AGE AND DENSITY MODIFY THE EFFECTS OF HABITAT QUALITY ON SURVIVAL AND MOVEMENTS OF ROE DEER

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Abstract. We analyzed spatial variations in movements and survival in a roe deer (*Capreolus capreolus*) population (Chizé, western France) by using recent developments of multistate capture–mark–recapture modeling in order to estimate transition and survival probabilities of individuals living in three habitats of contrasting quality. Irrespective of both population density and sex, habitat quality did not influence survivorship of prime-age or senescent roe deer. Likewise, habitat quality did not influence fawn survival at low density. On the other hand, fawn survival at high density was 20% higher in the resource-rich hornbeam-dominant coppices than in the other poorer habitats. We found, as expected, that fawns were mobile, whereas adults of both sexes were highly sedentary. Movements of roe deer among habitats were markedly influenced by habitat quality. Transition probabilities of individuals from the rich hornbeam coppices toward other habitats were lower than transition probabilities of individuals from the poor beech stand or from the medium-quality maple dominant coppices toward the rich hornbeam coppices.

Key words: Capreolus capreolus; fitness components; France; habitat quality; ideal despotic distribution; ideal free distribution; movements; multistate capture–mark–recapture analysis; roe deer; spatial heterogeneity; ungulates.

INTRODUCTION

Temporal and spatial fluctuations of ecological factors and population density have strong influences on the population dynamics of animals (Gilpin and Hanski 1991, Tuljapurkar and Caswell 1996, Tilman and Kareiva 1997). However, long-term studies of marked individuals have revealed that, at a particular place and time, individual variation may generate substantial variation in fitness components (Gaillard et al. 2000*b*). In mammals, among-individual heterogeneity is generally associated with differences in attributes such as sex (Clutton-Brock et al. 1982), age (Charlesworth 1980), or phenotypic quality (Festa-Bianchet et al. 1998, Gaillard et al. 2000*a*). The potential effects of spatial heterogeneity in habitat quality have generally been overlooked as an important component of individual variability in mammalian populations (Wahlström and Kjellander 1995, McCullough 1996; but see Coulson et al. 1997, 1999, Kohlmann and Risenhoover 1997). The absence of adequate data (i.e., from long-term studies of individually marked animals [Gaillard et al. 2000*b*]) and the widespread idea that negative effects of highest density in the best sites balance habitat quality among sites (ideal free distribution concept [IFD;

Fretwell and Lucas 1970]) have often led previous authors to neglect the influence of spatial heterogeneities in habitat quality on population dynamics. However, contrary to those expectations, recent work on red deer (*Cervus elaphus* Linnaeus, 1758) has shown that juveniles may have the lowest survival in the richest habitat (Coulson et al. 1997); accordingly, females show the lowest lifetime reproductive success in the richest habitat (Conradt et al. 1999). These recent results illustrate the need to consider habitat quality in studies of population processes (Milner-Gulland et al. 2000, Focardi et al. 2002).

We present here a detailed analysis of the influence of habitat quality on age- and sex-specific movements among habitats and survival in the enclosed roe deer (*Capreolus capreolus* Linnaeus, 1758) population of Chizé, France (see Fig. 1), which has been intensively monitored for 24 years. Roe deer are widespread small deer (~25 kg; Andersen et al. 1998) with few body reserves and a near-constant body mass throughout the year (income breeder strategy; Andersen et al. 2000), which make them very sensitive to resource availability. Adult males are territorial, whereas females live with their offspring in small groups, occupying small home ranges (Hewison et al. 1998).

The Chizé reserve has been stratified into three habitats contrasting in quality (N. Pettorelli, S. Dray, S. Villarubias, and D. Maillard, *unpublished data*; see *Study site*), so movements are assessed by estimating
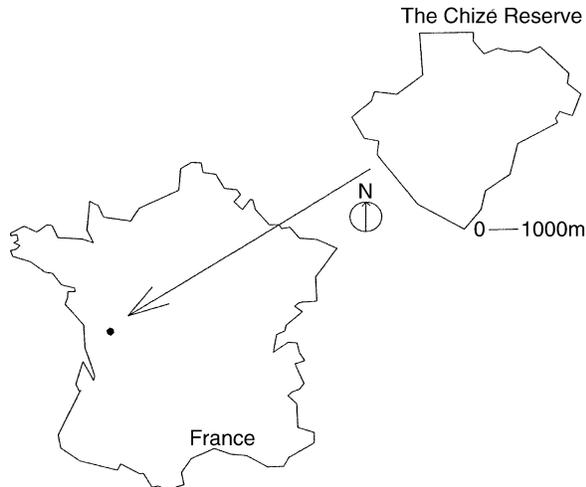
FIG. 1. The geographical location of the roe deer study area in France.

the transition probabilities among those three habitats, i.e., the probability of being recaptured in a different block of habitat. Age-specific survival rates of individuals living in each part of the reserve are also assessed.

Prime-age survival of female ungulates is highly resilient to changes in environmental conditions (Gaillard et al. 1998a, 2000b). In the weakly polygynous and almost monomorphic roe deer, survival of adult males, although lower than in females, was not influenced by yearly variation of environmental conditions (Gaillard et al. 1993). We therefore expected to find (1) the same high survival of prime-age roe deer of both sexes in all types of habitat. According to the ideal despotic distribution theory (Fretwell 1972), males defending territories should not show an ideal free distribution. Territorial males that live in the richest habitat are expected to have greater fitness than those living in the poorest habitat. Because prime-age survival is expected to be highly resilient to changes in environmental conditions in both sexes, we expected to find (2) an effect of habitat quality on survival rates of senescent bucks only. Fawn survival is highly variable over time (Gaillard et al. 1998b), and because winter fawn body mass is known to be affected by habitat quality (Pettorelli et al. 2001), we expected to find (3) an effect of habitat quality on fawn survival rate (see Plate 1).

According to our current knowledge of roe deer dispersal patterns, individuals generally leave their mothers at 1–2 years of age and are highly sedentary afterward (Strandgaard 1972, Linnell et al. 1998). We therefore expected (4) between-age differences in transition probabilities, with fawns being more mobile than other age classes.

According to Liberg et al. (1998), senescent males should be chased away from their territories by prime-age bucks. We thus expected to find (5) higher tran-

sition probabilities for senescent males than for prime-age ones. We did not expect that males and females would have the same possibilities of establishing their home ranges in each habitat: in the richest habitat, females could establish freely, whereas males would be prevented from settling there by established territorial males. We therefore expected to find (6) a sex effect on the individuals' first transition probabilities. Finally, according to both ideal free and despotic distributions, we also expected to find (7) directional transitions among habitats according to their quality. Transition from rich to poor habitat should be less frequent than the reverse, especially for females, which are not territorial.

MATERIALS AND METHODS

Study site

This study was carried out in the Chizé reserve, an enclosed 2614-ha forest located near the Atlantic Ocean in western France (46°05′ N, 0°25′ W). The climate is characterized by mild winters and hot, dry summers. The dominant trees are deciduous: oak (*Quercus* spp. Linnaeus, 1758) and beech (*Fagus sylvatica* Linnaeus, 1758). The northern part of the reserve is mainly composed of an oak stand, whereas the southern part of the reserve is mainly a beech stand. The abundance of the principal food plants for roe deer in spring and summer, plant nitrogen content, an index of population density, and fawn and adult body masses are all influenced by the type of timber stand (Pettorelli et al. 2001, 2002). Further, the oak stand has a shrub layer of contrasting quality, with resource-rich northeastern coppices dominated by hornbeam (*Carpinus betulus* Linnaeus, 1758) and northwestern coppices of medium quality dominated by Montpelier maple (*Acer monspessulanum* Linnaeus, 1758; N. Pettorelli, S. Dray, S. Villarubias, and D. Maillard, *unpublished data*). We decided to consider those three habitats in the present study because (1) hornbeam constitutes a major resource in spring and summer for roe deer at Chizé (the period of high energy requirements; [Mauget et al. 2000]) and is highly preferred (Tixier et al. 1997, Duncan et al. 1998), and (2) local population densities should differ among habitats, being higher in the rich hornbeam coppice (the northeastern part of the reserve encompassing >60% of the oak stand) than in the poor beech stand (Pettorelli et al. 2001), with the medium-quality maple coppice intermediate.

The roe deer population at Chizé fluctuated markedly during the study period, increasing from 350 deer older than 1 year in 1979 to >550 deer in 1983 and decreasing to <200 deer in 1993 (estimated by capture–mark–recapture methods; Gaillard et al. 1993). Since 1993, the population size has been maintained at ~200 roe deer older than 1 year. The population increased because few roe deer were removed annually, and decreased due both to high annual culling and to density-

PLATE 1. In juvenile ungulates, survival is more variable than adult female survival because young (here a newborn roe deer fawn) are more susceptible to adverse environmental conditions than adult females, but also because mothers adopt a selfish behavior and abandon their offspring as part as a risk-averse strategy of life. Photo by Guy van Laere (ONCFS).

dependent responses of population parameters. The intensity of annual culling tends to differ among habitats, being generally higher in the rich habitat (except during the high-density period, when no differences occurred [Pettorelli 2002]). Recruitment decreased from 1.7 to 1.3 fawns per doe following the population peak in 1983 (Boutin et al. 1987). Most does first gave birth as 2-year-olds, but does born during the peak first did so only as 3- or 4-year-olds (Gaillard et al. 1992), and the annual finite rate of increase (λ) averaged 1.25.

Data collection

The roe deer population at Chizé has been intensively monitored by using capture–mark–recapture (CMR) methods for more than 20 years (Gaillard et al. 1993, 1997). More than 70% of roe deer older than 1 year are individually marked using numbered collars (Strandgaard 1967) and ear tags. Every year animals are caught by drive-netting in winter (~25 capture drives per year in the reserve; Boisaubert and Boutin 1988). Each drive involves 150–300 persons and 2.5 km of nets, resulting in the capture of 120–300 roe deer every year. Mortality due to capture is low (<3%; Van Laere and Boutin 1990). To analyze the effect of habitat on survival and transition probabilities of roe deer, we used capture–recapture histories of 424 known-aged individuals that were first captured and marked during their first winter. Fawns were caught between 1978 and 1999 (see Plate 1); they were sexed and the site of capture (northeast, northwest, or south) was known. When an individual was captured more than once in a capture session, we considered the location at the first capture only because animals were not always released at their exact capture location; they may therefore have needed some time to regain their usual home range.

Statistical procedures

We used the multistate procedure in Mark 1.8 (White and Burnham 1999) to analyze variations in recapture,

survival, and transition probabilities among habitats. Two groups (males and females) and three states (the poor beech stand in the south, the rich oak stand with hornbeam coppices in the northeast, and the medium-quality oak stand with maple coppices in the northwest) were considered.

The procedure that we used followed three steps. As there is no goodness-of-fit test available for multistate models (White and Burnham 1999), we first fitted the one-state time-dependent model, the Cormack-Jolly-Seber model (Lebreton et al. 1992), to assess whether the assumptions of CMR models were fulfilled in our data set. We used the Release program (Burnham et al. 1987) using tests 2 and 3 as recommended by Lebreton et al. (1992). Because sample sizes in some cells were small, we used Fisher's exact tests. A general chi-square statistic was calculated as $-2\Sigma\ln(p_i)$ where p_i is the P value of Fisher's exact test of components of test 3.SR, test 3.Sm, and test 2 (for further details, see Gaillard et al. [1997]). The number of degrees of freedom was then equal to twice the number of components considered.

In a second step, we fitted the model previously selected at Chizé (for further details, see Gaillard et al. [1993, 1997] and Loison et al. [1999]) and added one transition probability between habitats by assuming that transition probabilities were constant across sexes, age classes, years, and habitats. Such a model involved an age-specific survival, the so-called Caughley's model (Caughley 1966, Gaillard et al. 1993) with three age classes (fawn, prime-age deer 2–7 years old, and senescent deer >7 years old), and a sex-specific survival for both prime-age and senescent roe deer. As in previous analyses, we considered three periods of capture (1978–1985, 1986–1999, and 2000) on the basis of differing capture efforts: half of the reserve was sampled between 1978 and 1985; between 1986 and 1999 an extra block was sampled each year (Gaillard et al. 1993), and a heavy storm hit France in late December 1999, causing a reduction in the capture probability in
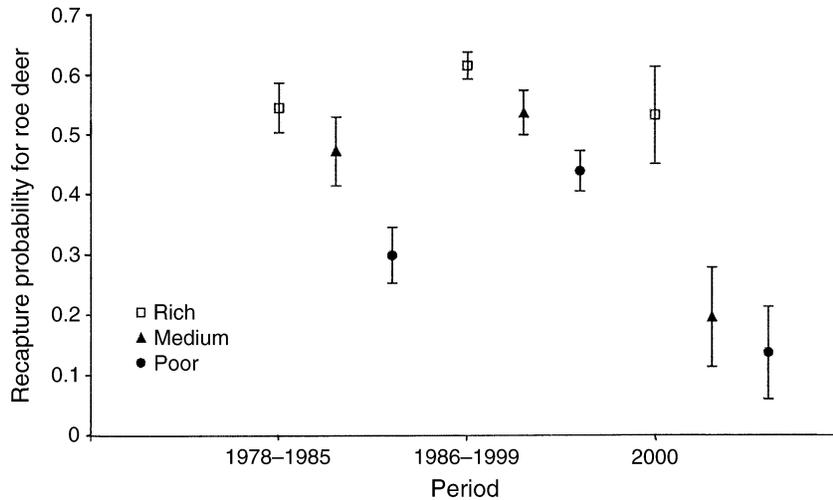
Fig. 2. The recapture probabilities (mean ± 1 SE) for individual roe deer living in the rich habitat (hornbeam coppices), the medium habitat (maple coppices), and the poor habitat (beech stand). The periods differ in capture effort (see *Materials and Methods: Statistical procedures*). Estimates are from the model involving effects of an interaction between age class and sex on adult survival and density dependence on survival of fawns living in the poorest habitats, an interaction between habitat and periods on recapture probability, and an interaction between age class and flux direction (two directions are considered: from the rich habitat and from the others) on transition probabilities (s(ac × sx(2.3.4) and densf × h), Pr(h × p), ψ(ac' × sens)).

the 2000 capture season because of practical problems when organizing the capture sessions (J. M. Gaillard, P. Duncan, D. Delorme, G. Van Laere, N. Pettorelli, D. Maillard, and G. Renaud, *unpublished data*). Because the reproductive output of females decreases after 12 years of age (Gaillard et al. 1998*b*), we also tested for differences of survival between 8–12 and >12 years of age. Because the recapture effort was unequal among the three habitats, we checked whether habitat influenced recapture probabilities. Finally, one constant transition probability between habitat was fitted. This second step allowed us to get a minimum model that we then used as a basis to test our predictions (see *Introduction*).

Finally, we tested whether habitat influenced survival probabilities. We checked for interactive effects of habitat and density on fawn survival because this latter has been reported to be density dependent at Chizé (Boisaubert et al. 1997) in response to marked changes in density throughout the study period (6–22 roe deer/100 ha; e.g., Pettorelli et al. 2001). We thus distinguished two periods of density, with a high-density period from 1982 to 1987 and a low-density period including all other years (as in Hewison et al. 2002). We also tested whether sex (males vs. females), age class (fawn, prime-age, and senescent), and direction influenced transition probabilities. To study age structure in transition probabilities, we focused on three age classes rather than four for survival: fawns, prime-age (2–7 years old), and senescent (>7 years old). Because (1) changes in density throughout the study period were similar in the three habitats and (2) population density was consistently highest in the rich hornbeam coppices

(Pettorelli 2002), we did not test for density effects in addition to habitat effects on transition probabilities.

Model selection was performed by using the corrected Akaike information criterion (AIC$_c$; Burnham and Anderson 1998). We selected the model that fitted the data satisfactorily with as few parameters as possible, making a trade-off between having too few parameters and poor accuracy of estimates, and having too many parameters and poor precision of estimates. In addition to AIC$_c$, we used likelihood ratio tests to test our predictions (Lebreton et al. 1992). Estimates are given as ±1 SE throughout, unless otherwise indicated.

RESULTS

The Cormack-Jolly-Seber model fitted the overall data set satisfactorily (χ^2 = 219.88, df = 244, P = 0.864). As expected from the model of Loison et al. (1999), survival decreased in both sexes from a mean of 0.803 [±0.048 SD] and 0.876 [±0.025] at 8–12 years of age to 0.422 [±0.187] and 0.673 [±0.068] at >12 years of age for males and females, respectively (Table 1A). Habitat quality influenced recapture probabilities, in addition to capture periods (Table 1B, C, E). Recapture probabilities in the three periods were highest in the rich habitat and lowest in the poor one (Fig. 2). The minimum model that we selected therefore included a fawn survival independent of sex, a yearly survival of older roe deer influenced by additive effects of age class (prime-age, 8–12, and >12 years of age) and sex (Table 1C, D), and capture probabilities influenced by additive effects of capture periods (1978–1985, 1986–1999, and 2000) and habitat (rich, medium,

TABLE 1. Finding a minimum model: for each hypothesis tested, the table shows the models compared, the Akaike information criterion after correction for sample size (AIC_c), the number of parameters considered for each model (*N*), the chi-square test (χ^2), degrees of freedom, and the *P* value of the comparison.

Hypothesis tested	Models	AIC_c	*N*	χ^2	df	*P*
1A) Effect of two stages of senescence on survival	ϕ (ac $\times$ sx(2.3)) Pr(2*p*) ψ ϕ (ac $\times$ sx(2.4.5)) Pr(2*p*) ψ	4878.02 4869.98	8 10	12.1	2	0.0024
1B) Habitat effect on recapture probabilities	ϕ (ac $\times$ sx(2.3)) Pr(2*p*) ψ ϕ (ac $\times$ sx(2.3)) Pr(2*p* $\times$ *h*) ψ	4878.02 4856.21	8 12	29.93	4	<0.0001
1C) Additive vs interactive effects	ϕ (ac $\times$ sx(2.4.5)) Pr(3*p* $\times$ *h*) ψ ϕ (ac + sx(2.4.5)) Pr(3*p* + *h*) ψ	4832.89 4829.87	17 11	9.24	6	0.16
1D) Interaction between sex and age on survival	ϕ (ac $\times$ sx(2.4.5)) Pr(3*p* $\times$ *h*) ψ ϕ (ac + sx(2.4.5)) Pr(3*p* $\times$ *h*) ψ	4832.89 **4829.04**	17 **15**	0.249	2	0.88
1E) Interaction between period and habitat on capture probabilities	ϕ (ac $\times$ sx(2.4.5)) Pr(3*p* $\times$ *h*) ψ ϕ (ac $\times$ sx(2.4.5)) Pr(3*p* + *h*) ψ	4832.89 4833.71	17 13	9.01	4	0.061

Notes: The model retained as the minimum model (i.e., the model with the lowest AIC_c) is in bold. Terms are as follows: ϕ, survival probability; Pr, probability of recapture; ψ, transition probability; ac, age class [(1) fawns, (2) prime age, (3) >8 years old, (4) 8–12 years of age, and (5) >12 years old]; *h*, habitat (rich hornbeam coppices, NE; medium maple coppices, NW; and poor beech stand, S); *p*, periods (2*p*, 1978–1985 and 1986–2000; 3*p*, 1978–1985, 1986–1999, and 2000); sx, sex.

and poor). Additive models include effects of different variables on survival and recapture probabilities, and these effects are cumulative and parallel across capture periods.

We did not observe any influence of habitat on prime-age survival (0.88 [±0.03] in the rich habitat vs. 0.85 [±0.04] in the medium one and 0.89 [±0.04] in the poor one for males; 0.93 [±0.02] in the rich vs. 0.90 [±0.03] in the medium and 0.94 [±0.03] in the poor habitat for females; see Table 2G, H, I, J). This result is consistent with our first prediction of a consistently high prime-age survival in both sexes irrespective of habitat quality. We did not find any significant influence of habitat quality on survival rate of old males (Table 2K, L, M). However, survival of males 8–12 years old tended to be higher in the medium than in the two other habitats (0.94 [±0.09] vs. 0.78 [±0.07] in the rich and 0.70 [±0.11] in the poor). For males >12 years old, the survival probability cannot be estimated in the poor habitat because only one individual was captured in this habitat during the 24 years of monitoring. Survival of males >12 years old was very similar in the two other habitats (0.35 [±0.29] in the rich vs. 0.30 [±0.25] in the medium habitat); hence, our second prediction, according to which old males should survive better in hornbeam coppices (the best habitat at Chizé), is rejected.

As expected in our third prediction, we found interactive effects of density and habitat quality on fawn survival (Table 2D). At low density, habitat quality did not influence fawn survival (0.85 [±0.04] in the rich habitat, 0.87 [±0.05] in the medium, and 0.83 [±0.06] in the poor). However, fawn survival in the rich habitat did not change according to density periods, whereas fawn survival in the two other habitats did. In those habitats, fawn survival decreased by >20% between low- and high-density periods (0.87 [±0.05] vs. 0.61

[±0.11] in the medium, and 0.83 [±0.06] vs. 0.58 [±0.13] in the poor habitat). At low density, the countervailing effects of density and habitat quality led fawn survival to be constant among habitats, but not at high density, when fawns that were raised in the best habitat survived much better.

As expected (fourth prediction), transition probabilities of roe deer among habitats were markedly age structured (Table 2A). Fawns moved among habitats to a much greater extent than did adults for all of the transition probabilities (from rich to medium, 0.2 and 0.13 for male and female fawns vs. 0.01 for prime-age adults of both sexes; from rich to poor, 0.18 and 0.27 for male and female fawns vs. 0.02 for prime-age adults of both sexes; from medium to rich, 0.26 and 0.38 for male and female fawns vs. 0.04 and 0.03 for prime-age males and females; from medium to poor, 0.26 and 0.30 for male and female fawns vs. 0.05 and 0.07 for prime-age males and females; from poor to rich, 0.32 for fawns of both sexes vs. 0.04 and 0.05 for prime-age males and females; from poor to medium, 0.29 and 0.35 for male and female fawns vs. 0.01 and 0.07 for prime-age males and females (Table 2A, Fig. 3). Contrary to our fifth prediction, we did not observe any detectable increase of transition probability between prime-age and senescent stages (transition probabilities of senescent stages of 0 and 0.02 for males and females from rich to medium habitat; of 0 and 0.009 for males and females from rich to poor habitat; of 0 and 0.07 for males and females from medium to rich habitat; of 0 for both males and females from medium to poor and from poor to rich habitat; and of 0.05 and 0.06 for males and females from poor to medium habitat). We therefore did not find any support for the suggestion of Liberg et al. (1998) that senescent males are chased away by prime-age ones, although the prediction of Liberg et al. was set at the level of individual territories

TABLE 2. Testing specific hypotheses: for each prediction, the table shows the models, the Akaike information criterion after correction for sample size (AIC$_c$), the number of parameters considered for each model (N), the chi-square test (χ^2), the degrees of freedom, and the P value of the comparison.

Assumption tested	Models	AIC$_c$	N	χ^2	df	P
2A) Age dependence in transition probabilities	ϕ (ac + sx(2.3.4)) Pr(3p + h)	4829.87	11	212.3	2	**<0.0001**
	ϕ (ac + sx(2.3.4)) Pr(3p + h) ψ (ac′)	4621.61	13			
2B) Additive effects of age and habitat on transition probabilities	ϕ (ac + sx(2.3.4)) Pr(3p + h) ψ (ac′)	4621.61	13	28.31	5	**<0.0001**
	ϕ (ac + sx(2.3.4)) Pr(3p + h) ψ (ac′ + h)	4603.54	18			
2C) Interaction between age and habitat on transition probabilities	ϕ (ac + sx(2.3.4)) Pr(3p + h) ψ (ac′)	24621.61	13	38.46	13	**0.0002**
	ϕ (ac + sx(2.3.4)) Pr(3p + h) ψ (ac′ × h)	4609.93	26			
2D) Interaction between habitat and density on fawn survival	ϕ (ac + sx(2.3.4)) Pr(3p + h) ψ (ac′ + h)	4603.54	18	10.07	2	**0.007**
	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	**4597.59**	20			
2E) Additive effects of sex and habitat on transition probabilities	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	2.42	1	0.12
	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h + sx)	4597.23	21			
2F) Interaction between sex and the cumulative effects of age and habitat on transition probabilities	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	5.07	6	0.53
	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ ((ac′ + h) × sx)	4604.94	26			
2G) Interaction between habitat and sex on prime age survival	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	2.809	4	0.59
	ϕ (ac + sx(2.3.4) + (densf × h) + h × PA) Pr(3p + h) ψ (ac′ + h)	4603.05	24			
2H) Additive effects of habitat and sex on prime age survival	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	2.63	2	0.27
	ϕ (ac + sx(2.3.4) + (densf × h) + (h + PA))Pr(3p + h) ψ (ac′ + h)	4599.08	22			
2I) Three-way interaction between density, sex and habitat on prime age survival	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	8.56	11	0.66
	ϕ (ac + sx(3.4) + (densf × h) + (densPA × sx × h)) Pr(3p + h) ψ (ac′ + h)	4611.9	31			
2J) Interaction between density and habitat on prime age survival	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	4.17	5	0.53
	ϕ (ac + sx(2.3.4) + (densf × h) + (densPA × h)) Pr(3p + h) ψ (ac′ + h)	4603.76	25			
2K) Additive effects of age and habitat on survival of males >8 years of age	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	0.404	2	0.82
	ϕ (ac + sx(2.3.4) + (densf × h) + (h + m(3.4)))Pr(3p + h) ψ (ac′ + h)	4601.31	22			
2L) Interaction between age and habitat on survival of males >8 years of age	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	2.19	4	0.70
	ϕ (ac + sx(2.3.4) + (densf × h) + h × m(3.4))Pr(3p + h) ψ (ac′ + h)	4603.67	24			
2M) Habitat dependence in survival of males aged 8–12	ϕ (ac + sx(2.3.4) + densf × h) Pr(3p + h) ψ (ac′ + h)	4597.59	20	1.50	2	0.47
	ϕ (ac + sx(2.3.4) + densf × h) + h(m(3))Pr(3p + h) ψ (ac′ + h)	4600.22	22			

Notes: The final model retained (the model with the lowest AIC$_c$), the prediction number, and all significant P values are in boldface. Terms are as follows: ϕ, survival probability; Pr, probability of recapture; ψ, transition probability; ac, age class [(1) fawns, (2) prime age, (3) senescent <12 years old, and (4) senescent >12 years old]; sx, sex, (m) males; ac′, age class [(1) fawns, (2) prime age, and (3) senescent]; h, habitat (hornbeam coppices, NE; maple coppices, NW; and beech stand, S); h(m(3.4)), additive effect of habitat type and age class only on senescent males; densf × h, interaction between habitat and density on fawn survival; densPA × h, interaction between habitat and density on prime-age survival.
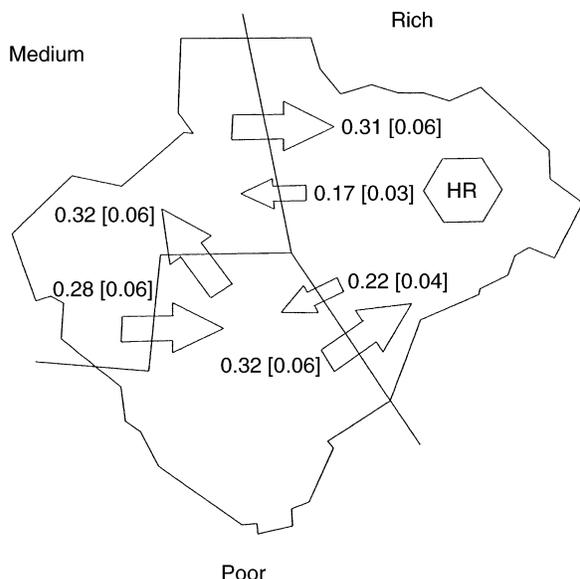
FIG. 3.　Movements of roe deer fawns between the three habitats considered, measured as the probability that an animal is recaptured in a different habitat (transition probabilities, mean with 1 SE in brackets). The size of the arrows increases with increasing transition probabilities. A typical roe deer home range (HR ~30 ha) is also represented. Estimates are from the model involving effects of an interaction between age class and sex on adult survival and density dependence on survival of fawns living in the poorest habitats, an interaction between habitat and periods on recapture probability, and an interaction between age class and flux direction (two directions are considered: from the rich habitat and from the others) on transition probabilities (s(ac $\times$ sx(2.3.4) and densf $\times$ h), Pr($h \times p$), ψ(ac′ $\times$ sens)).

rather than at the level of habitat types. We did not find evidence for between-sex differences in transition probabilities. However, there was a slight trend in all habitats for female fawns to have a greater transition probability than male fawns (Table 2E, F). Therefore we cannot formally reject our sixth prediction; according to which females have higher transition probabilities than males. Finally, the direction of fawn transitions among habitats was skewed in the expected di-

rection (Table 2B, C); fawns left the rich hornbeam coppices oak stand less often than other habitats. Therefore, in support of our seventh prediction, transitions from rich to poor habitats were less frequent than other transitions (see Fig. 3).

DISCUSSION

Of the seven predictions that we tested, four were clearly supported, one tended to be supported, and two were clearly rejected (Table 3). Considering the predictions related to variation in survival according to habitat quality, two out of the three predictions were supported by our analyses.

As expected for a large mammal (Eberhardt 1977), even the strongly contrasting habitat quality observed at Chizé did not influence survival of prime-age roe deer, which was consistently high, irrespective of both population density and habitat quality. Similar results have been reported for several ungulate species (for reviews, see Gaillard et al. [1998a, 2000b]).

Fawn survival varied markedly in response to variation in population density and habitat quality. At low density, fawns had high survival probabilities irrespective of habitat quality; at high density, fawns in the Chizé forest survived much better in the rich habitat than in any other. The interaction of density dependence and temporal sources of environmental variation (e.g., climatic factors) has previously been reported in ungulates for juvenile survival (Gaillard et al. [1997] for roe deer, Portier et al. [1998] for bighorn sheep *Ovis canadensis* Shaw 1804; Milner et al. [1999] for Soay sheep *Ovis aries* Linnaeus, 1758; Crête and Courtois [1997] for moose *Alces alces* Linnaeus, 1758). To our knowledge, this study provides the first empirical evidence that an interplay between density dependence and a spatial source of environmental variation (i.e., the habitat quality) occurs in an ungulate population. Habitat quality influences juvenile survival in caribou *Rangifer tarandus* Linnaeus, 1758 (Whitten et al. 1992), pronghorn *Antilocapra americana* Ord 1815 (Fairbanks 1993), and red deer (Coulson et al. 1997),

TABLE 3.　Outcomes of the tests of the seven predictions about the responses of survival and transition probabilities of roe deer to differences in habitat quality according to age and sex classes.

Predictions	Test used	Outcome
(i) Survival of prime-age roe deer of both sexes is consistently high and does not vary among habitats.	Table 2G,H,I,J	supported
(ii) Senescent males survive better in rich habitats than in poor ones.	Table 2K,L,M	rejected
(iii) Fawn survival varies according to habitat quality.	Table 2D	supported
(iv) Transition probabilities among habitats are age-structured.	Table 2A	supported
(v) Senescent males have higher transition probabilities than prime age males.	Table 2A	rejected
(vi) Transition probabilities for fawns are higher in females than in males.	Table 2E,F	partially supported
(vii) Transition probabilities from rich to poor habitats are lower than other transition probabilities.	Table 2B,C	supported

so such interactions may be widespread in ungulate populations: this warrants further investigation.

The last survival pattern in relation to habitat quality that we studied here concerned senescent males. Contrary to what we expected, we found little support for a higher survival for males aged 8–12 years living in the best habitat compared to those living in poorer ones. For the oldest males (>12 years old) it was not possible to test the hypothesis because too few individuals were caught, and none in the beech stand, over the 24-year period. The cost of maintaining a territory therefore appears to be quite similar in rich and poor habitats. This suggests either that males are able to adjust the energy expenditures allocated to territory defense in relation to the habitat quality, or that the costs of defending territory increase with density, which was higher in the high-quality habitat. Adjustment of male reproductive effort to resource availability recently has been suggested for highly polygynous red deer (Yoccoz et al. 2002) and bighorn sheep (M. Festa-Bianchet, J. M. Gaillard, and S. Coté, *unpublished manuscript*) and may also occur in a territorial species like the roe deer.

Of the four predictions related to variation in movements according to habitat quality, two were supported by our analyses. Our results confirmed previous work on roe deer home range dynamics, which found highly contrasted patterns according to age: fawns were much more mobile than adults, which were highly sedentary, as is usually reported for roe deer (Strandgaard 1972, Andersen et al. 1998). However, contrary to the suggestion of Liberg et al. (1998), senescent males did not move to a greater extent than prime-age ones. Senescent males may live in their territory over their lifetime, as territorials or satellites, at Chizé as has been observed in Norway (Linnell and Andersen 1998).

Transition probabilities of fawns were directional at Chizé, fluxes from the rich hornbeam coppices to the other parts being lower than the other fluxes. No clear effect of sex occurred on transition probabilities, although territorial males and nonterritorial females were expected to distribute themselves differently.

At Chizé, fawns survive better at high density (this study) and are, on average, ~0.9 kg heavier at the onset of winter (~6% of their body mass over the 24 years considered; N. Pettorelli, S. Dray, J. M. Gaillard, D. Chessel, P. Duncan, N. Guillon, A. W. Illius, F. Klein, and G. Van Laere, *unpublished data*) in the rich than in the poor habitat. We can thus conclude that female roe deer do not fit the ideal free distribution at Chizé, contrary to what was reported by Wahlström and Kjellander (1995) for a roe deer population living in an agricultural area.

Because the local density of roe deer was highest in the rich hornbeam habitat (Pettorelli et al. 2001; N. Pettorelli et al., *unpublished data*), transition probabilities showed an inverse density-dependent pattern. However, density in the rich habitat was not high enough to compensate for differences in habitat quality.

Fawns in the rich habitat had long-lasting fitness benefits over fawns in poorer habitats, especially when environmental harshness increased.

These results suggest that when density increases, females are not entirely free to move among habitats. This could be because of social constraints or perhaps because of lack of information. Many studies have reported deviations from an ideal free distribution, which can result from imperfect information about the habitats (Abrahams 1989, Kohlmann and Risenhoover 1997). In contrast to males, which are frequently involved in intraspecific contests, females are not chased off by reproductive individuals of any sex and female home ranges often overlap with those of relatives (Hewison et al. 1998), leading to clans at high population density (Kurt 1968). The fact that there was no clear effect of sex on transition probabilities, although territorial males and nonterritorial females were expected to distribute themselves differently, supports this interpretation.

In conclusion, it is likely that in conditions of nutritional stress, the reported difference in body mass reached at the onset of winter leads to a lower survival probability over their first winter for fawns living in poorest habitats (see also Gaillard et al. 1993). The abundance of key food resources in the highest quality habitat during the critical period of spring–summer (Pettorelli et al. 2001) may explain why fawns born in this part of the reserve survived even when density was high. Hornbeam constitutes a principal species in the diets of roe deer during periods when energy requirements of the females are high (~10% by mass of summer diets; Maizeret et al. 1991) and is highly preferred (eaten 10 times as much as its availability; Tixier et al. 1997). Further research is needed to determine whether hornbeam alone accounts for the spatial heterogeneity found for fawn survival at Chizé, or whether other plant species in the hornbeam coppices are involved.

This study underlines the importance of considering spatial heterogeneity in habitat quality when analyzing population dynamics (Milner-Gulland et al. 2000). It also provides a new empirical basis for further theoretical developments of spatially structured models of population dynamics.

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