

The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale

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Summary

1. Temporal and spatial variation can strongly affect life-history traits, but few studies to date have quantified the importance of the interplay between temporal and spatial components of population dynamics.
2. We analysed spatiotemporal variation in early survival of roe deer fawns over 15 years (1985–99) in an intensively monitored population in western France at two spatial scales: the maternal home range (a few tens of hectares) and the forest stand (a few hundreds of hectares).
3. Spatial variation in resource availability interacted with temporal variation to shape fawn survival. In good years, survival was not influenced by habitat quality (being 0.68 in the rich oak stand with hornbeam coppices vs. 0.64 in the poorer part of the reserve). At the home range scale, early survival of fawns during good years decreased with increasing occurrence of preferred plant species in the rich habitat; there was no effect in the poor habitat.
4. During bad years, however, there was a positive relationship between the occurrence of preferred plant species and survival of fawns in the poor habitat, whereas no relationship occurred in the rich habitat. Spatial variation in early survival during bad years was significant at the plot scale (from 0.19 to 0.40 in the poor habitat and from 0.49 to 0.61 in the rich habitat) even after accounting for the forest stand variations (from 0.27 to 0.51). The occurrence of key plant species therefore limits female reproductive success only in the poor habitat under harsh conditions.
5. Our findings highlight the crucial role of spatiotemporal interactions in shaping individual fitness in mammalian populations, and underline the importance of the scale of analysis when characterizing ecological processes.

Key-words: *Capreolus capreolus*, individual variability, population dynamics, spatiotemporal interactions.

Journal of Animal Ecology (2005) **74**, 972–981
doi: 10.1111/j.1365-2656.2005.00988.x

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Introduction

Variation in performance during early life has recently been reported to play a fundamental role in population dynamics of temperate herbivores (Coulson *et al.* 1997), especially for polytocous species (Gaillard *et al.* 2000). For example, juvenile survival is consistently lower and more sensitive to environmental variation

than adult survival in populations of large herbivores (Gaillard *et al.* 2000; Eberhardt 2002; Gaillard & Yoccoz 2003; for reviews). Conditions early in life can affect many aspects of adult life (Albon, Clutton-Brock & Guinness 1987; Stearns 1992; Pettorelli *et al.* 2002; Gaillard *et al.* 2003a) and variation in juvenile survival often explains a large part of the variance in lifetime reproductive success (Clutton-Brock, Albon & Guinness 1988) and other fitness measurements (Gaillard, Festa-Bianchet & Yoccoz 1998a). Identifying the environmental factors causing variation in early survival therefore constitutes a major issue for both evolutionary ecologists and managers.

High temporal variation in summer survival of juveniles has been reported in several populations of temperate ungulates (see Linnell, Aanes & Andersen 1995; Gaillard *et al.* 1998a; Gaillard *et al.* 2000; for reviews). Habitat quality, defined either according to resource availability, cover and hiding possibilities, or predation pressure has recently been identified as a significant source of variation in life-history traits of large herbivores: Coulson *et al.* (1997), and Milner-Gulland, Coulson & Clutton-Brock (2000) on red deer *Cervus elaphus* L.; Coulson *et al.* (1999) on Soay sheep *Ovis aries* L.; Pettorelli *et al.* (2001, 2002, 2003a,b), and Nilsen, Linnell & Andersen (2004) on roe deer *Capreolus capreolus* L. In this study we analysed spatiotemporal variation in early survival of fawns in the spatially contrasted reserve of Chizé, where the roe deer population has been intensively monitored for over 25 years. Roe deer are small (20–30 kg; Andersen, Duncan & Linnell 1998) and widespread cervids with both sexes being highly sedentary (Wahlström & Liberg 1995), and females living with their offspring in small home ranges (Hewison, Vincent & Reby 1998). Although spatio-temporal interactions are suspected to have a major effect on population dynamics, only circumstantial evidence is so far available (Gaillard *et al.* 2000; Haydon *et al.* 2003).

Previous studies of the spatial variation in phenotypic quality of roe deer at Chizé have shown that both fawns (Pettorelli *et al.* 2001) and adults (Pettorelli *et al.* 2002) have the highest body masses in the forest stand where plant species preferred by roe deer in spring are most abundant. Moreover, we previously showed that density negatively influenced winter survival of fawns only in poor habitats (Pettorelli *et al.* 2003b). However, no study has yet been performed on the effect of habitat quality on summer survival of fawns, the most influential vital rate of roe deer population dynamics (Gaillard *et al.* 2000). Indeed, the spring and summer seasons are critical for the nutrition of female deer in temperate habitats, especially for income breeders such as roe deer that can potentially raise successfully the two fawns they usually produce each year (Jönsson 1997; Andersen *et al.* 2000). In this period of high energy requirements, roe deer select food items that are both rich in soluble carbohydrates and highly digestible (Maizeret & Tran Manh Sung 1984). Hornbeam *Carpinus betulus* L. is

strongly selected in both spring and summer (eaten 10 times as much as its availability, Tixier *et al.* 1997; Duncan *et al.* 1998). Herbaceous species such as bluebells *Hyacinthoides* sp. L. (Maizeret *et al.* 1991; Tixier *et al.* 1997; Duncan *et al.* 1998) and star of Bethlehem *Ornithogalum* sp. L. (GVL, personal observations) are highly preferred in spring.

A recent study highlighted the crucial role of habitat quality at the home range scale for shaping variation in body mass and litter size of roe deer does in Norway (Nilsen *et al.* 2004). However, whether or not variation in habitat quality influenced female fitness cannot be answered in that study because the number of fawns produced (i.e. litter size) was not related to the number of fawns raised (a proxy for female fitness) in this population (Gaillard *et al.* 1998b). To assess the influence of habitat quality on individual fitness of roe deer females, we therefore tested whether spatial variation in the distribution of preferred plant species influenced early survival of roe deer fawns at two different scales (i.e. forest stand and maternal home range).

We expected that (H1) any variation in the availability of preferred resources should affect the reproductive success of females (i.e. summer survival of fawns) directly, because predation at Chizé is at the best weak and because roe deer are income breeders and cannot rely on body reserve to compensate a low availability of food resources during bad years. We then expected (H2) the influence of spatial variation in the abundance of preferred plant species to be stronger under poor conditions because the impact of environmental variation on life-history traits usually increases with environmental harshness (Lomnicki 1980; Pettorelli *et al.* 2003b). We finally expected (H3) the influence of spatial variation on the abundance of preferred plant species to be greater at the finer scale than at the scale of forest stands, as previously reported for winter body mass of fawns (Pettorelli *et al.* 2003a).

Materials and methods

STUDY AREA

The study was carried out in the fenced 2614 ha Chizé forest in western France (46°05'N, 0°25'W; see Gaillard *et al.* 1993 and Pettorelli *et al.* 2001 for descriptions). The climate is temperate oceanic, with mild winters (mean January temperature of 5 °C). The forest is managed by the Office National des Forêts, and is divided by forest trails into plots of about 10–15 ha (Fig. 1). The study area includes a variety of habitats, where the northern part of the reserve is mainly composed of an oak *Quercus* sp. L. stand while the southern part (S) of the reserve is mainly beech *Fagus sylvatica* L. (815 ha). Further, the oak stand has a contrasting shrub layer, with the north-eastern coppices (NE, 1046 ha) dominated by hornbeam associated with herbaceous species such as bluebells or star of Bethlehem, while north-western coppices (NW, 758 ha) are dominated by maple *Acer*

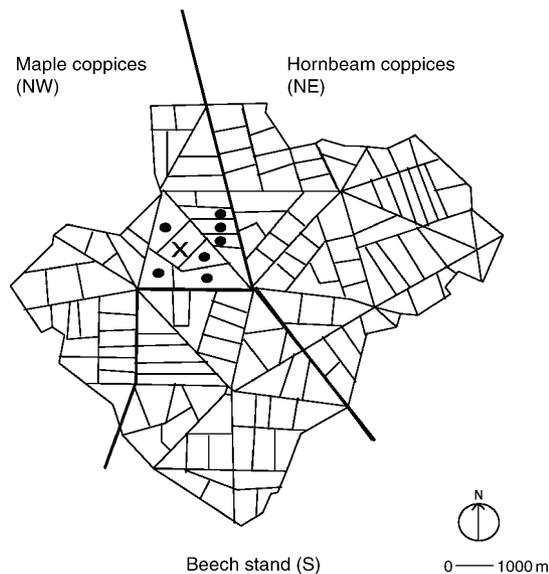


Fig. 1. The home range definition we used for the analysis at the finer spatial scale. The 155 forest plots and the three major plant communities (NE, NW and S) occurring within the reserve are represented. 'X' indicates the forest plot where a hypothetical fawn was found. The plots with bold points are those that were considered to belong to the mother's home range.

sp. L. (see Fig. 1). Such variations in the coppice type markedly influence both the abundance of food plants that roe deer select for strongly in their spring and summer diets (bluebells and star of Bethlehem being much more common in the NE part), and the winter body mass of fawns (Pettorelli *et al.* 2001). The major large-scale spatial pattern is an opposition between the richer hornbeam coppices in the NE part, and the rest of the reserve. In addition there is a spatial variability in the distribution of preferred species (hornbeam, bluebells, star of Bethlehem) within each of these major vegetation types (Pettorelli *et al.* 2003a).

DATA COLLECTION

Animals

From 1985 to 2002, systematic searches for newborn fawns were conducted from April 15 to June 30 (Delorme, Gaillard & Jullien 1988). For each fawn, the year of birth, the sex and the forestry plot where the fawn was found were noted. From 1985 to 1987, density-dependent responses consecutive to the population peak of 1983–84 were still reported (Pettorelli *et al.* 2003b). From 1988 onwards, the roe deer population density was about eight individuals per 100 ha and no density-dependent responses occurred (Pettorelli *et al.* 2003b).

The roe deer population at Chizé has been monitored by the Office National de la Chasse et de la Faune Sauvage using capture–mark–recapture (CMR) methods

for over 20 years (1978 onwards; Gaillard *et al.* 1993, 1997; Gaillard *et al.* 2003b). Each year, 150–350 roe deer were caught in January and February. During a particular capture session, groups of > 100 people drove animals into 3.5 km of nets enclosing selected forestry plots (*c.* 65 ha; Boutin & Van Laere 1990). When fawns marked as newborns during spring were captured in a subsequent winter capture (i.e. at 8 months of age, 20 months, 32 months, etc.) we knew they survived their first summer. To reduce the risk of underestimating the fawn survival rate, we did not consider the fawns that were marked after 1999. The high recapture probability (about 0.65 for fawns and about 0.50 for older individuals, Gaillard *et al.* 1997, 2003b) means that the chance of surviving fawns escaping captures for several years is low (see Gaillard *et al.* 1998b for further details). Indeed, the probability that a fawn born and marked in 1999 survived to 2002 without being controlled is 0.04.

One hundred and seventy-eight fawns were captured and marked during the 15-year period (1985–99, between three and 22 fawns per year), and fawns were found in 89 different plots in the reserve (of 155 plots, see Fig. 1). Previous work has shown that roe deer fawns do not leave their mother's home ranges before their first winter (i.e. before the first control; Hewison *et al.* 1998; Pettorelli *et al.* 2003b), so we are confident that the place where the fawn was caught at 8 months is the place where it was raised.

VEGETATION DATA

To measure the fine-scale variability in the abundance of the preferred plants, a plant survey was performed in 2001 by one of us (NP) in all vegetation types (NE, NW and S). A set of 578 stations on average 200 m apart was sampled from mid-May until mid-June, when all herbaceous and woody genera accessible to roe deer (< 1.20 m) were recognizable. At each station, a 1-m² quadrat was thrown at random, and the presence of 98 taxa of herbaceous and woody plants was noted. The coordinates of all sampling quadrats were calculated by a Global Positioning System (Magellan GPS 315, 12 parallel channels, 15 m RMS accuracy). We limited the analysis to hornbeam, bluebells and star of Bethlehem as these are known to be preferred by roe deer (Tixier *et al.* 1997) and to affect positively their body mass (Pettorelli *et al.* 2003a). For each forest plot we thus calculated the frequency of occurrence of hornbeam, bluebells and star of Bethlehem.

A limitation of this analysis is that different time-scales were used: the animal data were collected over 15 years, the vegetation data in only one (2001). However, all the information we have on this forest suggest that the important floristic community structures are stable over years. Previous studies have revealed strong positive relationships between data collected in 2001 from our vegetation survey and vegetation data collected in previous years: (1) at the stand level in 1993 by foresters

(Dray, Pettorelli & Chessel 2002); (2) for woody species in 1993 by GVL (Pettorelli *et al.* 2001); (3) again for woody plants in 1995 and 1997 (Pettorelli *et al.* 2001); and (4) from information gathered by foresters over the study period (ONF 1971, 1993). Moreover, hornbeam trees are long-lived and bluebells and star of Bethlehem are perennial bulbs (Rameau, Mansion & Dumé 1989), which implies a high repeatability of the spatial distributions over years. Although these species are perennial, the yearly above-ground biomass of those species could fluctuate from one year to another, due to yearly climatic conditions for example. However, if so this should affect equally the whole area and the three species at the same time (as they require roughly the same type of conditions to grow; Rameau *et al.* 1989), so that those yearly variations should be captured by our cohort type dichotomy. The different time-scales used in this study should not therefore hide important interactions between the animals and their resources.

STATISTICAL PROCEDURES

We considered fawns marked as newborn and never captured during subsequent winters to have died during their first summer. Although some newborn fawns could have survived the first summer, not been captured in their first winter and then subsequently died, this is a very unlikely possibility. According to the numerous studies performed on ungulates (reviewed in Gaillard *et al.* 2000), young ungulates are most likely to die either within their first weeks of life or after their first winter (March–May). Moreover, survival rates of roe deer fawn estimated by monitoring the reproductive success of roe deer females closely matched the fawn survival obtained by CMR analyses applied on marked fawns (see Gaillard *et al.* 1998b), meaning that most fawn mortalities occurred before weaning in September–October. To account for possible effects of density dependence, we also performed the same analyses considering only the cohorts born after 1987 (when no more density-dependent responses have been reported; Pettorelli *et al.* 2003b) and we obtained the same results. Lastly, fawns from the same litter are expected to have nonindependent fates in bad years (Gaillard *et al.* 1998b). To eliminate possible pseudoreplication, we performed the analyses on a restricted data set in which we included only one of the two fawns showing the same fate and found at a given location a given year. As the results were identical, we chose to present the analyses based on the total data set.

To explore possible spatiotemporal interactions in shaping summer survival of fawns, we distinguished good and bad cohorts. The overall survival probability in our dataset was 0.54 (97 of 178 fawns were considered to have survived their first summer, i.e. were subsequently captured at least once), the median of the annual estimates being 0.47 (see Appendix I for more details on the data). This probability is very close to the cut-off

value of 0.5 used for separating good from bad years in another roe deer population (Trois Fontaines; Gaillard *et al.* 1998b). We therefore used 0.5 as the cut-off value here: cohorts where less than 50% of fawns survived were considered as bad ones, the others as good ones. Our definition of ‘bad cohorts’ therefore included the effects of high density and climatic harshness (see Appendix I).

At the forest stand scale, we distinguished fawns captured in the rich habitat (i.e. the oak stand with hornbeam coppices, NE) from fawns caught in the poor habitat (i.e. the oak stand with maple coppices and the beech stand, NW + S).

Habitat quality and density are known to affect home range sizes in ungulates (for roe deer Tufto, Andersen & Linnell 1996). To account for the problem of variations in home range size according to habitat quality, we considered two different proxies for individual home ranges. We first combined data from each of the 89 plots with data from all the neighbouring plots (i.e. with at least one common border, see Fig. 1), to correct for the imprecision of the estimate of the living place. The average number of vegetation sampling sites per plot varied between nine and 70 when we included neighbouring plots (70 ha on average).

Female home range size estimated from the monitoring of 22 radio-collared adult females at Chizé during spring–summer is about 22 ha (Saïd *et al.* 2005). So our first proxy of the maternal home range measures the home range quality over an area three times larger than a typical spring–summer home range at Chizé.

We then considered only the forest plot where the fawn was caught. This estimate could have led to bias in the estimate of home range quality, as little correlation was reported between the proportion of preferred plant species in the forest plot and in the neighbouring plots in the NE part of the reserve ($R^2 = 0.0043$). Considering the forest plot only (about 10 ha) does not change the result (the effect is also present at that very fine scale), so we decided to present only results at the scale of our proxy of the maternal home range.

We counted for each proxy the number of sampling points for vegetation and the number with hornbeam, bluebells and star of Bethlehem. The distributions of those three plants have been the basis for the determination of our habitats (NE vs. NW + S). The weight of each plant in determining the quality of a habitat is unknown. Hornbeam has been traditionally mentioned as an important part of spring and summer roe deer diet (Duncan *et al.* 1998). Thus, to assess the quality of each home range, we considered three measurements. First, we used the proportion of hornbeam only as an indicator of home range quality. Then we considered the sum of the proportion of each of the three plants. Finally, we performed a Decentred Correspondence Analysis (Dolédec, Chessel & Olivier 1995). The Decentred CA can be viewed as an extension of Correspondence Analysis that extracts the main source of variation in

the vegetation, but corrects for varying sampling intensity by weighting the information on each area by the number of quadrats sampled. The first eigenvalue of the DCA was six times higher ($\lambda_1 = 0.29$) than the second one ($\lambda_2 = 0.05$), so we decided to conserve only the first axis. The distributions of the three species were highly spatially correlated, all these species having positive scores on the first axis. Note that the DCA axis corresponds to a weighted sum of all three species, the weights being chosen so as to describe best the vegetation patterns. Area scores ranged from 1.4 (high occurrence of hornbeam, bluebells and star of Bethlehem) to -0.80 (low occurrence of preferred food species).

We used a logistic regression model to assess the relationship between fawn survival (ϕ) and habitat type α (rich vs. poor), abundance of preferred plant species in the maternal home range β (measured either as: (1) the proportion of hornbeam; (2) the sum of the proportion of hornbeam, bluebells and star of Bethlehem; and (3) the first axis of the DCA) and cohort quality γ (good vs. bad cohorts):

$$\text{Logit}(\phi_{ijk}) = \phi + \alpha_i + \beta_j + \gamma_k + (\alpha \cdot \beta)_{ij} + (\alpha \cdot \gamma)_{ik} + (\beta \cdot \gamma)_{jk},$$

where terms into brackets correspond to interaction between factors.

To assess if nonindependence among observations within a year could affect estimates of uncertainty of parameters, we added to the selected model year as a random factor (i.e. a generalized linear mixed model). As yearly variation was mainly accounted for by cohort quality, considering a classical general linear model or a general mixed model had no effect on parameter estimates and standard deviation. We therefore chose to present results from the general linear model analyses. Goodness of fit of the logistic regression models was assessed using residual plots and the le Cessie-van Houwelingen normal test statistic for the unweighted sum of squared errors (Hosmer *et al.* 1997). To assess the predictive power of the different models, the Nagelkerke R^2 coefficient of determination (Nagelkerke 1991) was provided. Model selection was performed using Akaike's Information Criterion corrected for small sample size (AICc) and Akaike weights (Burnham & Anderson 1998). All analyses were done in R (R Development Core Team 2004), and the logistic regression diagnostics were calculated following Harrell (2001).

Results

The best model of summer fawn survival included the effect of cohort type, habitat type and the sum of the proportion of preferred plant species in spring and summer in the maternal home range. The best models all included the interaction between cohort quality and the amount of preferred plant species at the home range scale, and we therefore can conclude there is

strong evidence for this interaction. The interaction between habitat and cohort types was not consistently found in the best models, and the evidence for this interaction is not as strong (Tables 1 and 2).

According to our first prediction H1, the proportion of fawns that survived tended to be higher in the rich habitat ($p_{NE} = 0.61 \pm 0.05$) than in the poor habitat ($p_{NW+S} = 0.48 \pm 0.05$; $\chi^2 = 3.03$, d.f. = 1, $P = 0.08$; see Appendix II). When we removed 1985–87 (the last years with density-dependent responses reported), this trend completely vanished ($\chi^2 = 0.18$, d.f. = 1, $P = 0.67$).

According to our second prediction H2, we observed an interplay between cohort quality and habitat quality on early fawn survival at both scales. At the habitat scale (rich vs. poor) this interplay was not significant ($Z = -1.29$, $P = 0.19$). At the scale of maternal home range, we found clear evidence for interplay between home range richness and cohort quality on early fawn survival. In good years, the amount of preferred plant species, surprisingly, had a negative effect on early survival of fawns, whereas in bad years, the amount of preferred plants positively influenced the summer survival of fawns (see Table 2). These patterns were consistent irrespective of the definition of habitat quality we used (proportion of hornbeam, sum of the proportion of hornbeam, bluebells and star of Bethlehem, scores on the first axis of the DCA; see Table 2). This pattern was also observed when we removed the cohorts 1985–87.

In accordance with our third prediction (H3), spatial variation in the abundance of preferred plant species had an influence on fawn survival at the finer scale of maternal home range, even after correcting for forest stand variations. In bad years, the expected early survival of fawns varied positively with the sum of the proportions of preferred plant species from 0.49 to 0.61 (the sum of the proportions of preferred plant species varying from 0.72 to 1.81 in the NE) and from 0.19 to 0.40 (the sum of the proportions varying from 0.03 to 1.51 in the NW + S), while at the forest stand scale, the expected survival of fawns varied from 0.51 (in the rich area) to 0.27 (in the poor habitat).

Discussion

The present work reports a scale-dependent spatial structure in variation of early survival of roe deer fawns and shows that both cohort quality and habitat quality interplay to shape the most sensitive component of the roe deer population dynamics (Gaillard *et al.* 1998c), conforming to the previous patterns reported for winter fawn body mass (Pettorelli *et al.* 2001, 2003a) and winter fawn survival (Pettorelli *et al.* 2003b) in this study area. Indeed, we do not report any significant effect of habitat type in shaping summer survival of fawns in the absence of density dependence, which is directly in line with previous results on winter survival of fawns (Pettorelli *et al.* 2003b).

Table 1. Model selection procedure for the three measures of home range quality. The cohort factor distinguishes good (1) and bad (2) cohorts, the habitat factor rich (NE or 1) and poor (NW + S or 2) habitats, 'plants' corresponds to a variable summing up the proportion of hornbeam, bluebells and star of Bethlehem at the home range scale (a), 'DCA' corresponds to the score of the home range on the first axis of our Decentred Correspondence Analysis (b), 'hornbeam' corresponds to the proportion of hornbeam within the home range (c). The Nagelkerke coefficient of determination R^2 , and the Z and P -value for the le Cessie-van Houwelingen normal goodness-of-fit test are also provided. The selected models are in bold (i.e. the models with lowest AICc and P -values for the goodness-of-fit test > 0.05)

Model	AICc	dAICc	AIC weights	R^2	Z	P
(a) Cohort*plants + habitat	232.16	0.00	0.31	0.165	1.24	0.22
Cohort*plants + habitat*plants	233.29	1.13	0.17	0.172	0.28	0.78
Cohort*plants + habitat*cohort	233.93	1.77	0.13	0.168	0.90	0.37
Cohort*plants	234.46	2.30	0.10	0.136	0.47	0.64
Cohort*plants*habitat	234.97	2.81	0.07	0.189	-0.60	0.55
Cohort + habitat	235.39	3.23	0.06	—	—	—
Cohort + habitat + plants	235.60	3.44	0.05	0.128	-2.31	0.02
Cohort*habitat	235.79	3.63	0.05	—	—	—
Cohort	236.29	4.13	0.04	—	—	—
Cohort + plants	238.33	6.17	0.01	0.095	-2.30	0.02
(b) Cohort*DCA + habitat	232.69	0.00	0.30	0.162	0.95	0.34
Cohort*DCA	234.14	1.45	0.14	0.138	0.59	0.55
Cohort*DCA + habitat*DCA	234.31	1.62	0.13	0.165	0.48	0.63
Cohort*DCA + habitat*cohort	234.70	2.01	0.11	0.163	0.88	0.38
Cohort + habitat	235.39	2.70	0.08	—	—	—
Cohort*habitat	235.79	3.10	0.06	—	—	—
Cohort*DCA*habitat	235.95	3.26	0.06	0.183	-0.53	0.60
Cohort	236.29	3.60	0.05	—	—	—
Cohort + habitat + DCA	236.73	4.04	0.04	0.121	-2.09	0.04
Cohort + DCA	238.21	5.52	0.02	0.096	-1.93	0.05
(c) Cohort + habitat + hornbeam	234.78	0.00	0.20	0.134	-1.91	0.06
Cohort*hornbeam + habitat	234.97	0.19	0.18	0.147	-1.73	0.08
Cohort + habitat	235.39	0.61	0.15	0.115	-1.30	0.19
Cohort*habitat	235.79	1.01	0.12	0.127	-64.8	0
Cohort	236.29	1.51	0.09	0.095	-49.3	0
Cohort*hornbeam + habitat*hornbeam	236.86	2.08	0.07	0.148	-2.2	0.03
Cohort*hornbeam + habitat*cohort	237.09	2.31	0.06	0.147	-1.89	0.06
Cohort*hornbeam*habitat	237.43	2.65	0.05	0.173	-2.18	0.03
Cohort*hornbeam	238.15	3.37	0.04	0.111	1.42	0.15
Cohort + hornbeam	238.36	3.58	0.03	0.095	-1.48	0.14

Table 2. Parameter estimates for the three measures of home range quality. The cohort factor distinguishes (i.e. slope differences among categories) good (1) and bad (2) cohorts, the habitat factor rich (NE or 1) and poor (NW + S or 2) habitats, 'plants' corresponds to a variable summing up the proportion of hornbeam, bluebells and star of Bethlehem at the home range scale (a), 'DCA' corresponds to the score of the home range on the first axis of our Decentred Correspondence Analysis (b), 'hornbeam' corresponds to the proportion of hornbeam within the home range (c)

Parameter	Estimates	SE	Z	P
(a) Intercept	2.0926	0.6490	—	—
Cohort	-2.6963	0.7784	—	—
Habitat	-0.8950	0.4302	-2.08	0.04
Plants	-1.2084	0.5526	-2.19	0.03
Plants*cohort	1.9315	0.8452	2.28	0.02
(b) Intercept	1.0753	0.3061	—	—
Cohort	-1.1901	0.3307	—	—
Habitat	-0.7506	0.3996	-1.88	0.06
DCA	-0.8455	0.4434	-1.91	0.06
DCA*cohort	1.7004	0.7044	2.41	0.02
(c) Intercept	2.2297	0.7257	—	—
Cohort	-2.1437	0.8446	—	—
Habitat	-1.0126	0.4462	-2.27	0.02
Hornbeam	-2.3780	1.1757	-2.02	0.04
Hornbeam*cohort	2.3057	1.6892	1.36	0.17

The new result is that at the finest scale of the maternal home range, we highlight a beneficial effect of the abundance of preferred plant species when environmental harshness (due to density or to climate) increases. The importance of a group of plants for roe deer in Chizé also is underlined as the best model explaining summer survival of fawns includes bluebells and star of Bethlehem with hornbeam.

Our measures of quality based on the distribution of food resources were assumed to account for all the variability observed at the habitat scale: however, after having accounted for plant occurrence, variation in habitat quality still occurs for roe deer. Furthermore, we found a negative effect of the abundance of preferred plant species on early survival in the best habitat during good years. Even if the performance of roe deer is generally higher in our best habitat (Pettorelli *et al.* 2002, 2003a,b), local density within the rich habitat has been consistently higher in this best habitat (Pettorelli 2002). Moreover, the total density increased during the last years that were good years for fawn survival (Pettorelli 2002). Thus the negative effect of high density in the best patches could have overcompensated the positive effect of a greater availability of preferred food plants within the best habitat type.

Habitat quality has been reported to influence juvenile survival in other ungulate populations at the landscape level (caribou *Rangifer tarandus* L., Whitten *et al.* 1992; pronghorn *Antilocapra americana* Ord, Fairbanks 1993; red deer, Coulson *et al.* 1997) but less information is available at the finer scale of mother home range. In birds, Högstedt (1980) reported that 85% of the within-year variation in clutch size was associated with differences between territory qualities. For moose *Alces alces* L., Saether & Heim (1993) found that herb biomass in the mother's summer home range was correlated with calf body mass, showing the importance of summer conditions for calves as well as the importance of the abundance of particular plant species to determine the future performance of young female moose (Hjeljord & Histøl 1999). More recently, Nilsen *et al.* (2004) show that roe deer does with the highest home-range quality index (estimated by the availability of woodland) during winter produced the largest litters.

The significant interplay between plant distribution and cohort quality that shapes variation in summer survival of roe deer fawns underlines the quantitative importance of these interactions, and the necessity for further population dynamic studies to take them into account when analysing the effects of habitat quality on life-history traits. To our knowledge this study on roe deer provides the first empirical evidence that the abundance of preferred plant species limits early survival in a wild temperate ungulate in harsh environmental conditions (i.e. in bad years in the poor habitat) but not in favourable ones (i.e. no positive influence of the amount of preferred plant species in good years and/or in the rich habitat). Roe deer are income breed-

ers *sensu* Jönsson (1997), as their body mass is quite constant over time both within and among years (Andersen *et al.* 2000) making them especially sensitive to variations in resource availability. Thus any increase of the food supply available during the lactation period, when energy requirements are high, will greatly influence the energy provided to fawns by their mothers. The distribution of highly selected food items among home ranges could therefore affect the food supply of lactating females profoundly, and in turn have a strong effect on fawn survival over their first summer.

We show here that scale plays a major part in shaping the response of fitness components to changes in habitat quality (Levin 1992; Ray & Hastings 1996; Donalson & Nisbet 1999). Scale has been demonstrated as being a key determinant of ecological patterns and processes (Levin 1992), and the results obtained at different scales can be conflicting (Myserud *et al.* 2000). The scale (temporal and/or spatial) at which a study is carried out is usually determined by constraints of data collection (logistic problems, manpower availability; Wiens 1989). Sometimes, especially when dealing with space, the selected scale is based on assumptions by the observers that some particular areas are sufficiently homogeneous and different from one another to be distinguished (Myserud *et al.* 2001; Pettorelli *et al.* 2001, 2002; Focardi *et al.* 2002). As demonstrated here, such exploratory and sometimes convenient choices might reduce or even mask ecological patterns (Thomas & Kunin 1999).

Previous work on roe deer underlined a strong family effect on fawn survival (Gaillard *et al.* 1998b) in bad years: both twins survived or died together more often than expected by chance when the cohort survival was low (i.e. less than 0.5), leading to a threefold increase in the variance of female reproductive success over a 5-year period in the productive roe deer population at Trois Fontaines (eastern France). Genetic factors and/or mother's home range quality were considered as possible causes for such a relationship. Our findings that the distribution of resources influences the spatial distribution of summer survival of fawns in bad years suggest a likely mechanism to account for such family effects that only occur during bad years. More generally our results support the hypothesis that home range quality is a key determinant of female fitness.

Linking nutritional ecology and population dynamics is a major challenge in ecology (Myserud *et al.* 2001). The work reported here provides further evidence for the existence of 'key resources' in the ecology of temperate ungulates: 'key resources' (Illius & O'Connor 2000) are resources playing a fundamental role during sensitive periods in population dynamics such as the breeding period for temperate ruminants. Originally defined in the semiarid context, it seems that this concept also is relevant in temperate regions. Studies on roe deer (this paper), on red deer (Coulson *et al.* 1997; Conratt, Clutton-Brock & Guinness 1999), and on moose

(Hjeljord & Histøl 1999) indicate strong linkages between the abundance of highly preferred plant species during the rearing period and early survival. In conclusion, it seems that to understand the link between nutrition and population dynamics particular attention needs to be paid to the interplay between environmental harshness and resource availability during the most sensitive period of the year.

Acknowledgements

We thank the Office National de la Chasse et de la Faune Sauvage for organizing all the captures of roe deer at the Chizé reserve. We are grateful to all the students, field assistants, and volunteers that spent time catching and monitoring the roe deer fawns on the study site. Special thanks to Tim Coulson, Marco Festa-Bianchet, Andrew Illius, Atle Mysterud, Nils Christian Stenseth, Clément Calenge, Daniel Chessel, Mark Boyce for ideas, comments and suggestions on previous drafts of this work. This work benefited from the exchanges involved in the Programme International de Coopération Scientifique 1452 of the CNRS 'Plant-herbivore dynamics in changing environments'.

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Received 12 August 2004; accepted 22 March 2005

Appendix I

Summer survival according to year and habitat. The number of animals recaptured on the number of animals initially captured per habitat and per year are given

Years	NE	NW + S	Total	CMR estimates	Cohort quality	Nb fawns
1985	0/1 = 0	0/2 = 0	0	0	B	3
1986	4/9 = 0.44	0/3 = 0	0.33	0.38	B	12
1987	6/7 = 0.86	0/7 = 0	0.43	0.45	B	14
1988	7/8 = 0.87	4/4 = 1	0.92	0.94	G	12
1989	3/8 = 0.37	7/13 = 0.54	0.48	0.49	B	21
1990	3/5 = 0.6	2/6 = 0.33	0.45	0.48	B	11
1991	2/5 = 0.4	3/3 = 1	0.62	0.74	G	8
1992	1/2 = 0.5	2/5 = 0.4	0.43	0.43	B	7
1993	0/1 = 0	0/4 = 0	0	0	B	5
1994	4/5 = 0.8	1/2 = 0.5	0.71	0.82	G	7
1995	2/3 = 0.67	5/9 = 0.55	0.58	0.63	G	12
1996	5/6 = 0.83	7/11 = 0.64	0.71	0.78	G	17
1997	3/5 = 0.6	8/11 = 0.73	0.69	0.82	G	16
1998	3/5 = 0.6	2/6 = 0.33	0.45	0.64	G	11
1999	8/13 = 0.61	5/9 = 0.55	0.59	0.77	G	22

Appendix II

Parameter estimates for the three measures of home range quality (without the consideration of the years 1985–1987 when density-dependent responses still occurred in the roe deer population). The cohort factor distinguishes (i.e. slope differences among categories) good (1) and bad (2) cohorts, the habitat factor rich (NE or 1) and poor (NW + S or 2) habitats, 'plants' corresponds to a variable summing up the proportion of hornbeam, bluebells and star of Bethlehem at the home range scale (a), 'DCA' corresponds to the score of the home range on the first axis of our Decentred Correspondence Analysis (b), 'hornbeam' corresponds to the proportion of hornbeam within the home range (c)

	Estimate	SE	Z-value	$Pr(> Z)$
(a)				
Intercept	1.70	0.68	2.52	0.01
Cohort	-2.26	0.82	-2.75	0.006
Plants	-0.95	0.57	-1.67	0.09
Habitat	-0.56	0.46	-1.19	0.23
Cohort/plants	1.63	0.90	1.80	0.07
(b)				
Intercept	0.89	0.31	2.83	0.005
Cohort	-1.00	0.38	-2.64	0.008
DCA	-0.65	0.45	-1.44	0.15
Habitat	-0.43	0.43	-0.98	0.32
Cohort/DCA	1.46	0.77	1.90	0.05
(c)				
Intercept	1.65	0.76	2.17	0.03
Cohort	-1.81	0.86	-2.10	0.03
Hornbeam	-1.63	1.21	-1.34	0.18
Habitat	-0.55	0.49	-1.12	0.26
Cohort/hornbeam	1.94	1.77	1.10	0.27