixier and Duncan 1996). The positive relationship between hornbeam, bluebells, star of Bethlehem and body mass distributions we report here suggests that these plants, rather than brambles, are the important resources. Spatial differences in winter body mass are likely to be due mainly to differences in growth rates in the first months of life, as growth in roe deer follows a monomolecular model, involving a continuous decline in growth rate from birth (Portier et al. 2000). Growth rates in roe deer fawns are high [about 150 g/day during the first 3 weeks of life (Gaillard et al. 1993b)] so that about 65% of adult mass is usually reached at 8 months of age (Gaillard 1988). Growth rates are much lower in autumn than in spring and summer, so the resources used during the autumn and winter (principally brambles and ivy) are therefore for maintenance rather than for growth, which could explain the negative relationship between the distribution of brambles and fawn body mass.

In temperate ungulates, fawn survival is commonly the key factor in the dynamics of their populations (Gaillard et al. 2000). The causes of variation in this parameter are, therefore, of considerable interest. A recent study modelling ungulate population dynamics in arid and semi-arid grazing systems distinguished key resources, whose supply was shown to be crucial to dry season survival, from other resources that did not affect the key factor (Illius and O'Connor 2000). Key resources are thus defined as "resources whose supply determines the size of the key factor of the population". It is, of course, unlikely that the abundance of just a single resource would determine the population dynamics of a temperate generalist herbivore like the roe deer. Nevertheless, our results demonstrate that the abundance of resources which are preferred during the key season (spring and summer) shapes winter fawn body mass in roe deer.

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