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LIFETIME REPRODUCTIVE SUCCESS AND COMPOSITION OF THE HOME RANGE IN A LARGE HERBIVORE

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Abstract. The relationship between individual performance and nonrandom use of habitat is fundamental to ecology; however, empirical tests of this relationship remain limited, especially for higher orders of selection like that of the home range. We quantified the association between lifetime reproductive success (LRS) and variables describing lifetime home ranges during the period of maternal care (spring to autumn) for 77 female roe deer (*Capreolus capreolus*) at Trois-Fontaines, Champagne-Ardenne, France (1976–2000). We maintained population growth rate (adjusted to account for removals of non-focal animals) near $r_{\max}$, which enabled us to define the fitness–habitat relationship in the absence of density effects. Using a negative binomial model, we showed that a roe deer's incorporation into its home range of habitat components important to food, cover, and edge (meadows, thickets, and increased density of road allowances) was significantly related to LRS. Further, LRS decreased with increasing age of naturally reclaimed meadows at the time of a deer's birth, which may have reflected a cohort effect related to, but not entirely explained by, a decline in quality of meadows through time. Predictive capacity of the selected model, estimated as the median correlation (r_s) between predicted and observed LRS among deer of cross-validation samples, was 0.55. The strength of this relationship suggests that processes like selection of the site of a home range during dispersal may play a more important role in determining fitness of individuals than previously thought. Individual fitness of highly sedentary income breeders with high reproductive output such as roe deer should be more dependent on home range quality during the period of maternal care compared to capital breeders with low reproductive output. Identification of the most important habitat attributes to survival and reproduction at low density (low levels of intraspecific competition) may prove useful for defining habitat value ("intrinsic habitat value").

Key words: Capreolus capreolus; *fitness; habitat; home range; life history; lifetime reproductive success (LRS); resource selection function; roe deer; Trois-Fontaines, France.*

INTRODUCTION

The relationship between individual performance and nonrandom use of habitat is fundamental to our understanding of ecology. For example, niche theory (Hutchinson 1957, Vandermeer 1972), optimal foraging (MacArthur and Pianka 1966, Fretwell and Lucas 1970, Charnov 1976, Orians and Pearson 1979), and source–sink dynamics (Pulliam 1988) are all based on fitness–habitat associations. The concept of scale is also key to our interpretation of ecological pattern and process (Wiens 1989, Levin 1992, Schneider 2001); however, empirical tests of theories based on the relationship between performance and habitat selection have largely been conducted at relatively small spatial and temporal scales (reviews in Rosenzweig 1981, 1991, Stephens and Krebs 1986, Morris 2003). Patterns measured at small scales do not necessarily hold at larger scales, nor do processes prevailing at small scales necessarily prevail at large scales (Schneider 2001). Recent empirical analyses (Pettorelli et al. 2005, McLoughlin et al. 2006) support the hypothesis that scale dependence in habitat selection is the result of scale dependence in the link between performance and habitat selection (Orians and Wittenberger 1991). Despite the large body of literature describing the hierarchical nature of habitat selection (Hall et al. 1997, Garshelis 2000, Manly et al. 2002), studies demonstrating how observed patterns in selection might explain variation in performance at scales greater than that of the feeding site or patch continue to remain relatively uncommon. Moreover, after Morris (2006), we expect that processes operating over a long

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time (several years) at a large spatial scale (home range) are more likely to shape variation in population dynamics and individual fitness than processes operating over a short term (within a day) at a small spatial scale (food item or feeding place).

"Scaling up" of the fitness–habitat relationship to include larger spatial and temporal scales (e.g., selection for a home range or landscape features within the home range [higher-order habitat selection; Johnson 1980]) may offer new insights into both theoretical and applied ecology. First, research into the fitness–habitat link at higher orders of selection may help us to recognize that large-scale habitat or resource selection is a behavioral process (Johnson 1980, Hall et al. 1997) that, similar to the smaller scale resource selection examined by researchers of traditional foraging theory, can provide a mechanistic explanation of variation in individual performance. Second, longer periods of study allow for the calculation of more direct measures of Darwinian fitness, such as lifetime reproductive success (LRS; Brommer et al. 2004) or individual contributions to population growth (Coulson et al. 2006). Such analyses may permit more accurate tests of ecological theory founded on the link between fitness and habitat selection (e.g., ideal-free distribution; Fretwell and Lucas 1970), or development of new theory relevant to higher-order habitat selection. Key questions concern the role of density dependence in habitat selection (and the relationship between fitness and habitat selection) at higher (or multiple) scales of selection (McLoughlin et al. 2006, Morris 2006), and how the strength of relationships between performance and selected resources might depend on life history. Further, analyses incorporating habitat variables and performance measures assessed at larger spatial and temporal scales are likely to have increased relevance to conservation biology. For example, data may be used to identify resources most critical to survival and reproduction at scales amenable to habitat management, or instances of maladaptive habitat selection where landscapes have been modified by natural or anthropogenic disturbance (Delibes et al. 2001, Robertson and Hutto 2006).

Roe deer (*Capreolus capreolus*) at Trois-Fontaines, Champagne-Ardenne, France, have been the subject of considerable research in population dynamics (e.g., Gaillard et al. 1993, 2003*a*, *b*) and evolutionary ecology (e.g., Gaillard et al. 1998*a*, Hewison et al. 2005). Of particular relevance to the question of habitat selection, the population is unique in that, since commencement of research at Trois-Fontaines in the mid-1970s through 2000, deer were managed at a relatively constant level well below carrying capacity. In 2001, removals were relaxed, and the population was measured to subsequently increase at a per capita growth rate ($r = 0.35$; J.-M. Gaillard, *unpublished data*) close to the expected $r_{\max}$ for the species (Gaillard et al. 1998*a*). Hence, prior to 2001, density dependence is not likely to have influenced relationships between fitness of roe deer and selection of resources. Long-term data on LRS and boundaries of the lifetime home range are available from 1976 to 2000 for roe deer at Trois-Fontaines, enabling us to investigate relationships between performance and higher-order habitat selection independent of density effects.

Here we present an empirical analysis of the relationship between LRS of female roe deer at Trois-Fontaines and individual selection for a home range defined by unique compositions of available vegetation associations. Adult females maintain near constant body mass (~24 kg at Trois-Fontaines, Gaillard et al. 2003*b*) with low body reserves throughout most of the year, and rely on abundant, high-quality food to meet the high energy demands for producing and rearing fawns (i.e., income-breeder tactic; Andersen et al. 2000). Predation at Trois-Fontaines is very low (Gaillard et al. 1997), and the main cause of juvenile mortality in the study area is thought to be abandonment of fawns by mothers in response to nutritional stress. Fawn survival between birth and weaning is the most critical component of the roe deer life history cycle in temperate regions, accounting for most of the observed changes in population size over time (Gaillard et al. 1998*b*, 2000*b*). Through effects on juvenile survival, we thus predicted that a female's relative access to high-quality forage (artificially constructed meadows) during the period of maternal care (between spring and autumn) is likely to be an especially strong predictor of LRS. Further, because increasing edge density is thought to be an important component of home ranges of roe deer (Tufto et al. 1996, Saïd and Servanty 2005), compositional diversity of vegetation associations (McGarigal et al. 2002) and density of road allowances contained within the home range were predicted to relate with LRS. Finally, meadows established at the commencement of study at Trois-Fontaines were managed to undergo staged ecological succession, and their value to deer probably declined through time. We therefore expected a dynamic link in the association between LRS and selection for meadows.

METHODS

Study area and animals

Our study area was the Territoire d'Étude et d'Expérimentation at Trois-Fontaines, Champagne-Ardenne, France (48°43′ N, 4°55′ E), a reserve managed by the Office National de la Chasse et de la Faune Sauvage (Fig. 1). The fully enclosed, 1360-ha study area was divided into 172 forest census plots (7.3 ± 1.7 ha, mean ± SD) by a network of walking trails and road allowances (Fig. 1), and subdivided into vegetation classes by polygons averaging 2.0 ± 2.1 ha in size (Widmer et al. 1998). During the period of study (1976–2000), Trois-Fontaines was dominated by mature oak (*Quercus* spp.) and beech (*Fagus sylvatica*) forest with little or no understory (mature closed forest; 50.3% coverage). Remaining vegetation associations were

FIG. 1. Distribution of forest plots, roads and trails, and vegetation associations within the Territoire d'Etude et d'Expérimentation at Trois-Fontaines, Champagne-Ardenne, France (map year 1996). Forest plots occupied by a deer between spring and autumn during its lifetime were used to define the home range (Pettorelli et al. 2005). An example home range is presented in the center of the map (stippled polygon). Different gray scale shadings illustrate heterogeneity in forest types.

largely composed of more open forest stands containing mature trees without understory and openings of <1 ha (mature open forest; 13.4% coverage), patches of relatively young forest typically containing hornbeam (*Carpinus betulus*) and ivy (*Hedera helix*) and bramble (*Rubus* spp.) understory (18.3% coverage), and dense thickets of ivy and bramble (16.4% coverage). Clearings dominated by forbs and grasses occurred as artificially constructed meadows (1.6% coverage), but also along a network of road allowances in the study area (Fig. 1). Meadows at Trois-Fontaines were created in 1973 when 10 patches of 1–3 ha each within the reserve were cleared and planted with grasses to improve food resources for roe deer. Meadows were fertilized each year from 1975 until 1982, maintained (regularly cut) but no longer fertilized through 1991, and then allowed to progressively undergo succession until the year 2000, when hurricane Lothar substantially reopened the forest (Widmer et al. 2004). We used the hurricane to mark the end of our period of study. Vegetation associations other than meadows largely remained consistent in area and structure from 1976 to 2000.

Excepting the initial years of 1976 and 1977, at any moment during the course of study, ~70% of adult roe deer at Trois-Fontaines were marked with ear tags and highly visible, numbered collars (Gaillard et al. 1993). Each year from 15 April to 30 June we caught and marked fawns (20–70/year; Gaillard et al. 1997, 1998*a*). We fit collars on surviving fawns at ~8 months of age. We sampled the entire study area every year, so that focal animals were randomly distributed within the reserve. For known-aged females (i.e., those marked as fawns), we collected location information and complete life histories (from birth to death) from repeated observations (Gaillard et al. 1998*a*, 2000*a*). We maintained the population of roe deer in the reserve at a relatively constant size of 200–250 adult deer (15–18 animals >1 yr old per square kilometer in March) by having reserve managers regularly translocate unmarked animals (Gaillard et al. 1993, 1998*a*). All removals were carried out in winter from January to February (Gaillard et al. 1993). If previously unmarked fawns were detected during removal operations, we ensured no bias when deciding whether a fawn was to be translocated or released back into the study area after being marked. Removals were relaxed only after hurricane Lothar, and no evidence of density-dependent effects on deer were observed during the period of study (Gaillard et al. 1993, 1997, 1998*a*, *b*, 2003*a*).

Lifetime reproductive success

We planned to use a generalized linear model (GLM; McCullagh and Nelder 1989) to relate LRS (discrete response variable) to individual-based measures describing lifetime selection of the home range (predictor variables). We calculated LRS as the number of fawns to which a female gave birth that survived past weaning. We limited our analysis to deer that lived at least to 2.5 years (the youngest age at which we observed successful recruitment of offspring) to avoid including animals that died before adulthood, and thus would not have had an opportunity to establish a home range comparable with that of adult deer. We restricted the latest cohort in our sample to deer born in 1987, because some members of subsequent cohorts lived beyond the end of the period of study (2000). Our sample size was 77 deer spanning 575 animal-years.

Habitat selection

We defined habitat as the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism (Hall et al. 1997). Habitat selection is the hierarchical, nonrandom process of innate and learned behavioral decisions made by an animal, at different geographic scales, leading to occupancy of a location or use of a habitat resource (Hall et al. 1997, Manly et al. 2002). Here, our concern was second-order habitat selection (according to Johnson's [1980] scale of hierarchical orders of selection), specifically, establishment of the home range during the critical period of parturition and postnatal care between spring and autumn (hereafter, "home range"). In determining selection of the home range for each roe deer, grain of analysis was the smallest polygon of a discrete vegetation association in our map (61 m^2); the extent of study was the enclosed portion of the Trois-Fontaines reserve (Fig. 1).

Female roe deer occupy small, extremely stable, overlapping home ranges (Strandgaard 1972, Saïd et al. 2005) that can be determined from a relatively low frequency of relocations (<10; Börger et al. 2006). We estimated home ranges as boundaries of the aggregate of forest plots in which deer were observed (Pettorelli et al. 2005) between spring and autumn during their lifetime (7.4 ± 4.0 plots encompassing 54.5 ± 29.3 ha per home range; Fig. 1), based on 27.6 ± 2.8 locations per individual (mean ± SD). Aggregating forest plots to assess home range size in roe deer has previously been shown to be highly reliable (roe deer at Chizé, France [Pettorelli et al. 2005]); however, we note that in some cases not all parts of all forest plots may have been used by deer. That said, this approach is also likely to have mitigated potential underestimation of home range size for females with fewer observations.

TABLE 1. Estimated availability of vegetation associations (a_i) at Trois-Fontaines, France, and population means and variation in use ($\bar{u}_i$ ± SD) and relative selection ($\bar{B}_i$ and 95% confidence interval) for vegetation associations in lifetime home ranges (spring–autumn) of female roe deer (n = 77), 1976–2000.

Vegetation association	a	$\bar{u}$	$\bar{B}$ (95% CI)
Mature closed forest	0.503	0.491 ± 0.246	0.201 (0.161–0.241)
Mature open forest	0.134	0.108 ± 0.166	0.135 (0.091–0.179)†
Young forest	0.183	0.184 ± 0.201	0.176 (0.132–0.220)
Thicket	0.164	0.184 ± 0.155	0.193 (0.156–0.231)
Meadow	0.016	0.033 ± 0.033	0.294 (0.242–0.346)†

† Significantly different from the random expectation of $1/R$ (i.e., 0.20).

In each forest plot, dominant vegetation associations and their coverages (in square meters) were identified using aerial photographs (Table 1). For each home range, for $i = 1$ to R vegetation associations (resources), we then calculated a resource selection index (Manly et al. 2002:9–11). Selection indices for home ranges were first calculated as

$$w_i = \frac{u_i}{a_i} \tag{1}$$

where u_i is the proportion of vegetation association i within the home range and a_i is the proportional availability of i in the study area. We standardized estimates of w_i such that the set of use : availability ratios for each deer summed to 1.0:

$$B_i = \frac{w_i}{\sum_{i=1}^{R} w_i}. \tag{2}$$

A B_i value can be interpreted as the probability that, for any selection event, an animal would choose resource i over all others, assuming all resources were available to the animal in equal proportion; hence, the set of B_i's for an individual relate directly to the coefficients of a resource selection function (Manly et al. 2002:11). Although largely limited to the quantification of selection for discrete-resource variables (e.g., vegetation association or type of food), B_i values, compared to coefficients of resource selection functions computed using logistic regression (Boyce et al. 2002, Manly et al. 2002), were particularly amenable to our purposes because of their ease of calculation and suitability for individual-based modeling.

We considered that the choice of a home range by deer (and their subsequent LRS) would not be based solely on selection for vegetation associations relative to the study area, but also with respect to linear features in the form of road allowances. Major road allowances (15–20 m width) at Trois-Fontaines consisted of low-traffic clearings similar in vegetation composition to meadows (excluding road surfaces), but they also contributed to increasing the amount of potentially important edge habitat in the reserve. Although comprising an estimated 46.4 ha in Trois-Fontaines, due to their linear nature we did not consider road allowances as areas used by deer in the home range (i.e., we did not compute a B_i value); rather, we assessed their use by measuring the density of road allowances (m/ha) in each home range (20.1 ± 13.6 m/ha, mean ± SD; $n = 77$), and included this value as a covariate in our analysis. Minor trails and paths used to subdivide forest census plots (Fig. 1) showed little variation in density across the study area; we did not consider these linear features when computing road density in a deer's home range.

We also considered that habitat diversity in the home range (McLoughlin and Ferguson 2000) might be an important covariate in our analysis of relationships with LRS. Using Shannon's H index (McGarigal et al. 2002), for each home range we calculated the proportion of vegetation association i relative to the total number of associations contained in the home range (p_i), and then multiplied by the natural logarithm of this proportion ($\ln p_i$). We summed the resulting product across vegetation associations, and multiplied by -1. Females with all vegetation associations represented within the home range in similar proportions had highest diversity; those having home ranges that focused on a single association had lowest. Strong selection for one vegetation association did not, however, necessitate low diversity in the home range: a value of B_i was dependent on habitat availability in the study area, whereas H was not. We controlled for effects of home range size on H by presenting the diversity index as the residual between H and home range size (H_r).

We wished to model effects of ecological succession in meadows on a deer's response to selecting meadows (B_{mead}); hence, for each deer we calculated the age of meadows when a deer was born (setting the origin in 1976 when monitoring commenced), and planned to include this variable in the relationship between LRS and selection for the home range. The history of meadows probably followed a nonlinear pattern in terms of quality for deer: initially meadows were mowed and fertilized (1976–1982), then just mowed (1982–1991), and finally allowed to undergo succession without management intervention (1991–2000). To reflect this dynamic, we transformed age of meadows in which a deer was born as its natural logarithm. We used this variable to provide an index of the state of meadows during the life span of a deer; however, because conditions early in life are known to influence many aspects of adult life (Albon et al. 1987, 1992, for roe deer see Pettorelli et al. 2002, 2005, Gaillard et al. 2003*b*), we hypothesized that quality of meadows during the first year of life might also engender a cohort effect on LRS. Further, we hypothesized that ln(meadow age) might interact with B_{mead}: as quality changed within meadows through time, LRS of deer may have been affected by their strength of selection for the resource. Therefore, we included ln(meadow age) × B_{mead} as a potential second-order effect in the relationship between LRS and composition of the home range.

Analysis and model selection

Standardized resource selection indices (B_i values) summed to 1.0; hence, due to problems with multicollinearity, we could not include all values in a GLM with LRS. We also wished to examine only plausible relationships between LRS and B_i values, rather than all models described by all possible combinations of predictors. We had a priori expectations that selection for meadows rich in forage would positively relate to LRS; however, we had no data to presume relationships with remaining B_i values, which may have been based on attributes of cover or, in some cases, seasonal food availability. Therefore, we used principal components analysis (PCA) in combination with the negative binomial model outlined below to initially suggest B_i values most likely to explain variation in LRS. Based on Akaike's Information Criterion adjusted for sample size (AIC$_c$; Burnham and Anderson 2002), we determined which B_i values associated with principal components (first two axes) were more or less likely to explain variation in LRS, and incorporated only the likely predictors of LRS in subsequent analyses.

We had initially considered a Poisson regression model to relate LRS to variables describing individual-based habitat selection (McLoughlin et al. 2006). However, the high variance of LRS among female roe deer (Gaillard et al. 1998*a*, 2000*a*) led to a marked deviation from a Poisson distribution. The most complex model considered was thus strongly overdispersed (residual deviance was 318.96 on 69 degrees of freedom, ratio 4.62); therefore, we elected to fit a negative binomial (overdispersed Poisson) model to the data (McCullagh and Nelder 1989).

Following the preliminary considerations just outlined, we used AIC$_c$ to identify the most likely subsets of a negative binomial model containing: (1) standardized resource selection indices (identified a priori for meadow, thicket, and mature open forest, respectively: B_{mead}, B_{thick}, and B_{mof}; see *Results*); (2) density of road allowances in the home range (m/ha); (3) habitat diversity within the home range controlling for home range size (H_r); (4) ln(meadow age); and (5) the interaction term ln(meadow age) × B_{mead} (Table 2). We computed Akaike weights (w_i) to provide an approximate probability that each candidate model was the best of the proposed set (Burnham and Anderson 2002). We adopted a bootstrapping approach to cross-validation to evaluate predictive success of the selected model, whereby for each of 1000 iterations we randomly divided our sample into two groups with ratio 3:1, and trained the selected model on the larger of the two samples (75% of the data). For each iteration, validation was based on the remaining testing set (25%

TABLE 2. Ranking of the top eight candidate negative binomial models describing the relationship between LRS and composition of the home range for female roe deer ($n = 77$) at Trois-Fontaines, France, 1976–2000.

Model	Model predictors†	k	$\mathrm{AIC_c}$	$\Delta_i\mathrm{AIC_c}$	w_i
1	B_j + road allowance + ln(meadow age)	7	473.65	0.00	0.57
2	B_j + road allowance + H_r + ln(meadow age)	8	476.04	2.39	0.17
3	$B_j + H_r + B_{\mathrm{mead}} \times$ ln(meadow age)	8	476.14	2.49	0.16
4	B_j + road allowance + $H_r + B_{\mathrm{mead}} \times$ ln(meadow age)	9	478.60	4.96	0.05
5	B_j + road allowance + H_r	7	479.50	5.85	0.03
6	B_j + ln(meadow age)	6	482.84	9.19	0.01
7	B_j	5	483.61	9.96	0.00
8	road allowance + ln(meadow age)	4	484.66	11.01	0.00

Notes: Predictors included B_i values selected a priori (B_j) for meadow, thicket, and mature open forest, respectively (B_{mead}, B_{thick}, and B_{mof}), density of road allowances in the home range (road density), diversity in composition of the home range standardized by home range size (H_r), the age of meadows in the year a deer was born (ln[meadow age]), and the interaction between a deer's selection for meadows (B_{mead}) and modifying effects of ln(meadow age). The number of parameters (k) includes the model intercept, predictors, and the overdispersion parameter, Θ. The parameter $\Delta_i\mathrm{AIC_c}$ refers to the change in $\mathrm{AIC_c}$ between model i and the model with lowest $\mathrm{AIC_c}$ score. $\mathrm{AIC_c}$ weights (w_i) sum to 1.0 over all possible models. The $\mathrm{AIC_c}$ of the null model was 489.87.

† For models with interactions, first-order terms of interacting parameters are included in model subsets.

of data). We used the Spearman rank correlation coefficient (r_s) between predicted and observed LRS among withheld deer (testing set) to assess the predictive capacity of the selected model, which we presented as a distribution of bootstrapped estimates of r_s.

Statistical analyses were conducted using the open-source programming application R, version 2.3.1 (R Foundation for Statistical Computing 2006). Relevant software included that of the "ade4" library (Chessel et al. 2004) and the "glm.nb" routine of the "MASS" library (Venables and Ripley 2002). Our cross-validation routine was also written in R 2.3.1.

RESULTS

Habitat use (and thus selection) at the level of the home range was highly variable among female roe deer (Table 1). On average, however, study animals significantly preferred meadow habitat and avoided mature open forest (95% confidence intervals did not overlap the random expectation of $1/R$ [i.e., 0.20]). The first two components of PCA incorporating B_i values explained 62.9% of the variance (Fig. 2). The first component (39.6% of variance explained) reflected results presented in Table 1, and opposed selection for meadows and mature open forest. The second component described a gradient of selection for mature closed forest to that of young forest. $\mathrm{AIC_c}$ of regression models of LRS vs. the first and second principal components indicated that variables correlating with the first axis were expected to have the largest influence on LRS: $\mathrm{AIC_c}$ was 486.56 for the first component-only model ($w = 0.91$), and 491.23 for the second component-only model ($w = 0.09$). For subsequent analysis of relationships with LRS, we excluded the main opposing variables of the second axis and retained B_i values for meadows, thickets, and mature open forest. Minimum tolerance among these variables, road density, diversity (H_r), and ln(meadow age) was 0.58.

The most parsimonious of subsequent regression models related an individual's LRS to first-order effects of selection for meadows, thickets, and mature open forest; density of road allowances; and age of meadows in the year of a deer's birth (Table 2). We concluded that the top model was sufficiently distant from competing models to be presented as our final model (Table 2); we did not compute a model average. Predictive capacity of this model, estimated as the median correlation (r_s) between predicted and observed LRS among deer of cross-validation samples, was 0.55 (0.38–0.63, upper and lower quartiles).

In the final model, LRS of roe deer was significantly and positively related to their selection for meadows (Table 3). LRS of animals that established home ranges containing any degree of meadows was substantially higher compared to deer that did not (9.71 [8.11–11.31]

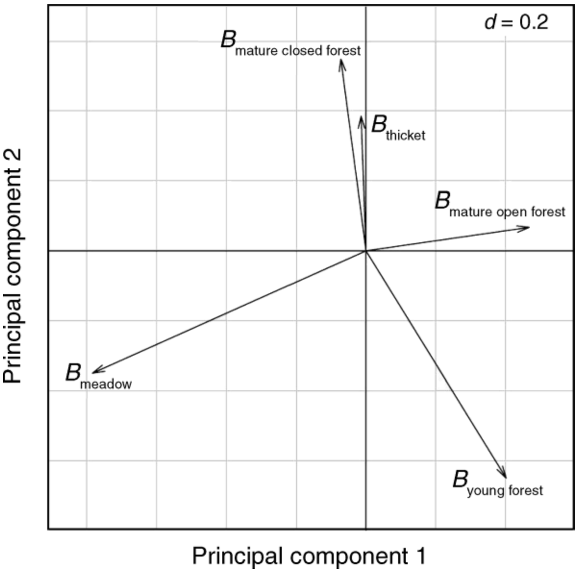

FIG. 2. Projection of values of B_i (probability that an individual would choose resource i over all others, assuming all resources were available in equal proportion) for roe deer ($n = 77$ deer) on the factor plane (1×2), illustrating gradients in patterns of selection for vegetation associations included in the home range. The scale of the plot is indicated by the grid, with dimensions d (unitless, from PCA) of 0.2.

TABLE 3. Estimates, standard errors of the mean, and significance of parameters of Model 1 in Table 2.

Parameter	Estimate	SE	z	P
Intercept	1.367	0.351	3.90	0.0001
B_{mead}	1.316	0.506	2.60	0.009
B_{thick}	1.298	0.646	2.01	0.045
B_{mof}	−1.213	0.674	−1.80	0.072
Road density	0.030	0.008	3.97	<0.0001
ln(meadow age)	−0.320	0.126	−2.55	0.011

Notes: The model describes the relationship between LRS and effects of selection for meadows, thickets, mature open forest (B_{mead}, B_{thick}, and B_{mof}), density of road allowances within the home range (road density), and the age of meadows in the year a deer was born (ln[meadow age]) for female roe deer ($n = 77$) at Trois-Fontaines, France, 1976–2000. The dispersion parameter, Θ, was 2.053 (SE = 0.478).

vs. 3.58 [1.15–6.01], respectively [mean and 95% CI]). LRS was also positively related to a deer's selection for thickets (Table 3). Avoidance of mature open forest significantly improved LRS (Table 3). LRS was strongly related to the density of road allowances within the home range, and inversely associated with the age of meadows when a deer was born (Table 3).

DISCUSSION

The literature is replete with examples of studies linking small-scale resource selection and short-term measures of performance such as energy gained from the environment per unit time (Stephens and Krebs 1986). Only recently, however, has it become more common for researchers to test fitness–habitat relationships using long-term, individual-based components of fitness, such as survival and reproduction, which generally corresponds to an increase in scale of observation (e.g., Conradt et al. 1999, Morris and Davidson 2000, Pettorelli et al. 2003, 2005, McLoughlin et al. 2005, 2006, Fontaine and Martin 2007). To the best of our knowledge, however, no previous study has explained as much variation in LRS using variables of habitat selection as we do here. This suggests to us that higher-order resource selection, such as the selection of the site of a home range during the process of dispersal and the establishment of the bounds of the home range during adulthood, may play a more important role in determining fitness of individuals than previously thought. These results thus support the contention of Morris (2006), based on results of the study by Haugen et al. (2006) of ideal free distribution in pike (*Esox lucius*) among lake basins, that habitat selection at larger spatial scales may be a primary determinant of population dynamics.

Our results suggest a strong association between LRS of female roe deer and home ranges containing high-quality forage, cover, and high contrast or edge (i.e., meadows, thickets, and road allowances). Negative effects of including open mature forest in the home range were probably due to a combination of low food and low cover in this forest type. Compared to other large herbivores, a strong fitness–habitat relationship was expected in response to the life history strategy adopted by roe deer. More specifically, three life history traits of roe deer may explain why females in this species are so dependent on access to habitat of high quality between spring and autumn. First, being income breeders (Andersen et al. 2000), female roe deer cannot rely on body reserves to meet the high energy demands at the end of gestation and early lactation common to most large herbivores (Clutton-Brock et al. 1989). Second, such energy expenditures are comparatively high in roe deer that usually produce twins, whereas most other large herbivores produce singletons (Robbins and Robbins 1979). Lastly, the observed variation in individual fitness of female roe deer is largely determined by the ability of females to wean fawns successfully (Gaillard et al. 1998*a*, *b*, 2000*a*). At least in temperate regions, little among-female variation occurs in litter size (Gaillard et al. 1998*a*) and adult survival is very high throughout most of the reproductive life span (Gaillard et al. 1993, 1998*b*). Pre-weaning survival is thus more sensitive to environmental variation and thereby more variable in polycotous income breeders like roe deer than in monocotous capital breeders like red deer (*Cervus elaphus*) or bighorn sheep (*Ovis canadensis*) (Gaillard et al. 1997, 2000*a*, *b*). Our results agree with the hypothesis that through the close link between access to resources and fawn survival, the relationship between LRS and selection of the home range in roe deer is especially strong.

This conclusion is supported by the less marked predictive capacity of a model of LRS and habitat selection reported for red deer ($r_s = 0.44$; McLoughlin et al. 2006) vs. results of this study ($r_s = 0.55$). Note, however, that in comparison to McLoughlin et al. (2006), the analysis presented here was constrained to include data only from the seasonally critical period of maternal care (i.e., from spring to autumn). This approach may have increased the power of analysis or the effect size of coefficients of independent variables that covaried with juvenile survival, although seasonal variation in the home range of female roe deer in temperate forests remains very low (the only exception being a slight increase in size during winter; Pellerin [2005]). Further, we conducted our analysis while controlling for density, and in so doing probably avoided density-related deterioration of the fitness–habitat relationship, as was shown by McLoughlin et al. (2006).

Our demonstration of a strong relationship between LRS and habitat selection suggests that, at least when it comes to selection for the home range during the period of maternal care, female roe deer at Trois-Fontaines do not fit the ideal-free distribution model of Fretwell and Lucas (1970), which predicts equal fitness among deer, irrespective of habitat selection. Results of Pettorelli et al. (2003) and Nilsen et al. (2004) suggest that female roe deer are likely to deviate from ideal-free distribution because of less-than-free movement among available vegetation associations. This is supported by our finding that, for most vegetation associations, mean values of use correlated strongly with availability (Table 1), an observation expected if randomly sampled animals were not free to disperse and establish home ranges throughout the study area. The sedentary nature of roe deer (Strandgaard 1972) is likely to have influenced our results by increasing among-individual variation in resource selection patterns. This might explain why 24.7% (19/77) of female roe deer did not possess any meadows in the home range, despite the obvious advantages of meadows to LRS. Hence, higher-order (home range) selection in roe deer, in addition to reflecting learned and innate preferences (Hall et al. 1997), is also likely to be constrained by factors independent of individual behavior. One obvious contributing factor is the maternal environmental effect of where an individual is born. The potentially important role of maternal environmental effects on the process of higher-order habitat selection invites further research (e.g., Brown and Shine 2007), including how such effects may lead to violations of the assumptions of the ideal-free distribution. In this sense, the "selection" of a home range may be better qualified as "use" of a home range.

Gaillard et al. (2003*b*) reported a decline in year-specific reproductive success with time for female roe deer at Trois-Fontaines. Our results suggest that this density-independent decline in reproductive success may, in part, be explained by a decline in quality of meadows during the course of study. However, not all deer in our sample possessed meadows in their home range; yet, these animals also exhibited a cohort effect in LRS. Interestingly, declines in LRS through time (negative binomial model of LRS vs. year of cohort) were stronger for females without meadows in their home range (slope -0.247 ± 0.106, mean ± SE; $n = 19$, $P = 0.020$) compared to females with access to meadows (slope -0.044 ± 0.028, $n = 58$, $P = 0.121$). These results suggest that, despite declines in meadow quality through time, meadows may have acted as a buffer of the time-dependent cohort effect observed by Gaillard et al. (2003*b*). We have yet to develop a complete understanding of cohort effects on roe deer survival and reproduction at Trois-Fontaines.

Through annual removals of unmarked deer, observed patterns in habitat selection were probably freed from constraints imposed by intraspecific competition, permitting individuals, dependent on individual perceptions of availability, to select those resources intrinsically valuable to them for survival and reproduction. The concept of "intrinsic habitat value," defined here as the most important resources to individual survival and reproduction in the absence of density dependence in habitat selection, warrants further research. Due to density effects, it may not be unusual to find a lack of a relationship (or even a negative association) between individual performance and habitat selection (e.g., LRS and red deer; Conradt et al. 1999, McLoughlin et al. 2006). The value of habitat to animals is the subject of much debate (Garshelis 2000), and merit in the concept of intrinsic habitat value may lie in its application as a definition. Further, the concept might provide guidance to conservation planning and habitat protection by highlighting resources most beneficial to population growth when abundance is at its most critical (lowest) level. Determination of intrinsically valuable habitat may be accomplished through study design (this study) or by controlling for density effects in models of fitness and habitat selection (McLoughlin et al. 2006). From a practical perspective, analyses of intrinsic habitat value may be best directed at larger ecological scales (higher-order habitat selection), which may make it easier to identify landscape features amenable to reserve design and habitat conservation. However, the scale of habitat selection that best relates to individual fitness has yet to be determined. How best to match scales of habitat selection with the many different measures of performance is an issue of potential importance to habitat ecology.

Expanding the search for links between fitness and habitat to higher orders of selection allows for the inclusion of direct measures of Darwinian fitness in testing the fitness–habitat relationship, and the exploration of new concepts in habitat ecology. Here we present a particularly strong relationship between LRS of female roe deer and selection of the home range during the period of maternal care. We believe this to reflect, in part, the life history and space use tactics of roe deer relative to other related species, although the way in which we conducted our analysis (controlling for density effects, choice of model, focusing on the home range during the critical period of fawn development) was also probably important. We identify attributes of the home range that are most important to fitness of female roe deer in the absence of density dependence in habitat selection. Identification of important resources in this context ("intrinsic habitat value") may have merit in providing a standard definition of the value of habitat to animals.

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