



Partial migration or just habitat selection? Seasonal movements of roe deer in an Alpine population

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The European roe deer (*Capreolus capreolus*) responds to environmental conditions that vary in time and space across its distributional range, generating many different space use patterns. To test the expectation that variation in movement patterns should track changes in environmental conditions, we used the net squared displacement metric to identify the factors shaping observed movement patterns of roe deer in the French Alps. Based on 5 years of data from 25 radiomonitored roe deer (54 individual-years), we found that movements were longest in spring and summer when the normalized difference vegetation index (NDVI) was higher and shortest in autumn and winter when NDVI was lower and snow cover was present. Roe deer displayed long displacements toward high elevations with gentle slope when the NDVI was higher. The higher quality food resources at higher elevations may have compensated for the energy costs of those movements. Contrary to previous studies on roe deer in mountain ranges, we showed that roe deer movements in the northern French Alps should be interpreted as within home range habitat selection (48 cases; 89%) rather than as partial migration because very few deer (6 cases; 11%) stabilized their activity in distinct home ranges across seasons.

Au sein de son aire de répartition, le chevreuil (*Capreolus capreolus*) rencontre des conditions environnementales variables et contrastées qui engendrent une grande variété de patrons d'utilisation de l'espace. Pour tester la prédiction que les chevreuils devraient ajuster leurs mouvements en fonction des variations spatio-temporelles de leurs ressources, nous avons identifié les facteurs expliquant les mouvements de chevreuils en milieu de montagne. Nous avons pour cela utilisé la métrique du Déplacement Net élevé au carré (NSD). Grâce au cinq années de suivi télémétrique de chevreuils dans les Alpes françaises (54 individus.années), nous avons démontré que les mouvements des animaux étaient plus grands au printemps et en été lorsque l'indice de végétation (NDVI) augmentait puis plus courts en automne et en hiver lorsque le NDVI diminuait et que le couvert nival était présent. Lorsque le NDVI augmentait, les chevreuils orientaient leurs longs déplacements vers des milieux situés en altitude avec une faible pente. Ce type de mouvement suggère que les bénéfices associés à l'utilisation de ressources de meilleure qualité dans les habitats en altitude permettent de compenser l'augmentation des coûts énergétiques provoqués par le déplacement. Contrairement aux précédentes études sur l'utilisation de l'espace par le chevreuil en milieu de montagne, nous avons montré que les mouvements des chevreuils au sein de notre aire d'étude correspondaient au processus de sélection d'habitat de troisième ordre (48 cas; 89%) plutôt qu'à de la migration partielle, puisque très peu d'individus (6 cas; 11%) avaient stabilisé leurs déplacements au sein de domaines vitaux distincts au cours des saisons.

Key words: displacement, elevation, home range, migration, NDVI, net squared displacement, resource availability

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Identifying the factors influencing movements of animals is currently one of the main challenges of ecology (e.g., Dingle and Drake 2007; Nathan et al. 2008). Most previous works have focused on the influence of environmental factors such as landscape structures, cover types, or climate on patterns of both movements (e.g., Börger et al. 2008; Nathan et al. 2008) and space use (Hewison et al. 2001; Morellet et al. 2013) across different spatiotemporal scales (see Owen-Smith et al. 2010 for a review). In large herbivores, previous studies have consistently demonstrated that individuals adjust their pattern of space use in response to environmental conditions that influence both habitat quality and resource availability (e.g., Cagnacci et al. 2011; Bischof et al. 2012).

Resources vary greatly in space and time in strongly seasonal environments found at high elevations or at high latitudes (Albon and Langvatn 1992). This leads large herbivores to track environmental changes to benefit from higher resource quality in spite of the energetic costs associated with movements (Myrsterud et al. 2001; Bocci et al. 2010; Bischof et al. 2012). As a general rule, large herbivores move from low-elevation winter ranges to distinct high-elevation summer ranges to track increasing resource quality and availability (e.g., red deer *Cervus elaphus*—Myrsterud et al. 2001; Bischof et al. 2012, roe deer *Capreolus capreolus*—Ramanzin et al. 2007, moose *Alces alces*—Bunnfeld et al. 2011, and white-tailed deer *Odocoileus virginianus*—Sabine et al. 2002). These seasonal movements are mainly driven by food availability (Bischof et al. 2012), temperature (Morellet et al. 2013), day length (Morellet et al. 2013), and snow accumulation (Myrsterud et al. 1997).

Roe deer are the most widespread ungulates in Europe with a distributional range extending from southern Spain to northern Scandinavia, leading different populations to experience a large diversity of environmental conditions (Linnell et al. 1998). Such high variation in environmental conditions generates a large range of population-specific space use patterns, demonstrating the behavioral plasticity of roe deer (Hewison et al. 1998). Because female roe deer are income breeders (they do not store any body reserve to meet the high energetic expenditures required by reproduction—Andersen et al. 2000), they should be especially responsive to spatiotemporal variation in resource availability during spring–summer, when energetic costs of late gestation–early lactation peak (Mauget et al. 1999). Although seasonal migration is commonly observed in roe deer populations occupying mountainous and northern environments (Wahlstrom and Liberg 1995; Myrsterud 1999; Ramanzin et al. 2007; Carvalho et al. 2008), the proportion of migrants is quite variable both between and within populations (Cagnacci et al. 2011). Partial migration (only a proportion of individuals migrate, whereas the others remain within their home range—Dingle and Drake 2007) seems to be the rule in roe deer populations inhabiting highly seasonal environments (Myrsterud 1999; Ramanzin et al. 2007), but roe deer may also make frequent shifts between different ranges within a season in response to the benefit/cost ratio associated with movements. The occurrence of multiple shifts between ranges for a given individual within

a given season might be interpreted as 3rd-order habitat selection (sensu Johnson 1980), whereas a stabilization of a given individual within one well-defined range in a given season might rather be interpreted as conditional or facultative migration (sensu Dingle and Drake 2007).

In the northern Italian Alps, Ramanzin et al. (2007) reported that 40% of monitored roe deer displayed migration. However, methods used to classify an individual as resident or migratory have not been consistent across studies, which prevent reliable comparisons (Myrsterud 1999; Ramanzin et al. 2007; Cagnacci et al. 2011; Bischof et al. 2012). As an example, both Myrsterud (1999) and Ramanzin et al. (2007) considered individuals having nonoverlapping seasonal home ranges as migratory, whereas Cagnacci et al. (2011) used a clustering procedure to identify nonoverlapping ranges. Moreover, the interpretation of movements between ranges is disputable because individuals that shift between ranges can be classified as migratory (Ramanzin et al. 2007; Cagnacci et al. 2011), resident, or belonging to an “other category” (Bischof et al. 2012).

Based on 5 years of radiolocating roe deer equipped with VHF radiotransmitters in the northern French Alps, we aimed to identify the specific factors shaping roe deer movements. To do that we used, the net squared displacement (NSD—Bunnfeld et al. 2011; Börger and Fryxell 2012). One of the main advantages of this method is its capability to distinguish between various movement behaviors of an animal without using arbitrary cutoff criteria (Bunnfeld et al. 2011). Roe deer should adapt their movements according to topography and snow accumulation during winter (Myrsterud 1999; Cagnacci et al. 2011). Roe deer we studied faced a variable topography and experienced harsh winter conditions, low temperature, and high snow accumulation. As a consequence, we expected roe deer to adjust their movements in relation to seasonal changes in climatic conditions and spatiotemporal variation in resource availability and quality. More specifically, we tested 5 predictions. First, we expected the range of movement to vary across seasons, with shorter movements during the autumn–winter period when energetic cost associated with movements is not compensated by benefits (access to high-quality resource) than during the spring–summer period. Second, because increasing snow depth increases the costs of locomotion, we expected movements to be restricted above a snow depth threshold (Parker et al. 1984). Third, because female roe deer require high forage quality in spring–summer to meet their high energetic needs (Andersen et al. 2000), we expected roe deer to benefit from larger movements with higher resource availability (Cagnacci et al. 2011). Fourth, we expected increased movements toward high elevation during the growing vegetation period because the energetic costs of movements should be then compensated by benefits of reaching high forage quality at high elevation (Albon and Langvatn 1992; Bocci et al. 2010). Finally, because moving in steep slope is energetically costly (Parker et al. 1984), we expected the magnitude of roe deer movements to be inversely related to the slope (Cagnacci et al. 2011).

MATERIALS AND METHODS

Study area.—We conducted this study in the National Game and Wildlife Reserve of Les Bauges (hereafter referred as NGWR, 45°40'N, 6°13'E), which is part of Les Bauges Natural Regional Park in Les Bauges mountain range, a typical prealpine range of the northern French Alps. Les Bauges Natural Regional Park covers a total of 81,000 ha including the 5,205 ha of the NGWR. Because of mountain topography, the NGWR experiences typical Alpine climate with a mean annual temperature of 7.9°C, lowest temperature (in January) of -1.1°C, warmest temperature (in July) of 17.2°C, and total annual rainfall of 1,519 mm. The average daily temperature is below 0°C for about 148 days a year, and snow accumulation reaches up to 2.8 m between mid-November and late April. Elevations of the NGWR vary from 700 to 2,200 m and 4 distinct plant assemblages are found along this elevation gradient. At lower elevation, the landscape is composed of a mosaic of agricultural lands, separated by forest patches made of a large diversity of ligneous and semiligneous species preferred by roe deer. Between 700 and 1,400 m, the forest cover provides a poor habitat for roe deer by being largely dominated by ligneous species like beech (*Fagus sylvatica*) and fir (*Abies alba*), with only few fragmented patches of plants preferred by roe deer like green alder (*Alnus viridis*) and semiligneous species such as ivy (*Hedera helix*), hazel bush (*Corylus avellana*), and bramble (*Rubus* sp.). Up to 1,400 m, the forest is replaced with open pastures, which are grazed by domestic animals (cattle: *Bos taurus*, goats: *Capra aegagrus*, and sheep: *Ovis aries*) from June to September. Other shrubby species preferred by roe deer are present, including green alder, maple (*Acer* sp.), willow (*Salix* sp.), bilberry (*Vaccinium myrtillus*), and rhododendron (*Rhododendron ferrugineum*), which are scattered up to 1,400 m. Between 1,600 and 1,900 m, the vegetation becomes scarce with cliffs including only small patches of alpine grassland. In addition to roe deer, the NGWR hosts populations of chamois (*Rupicapra rupicapra*; $n = 2,000$), mouflons (*Ovis gmelini musimon*; $n = 500$), and wild boars (*Sus scrofa*). Red deer are occasionally found in the study area. Although red deer can have negative effects on roe deer performance (Richard et al. 2010), Redjadj et al. (2014) did not detect any evidence of food competition between deer species in the study area.

Monitoring roe deer using VHF collars.—To monitor their movements, we captured roe deer during winters 2003–2004, 2004–2005, and 2005–2006 using both drive netting and falling nets baited with salt licks. Twenty-two adult (11 males and 11 females) and 3 juvenile (< 1 year, all males) roe deer were caught and fitted with a Televilt TXH-3 radiocollar (Followit, Lindesberg, Sweden). Roe deer were monitored between January 2004 and November 2008 with a TONNA 5-element antenna attached to a Televilt RX 900 (Followit) or to a Yaesu FT-290R receiver (Yaesu, Cypress, California). From April to October, when roe deer are the most active (Cederlund 1989), animals were located once a day, whereas from November to April, when the presence of snow was expected to limit roe deer movements (Mysterud 1999), animals were only located once a week. Equal numbers of locations were obtained for each roe

deer in each of the following periods: 0100–0500, 0500–0900, 0900–1300, 1300–1700, 1700–2100, and 2100–0100h. These periods accounted for possible variation in the daily activity patterns (Carvalho et al. 2008). When locating an animal, a minimum of 3 azimuths were recorded to obtain precise location coordinates (confidence area: 0.61 ± 1.23 [SD] ha—White and Garrott 1990). Because 3 individuals died just after release, the final data set included 22 roe deer (9 adult males, 11 adult females, and 2 juvenile males) for a total of 11,439 locations (18.1 ± 15.2 locations individual⁻¹ month⁻¹ year⁻¹). Since roe deer were monitored for consecutive years, we obtained a total of 54 individual-years (10 individuals in 2004, 14 in 2005, 16 in 2006, 10 in 2007, and 4 in 2008, with 211.8 ± 91.9 locations individual⁻¹ year⁻¹). Because both juvenile males dispersed 1 year after they were captured, we decided to remove every location before this event from the analyses to avoid any confounding effect of natal dispersal (Cagnacci et al. 2011).

Explanatory variables.—We selected normalized difference vegetation index (hereafter referred as NDVI), temperature, snow depth, slope, and elevation to model roe deer movements because they are all likely to shape spatiotemporal variation in resource availability (Pettorelli et al. 2005; Cagnacci et al. 2011; Morellet et al. 2013). Weather stations within the study area were mostly located in valleys and did not correspond to weather conditions at roe deer locations. We thus measured snow depth each day directly on site during the telemetry survey. Snow depth was categorized into 5 classes (0, 1–20, 21–40, 41–60, and > 60 cm). We measured slope and elevation at each location using digital elevation models with a resolution of 30 m. Slope and elevation were extracted using the “adehabitat” package in R (Calenge 2006). Slope and elevation were included as the difference of slope value and elevation value for each subsequent location. As the forest cover situated between 700 and 1,400 m is mainly composed of beech, a plant species not preferred by roe deer (Pellerin et al. 2010), we expected individuals that move toward high elevation to make long movements to reach rapidly the more suitable habitat situated at higher elevations. As we expected a nonlinear relationship between NSD and elevation, we included this variable using both linear and quadratic terms in the models. NDVI being a relevant metric to describe plant phenology (Pettorelli et al. 2005), we used the NDVI to estimate variation in resource availability across the study period. The NDVI was calculated every 15 days with a pixel resolution of 250 m. We then calculated the mean NDVI value for the entire study area and assigned it to the appropriate group of locations. Variables such as temperature or day length are also tightly linked to resource availability and are thereby likely to affect roe deer space use pattern (Cagnacci et al. 2011; Morellet et al. 2013). Thus, NDVI was highly correlated with both day length ($r = 0.727$) and temperature ($r = 0.731$). To avoid multicollinearity problems (Graham 2003), we only retained NDVI in the analyses because it provides an accurate index of temporal variation in resource availability (Pettorelli et al. 2005). Moreover, we also included year as a fixed factor (5 levels) to account for yearly differences in NSD caused by factors that

have not been measured in this study (e.g., roe deer density—Cagnacci et al. 2011). Finally, we included sex as a fixed factor (2 levels) to account for sex differences in behavior (Hewison et al. 1998; Liberg et al. 1998).

Using the NSD as a measure of movement.—We quantified individual movements using the NSD because it is especially well suited to different sampling intervals between locations and can be applied to a wide range of data (Börger and Fryxell 2012). We used the north $N(t)$ and east $E(t)$ coordinates of the 1st location, and then the $N(t + n)$ and $E(t + n)$ coordinates of subsequent locations, with n being the total number of VHF locations for a given roe deer (Bunnefeld et al. 2011). The NSD was calculated separately for each individual-year as the square net Euclidian distances (assuming a straight line) between the 1st location and the subsequent locations (see Supporting Information S1). The 1st location of each animal was recorded in the winter range at least 1 month after they had been captured to avoid any confounding effect of stress related to capture. Because NSD values are sensitive to the 1st location of an animal, we checked visually for each individual that the 1st location was situated inside the home range (Bunnefeld et al. 2011) and had not been collected during a migration period or

an excursion (see Supporting Information S1). We computed NSD by using the “adehabitat” package (Calenge 2006).

Data analyses.—We used linear mixed models using the nlme package (Pinheiro et al. 2015) in R (version 3.0.1—R Development Core Team 2013) to model the influence of environmental factors on the NSD (Table 1). We log-transformed the NSD to obtain a Gaussian distribution. Our independent variables included continuous variables such as difference in elevation between subsequent locations and difference in slope between subsequent locations and NDVI to account for seasonal variation in NSD (Table 1). We also included sex (2-level factor) and snow depth (5-level factor) as fixed factors. We developed 14 a priori candidate models that included the environmental variables most likely to describe variation in NSD and we presented the 4 best models and the null model (Table 2). We ranked candidate models using the Akaike information criterion (AIC) and determined ΔAIC and AIC weights (Table 2; Burnham and Anderson 2002). When 2 candidate models had a $\Delta AIC < 2$, they were considered as equivalent and we retained the model with the smallest number of parameters to satisfy parsimony rules (Burnham and Anderson 2002). We built a general model that included individual identity as a

Table 1.—Variables expected to influence roe deer (*Capreolus capreolus*) movements in the National Game and Wildlife Reserve of Les Bauges mountain range (Savoie, France) during the monitoring period (2004–2008) that were included in the models. NDVI represents the normalized difference vegetation index.

Independent variable	Biological effect	Expectation
Elevation (difference in elevation)	Positively associated with resource quality	Presence of high-quality forage at high elevation should influence movement patterns of roe deer during the growing season
Slope (difference in slope)	Negatively associated with the energetic costs of movements	Movements should be less costly with gentle slope and more with steep slope
NDVI	Positively associated with resource availability because it measures the photosynthetic activity. Also associated with seasonality	Resource availability increases with photosynthetic activity. Movement should vary depending on seasonal constraints with shorter movement when snow depth increases and NDVI index decreases
Snow depth	Negatively associated with resource availability. Increase in the energy costs of movements	Resource availability should decrease when snow cover is present. The energetic costs associated with movements should increase with snow depth
Sex	Associated with deer behavior	Roe deer movement should differ between sexes during rut. Males are known to perform longer movements than females during this period
Year	Movement pattern should also vary according to factors that are year-dependent (other than those cited above)	Roe deer movement should differ according to yearly variation in factors that have not been measured in this study (like reproductive status, roe deer density, home range quality, or environmental conditions)

Table 2.—Candidate general linear mixed models to investigate variation in the net squared displacement (NSD, on a log-scale) of roe deer (*Capreolus capreolus*) in the National Game and Wildlife Reserve of Les Bauges mountain range (Savoie, France) monitored between 2004 and 2008. Roe deer identity ($n = 22$ individuals) was included as a random factor. Candidate models i are ranked according to the Akaike information criterion (AIC). k_i represents the number of parameters of model i , ΔAIC_i is the difference in AIC compared to the most parsimonious model, and w_i refers to the Akaike weight. NDVI represents the normalized difference vegetation index.

No.	Model	k_i	AIC	ΔAIC_i	w_i
2	NSD ~ NDVI + Elevation ² + Slope + Snow + Year	5	37481.78	0	0.58
1	NSD ~ NDVI + Elevation ² + Slope + Snow + Sex + Year	6	37482.44	0.66	0.42
3	NSD ~ NDVI + Elevation ² + Snow + Year	4	37495.81	-14.03	0.00
4	NSD ~ NDVI + Elevation ² + Snow + Year + Sex	5	37496.47	-14.69	0.00
Intercept	NSD ~ 1	0	38353.91	-872.13	0.00

random factor to account for pseudoreplication (sensu Hurlbert 1984) and individual heterogeneity, which is usually large in spatial ecology (Cagnacci et al. 2011; Bischof et al. 2012). We also included a 1st-order autoregressive process (AR1) using Julian date as a measure of time to account for the positive autocorrelation between successive locations. Finally, we used a variance inflation factor (VIF) by removing independent variables that had a VIF > 10 (Neter et al. 1996) to account for colinearity problems (Graham 2003). According to Bunnefeld et al. (2011), we considered that an individual migrated when NSD was close to zero during winter (animal within its winter range), then during spring its NSD increases (animal migrating) to remain stable during summer (animal within its summer range), and then decreases during the autumn (animal migrating) to return to a value close to zero (animal back to its winter range). When an animal had a NSD value equal or close to zero

during the summer period (return to its original position), we considered any movement as belonging to a 3rd habitat selection process.

RESULTS

As we predicted, NSD varied among seasons. Roe deer had longer movements in spring and summer and shorter ones in autumn and winter when energetic costs associated with locomotion were highest (Fig. 1A). Model 2, which included the effects of elevation, slope, NDVI, snow depth, and year on observed variation in NSD, was the most parsimonious model for predicting NSD, with the highest AIC weight (Table 2). As expected, NSD was negatively influenced by snow depth, indicating that the costs of movements increased when snow depth was above 20cm (Table 3). Likewise the positive relationships between

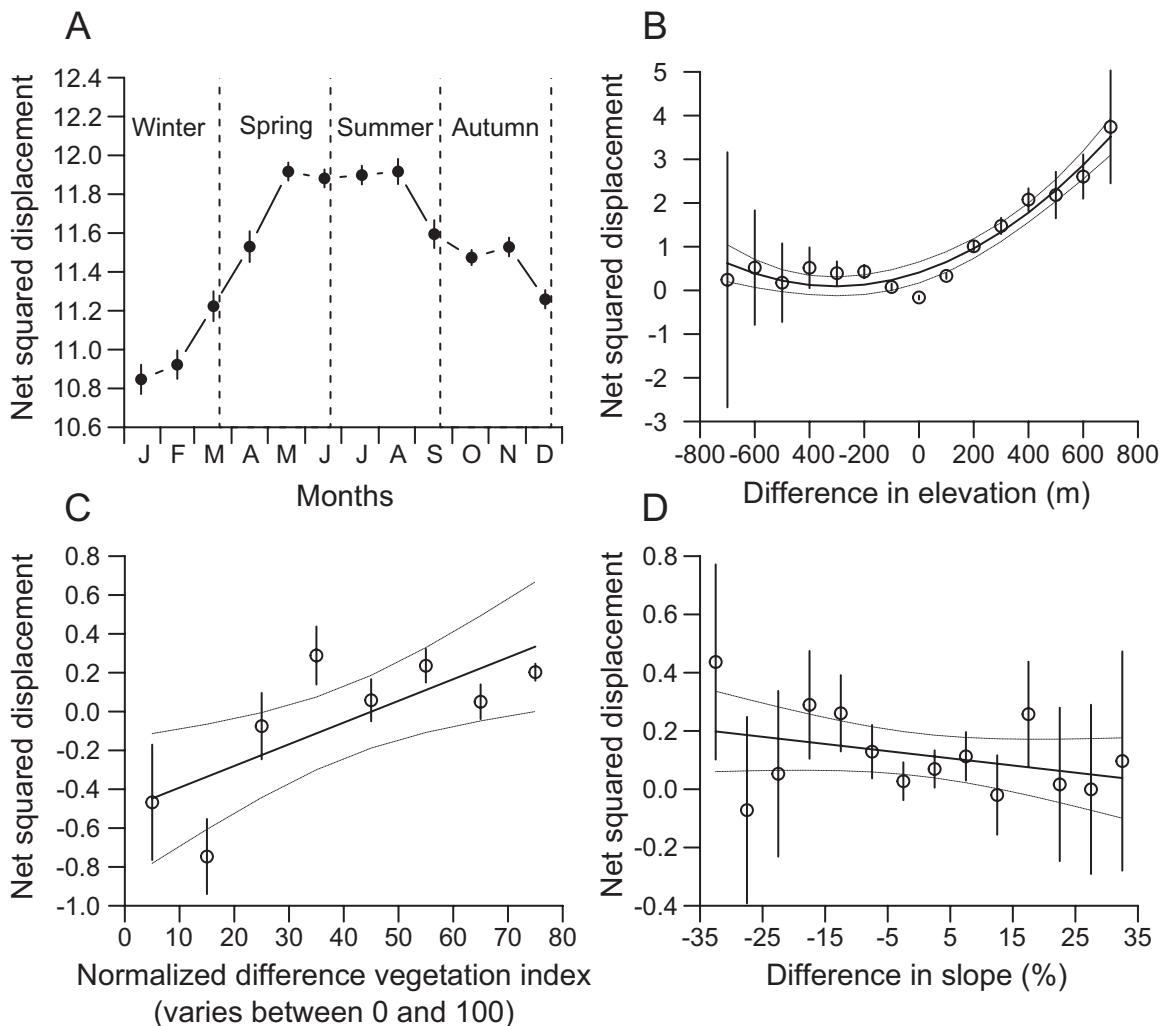


Fig. 1.—A) Mean time-specific variation in the net squared displacement (NSD) of the 22 roe deer (*Capreolus capreolus*) monitored in the National Game and Wildlife Reserve of Les Bauges mountain range (Savoie, France) between 2004 and 2008 (dots represent the mean NSD value for each month and the thin vertical black lines represent their standard errors). B), C), and D) The relationship between the NSD of the 22 roe deer and the covariates included in the selected model: difference in elevation (m), normalized difference vegetation index (NDVI; variation from 0 to 100), and difference in slope (percent). The middle curve corresponds to the NSD values estimated by the selected model according to the residuals effect of the focal covariate, whereas upper and lower curves correspond to the 95% confidence limits. The empty dots represent the mean NSD values and the thin vertical black lines represent their standard errors.

Table 3.—Coefficient (β) and associated standard error (SE) of environmental factors that best explained observed variation in the net squared displacement of roe deer (*Capreolus capreolus*) in the National Game and Wildlife Reserve of Les Bauges mountain range (Savoie, France) monitored between 2004 and 2008. The value of temporal autocorrelation in successive locations was $\phi = 0.72$. NDVI represents the normalized difference vegetation index.

Variables	Terms	β	SE	P
	Random effect	—	1.24	—
Covariates	Intercept	10.10	0.24	< 0.001
	NDVI	0.013	0.0016	< 0.001
	Elevation	0.002	0.00001	< 0.001
	Elevation ²	0.000004	0.0000004	< 0.001
	Slope	-0.003	0.0008	< 0.001
Snow depth	1–20 cm	0.088	0.063	0.16
	21–40 cm	-0.380	0.103	< 0.001
	41–60 cm	-0.259	0.119	0.029
	> 60 cm	-0.653	0.199	< 0.01
Year	2005	0.582	0.0934	< 0.001
	2006	-0.559	0.100	< 0.001
	2007	-0.692	0.124	< 0.001
	2008	-0.958	0.178	< 0.001

NSD and elevation (Fig. 1B) and between NSD and NDVI (Fig. 1C) supported our hypothesis (Table 3) and indicated that long movements were oriented toward high elevation (range of elevation used by roe deer varied from 724 to 1,825 m) mostly during the vegetation growth period when resource availability was highest. Finally, we found that NSD declined with slope, meaning that long movements potentially costly in energy were oriented away from areas with lower slope (Table 3; Fig. 1D). Sex did not have any detectable influence on NSD. The value of temporal autocorrelation in successive locations was $\phi = 0.72$. When interpreting NSD pattern of each individual (Supporting Information S1), we found that for a total of 54 individual-years, 6 migrated (11%) and 48 (89%) had movement patterns that matched a 3rd-order habitat selection process.

DISCUSSION

Consistent with our 1st expectation, roe deer movement patterns were associated with seasonal variation in environmental conditions. Movements were shorter during autumn and winter and longer during spring and summer when photosynthetic activities were highest. Roe deer were thus able to adjust their movements in response to seasonal constraints that influence the cost/benefit ratio associated with movements (Mysterud 1999; Ramanzin et al. 2007). During winter, roe deer moved shorter distances when snow depth was deeper than 20 cm. Roe deer thus reduced their movements when snow depth reached a critical level, likely because of increased energetic movement cost in deep snow, as previously reported for other large herbivores (Parker et al. 1984; Telfer and Kelsall 1984; Holand et al. 1998; Massé and Coté 2013). Snow depth in highly seasonal environments plays a major role on spatial use not only by roe deer (Mysterud et al. 1997; Ramanzin et al. 2007) but also by other large herbivores (e.g., mule deer *Odocoileus hemionus*—Nicholson et al. 1997, white-tailed deer—Telfer and Kelsall 1984; Sabine et al. 2002; Massé and Coté 2013, and red deer—Bocci et al. 2010) and by carnivores (e.g., lynx *Lynx lynx*—Murray and Boutin 1991 and coyote *Canis latrans*—Crête and

Larivière 2003) by influencing both resource availability and energetic costs of locomotion.

Moreover, our results demonstrated that the increase in winter home range size previously reported in roe deer inhabiting strongly seasonal environments (Ramanzin et al. 2007; Morellet et al. 2013) did not necessarily involve longer movements but could rather result from increased frequency of short movements over a larger range (Cederlund 1982; Guillet et al. 1996). Such behaviors might correspond to a general tactic of space use by roe deer inhabiting seasonal environments with snowy winters probably to maximize resource access while attempting to decrease the costs of locomotion. Indeed, Guillet et al. (1996) found that roe deer home range size increased during winter, whereas they tended to reduce their movements in severe snow conditions (Cederlund 1982; Ramanzin et al. 2007). Such a decrease in the activity pattern during the winter season is a common tactic for other large herbivores to reduce energy costs associated with severe winter conditions (e.g., moose—Cederlund 1989 and white-tailed deer—Beier 1990; Massé and Coté 2013). However, contrary to roe deer, moose and white-tailed deer also reduced their home range size during this period.

When NDVI increased, roe deer movements became longer. Roe deer movements increased with NDVI in spring and summer probably because snow did not restrain movements any longer. Moreover, the availability of high-quality food is higher in spring and summer than winter in mountainous environments. When food resources are abundant, ungulates tend to move less (Owen-Smith et al. 2010) and have smaller home ranges (Saïd et al. 2005; Morellet et al. 2013). Nevertheless, roe deer behavioral responses to increased resource availability were likely to include drivers other than food resources and snow conditions. Roe deer mate in summer, when both sexes increase movements (Hewison et al. 1998). Males show increased daily activity during the rut period for territorial defense, which includes marking and patrolling behavior (Liberg et al. 1998), and a substantial proportion of females make breeding excursions outside their home range (Richard et al. 2012).

As we expected, roe deer moved toward areas of high elevation, where NDVI was high (Supporting Information S1; Fig. 1). Because animals move to increase their access to high-quality resources (Fryxell and Sinclair 1988; Albon and Langvatn 1992), in our study area, roe deer likely moved toward higher elevations to search for high-quality food. Indeed, above 1,400 m of elevation, the beech forest, of poor nutritional value for roe deer (Pellerin et al. 2010), is replaced by a mosaic of open pastures with maple, willow, or bilberry that are all highly preferred plants of roe deer (Duncan et al. 1998). Because moving is energetically costly, moving along an elevation gradient should be compensated by a better access to high-quality resources. This interpretation is consistent with the forage-maturation hypothesis that herbivores migrate along a phenological gradient of plant development to maximize energy intake (Fryxell 1991; Albon and Langvatn 1992; Bischof et al. 2012).

As expected, we also found that roe deer avoided steeper slopes when moving long distances. The use of gentle slopes for long movements likely corresponds to a tactic of energy saving when moving between patches of various elevations (Cagnacci et al. 2011). We also found a strong year effect on NSD. Climatic factors (temperature, rainfall) acting on animal activity rather than on food resources might partly account for such yearly differences (Morellet et al. 2013). Moreover, annual variation in human disturbances (Hewison et al. 2001), population abundance (Cagnacci et al. 2011), and interactions with sympatric large herbivores that compete with roe deer (Redjadj et al. 2014) could all account for observed yearly variation in roe deer movements.

Although moving or migrating along an elevation gradient has been commonly observed in large herbivores (e.g., roe deer—Mysterud 1999; Ramanzin et al. 2007, red deer—Mysterud et al. 2001; Bocci et al. 2010; Bischof et al. 2012, mountain goat *Oreamnos americanus*—Rice 2008, and mule deer—Nicholson et al. 1997), not all movements of roe deer between low and high elevation should be interpreted as seasonal migration (sensu Dingle and Drake 2007). The typical movement pattern of a migrant should be characterized by a movement away from the winter range in spring, with a stabilization in the summer range for an extended period of time, followed by a return to the point of origin in the autumn (Bunnfeld et al. 2011; Bischof et al. 2012). We found that very few roe deer stabilized their ranges at high elevation during summer (only 6 of 54 individual-years representing 11%). The low proportion of migrants we reported markedly contrasts with previous studies in highly seasonal environments, in which as much as 40–70% of roe deer were found to migrate between distinct seasonal home ranges (Mysterud 1999; Ramanzin et al. 2007). In most previous studies, roe deer movements have been interpreted as being a response to either variation in resource availability or cost/benefit ratio associated with movements (Cagnacci et al. 2011). Consequently, differences in the spatial distribution of seasonal resources are probably the main factor responsible for the variation we observed in space use. In our study area, the presence of a steep slope associated with a large elevation gradient generated marked habitat heterogeneity at a small spatial scale. Consequently, roe deer were able to access a large diversity

of resources by moving only short distances. Such small-scale movements contrast with the long distances travelled by deer in less heterogeneous landscapes where seasonal migration constitutes a response to variation in the spatial distribution of seasonal resources (Mysterud 1999; Mysterud et al. 2012). Such space use patterns thus correspond to a 3rd-order habitat selection process (sensu Johnson 1980) rather than to a seasonal migration process. Furthermore, avoiding competition with other herbivores is also a common explanation for ungulates moving from low to high elevation (Bocci et al. 2010). This avoidance was unlikely because the density of the focal hunted roe deer population was quite low and roe deer moving to high elevation have to compete with chamois and mouflon present in the NGWR (Redjadj et al. 2014).

Our study highlights how climatic conditions (in particular snow depth), spatiotemporal variation in resource availability, and topography all shaped roe deer movements in mountainous areas. Understanding how roe deer adjust their movements to track variation in resources is crucial for managers, especially in the current context of climate change, which is especially marked at high elevation (Lenoir et al. 2008). Moreover, different movement tactics seem to coexist among individuals and for a given individual among years (see Supporting Information S1). To understand better the ecology of movements, future studies should take into account factors that influence mobility such as the presence of dependent offspring for females (Bongi et al. 2008), reproductive status (Liberg et al. 1998), population density (Cagnacci et al. 2011), and changes in home range quality among years (Pellerin et al. 2010). Finally, understanding the ultimate consequences of variable movement tactics on individual fitness is of prime importance (Gaillard et al. 2010) to understand better how different movement tactics can still coexist within and among species (Bischof et al. 2012).

ACKNOWLEDGMENTS

We sincerely thank all the volunteers, students, and the officers from the Office National de la Chasse et de la Faune Sauvage and Parc Naturel Régional du Massif des Bauges for helping with the capture and marking of the animals and for the recovery of collars. We are also grateful to Météo-France for providing us with the weather data. We thank M. Garel, P. Marchand, A. Duparc, M.-H. St-Laurent, and 2 anonymous reviewers for their valuable comments on a previous draft of this manuscript. We acknowledge the financial support of the Centre National de Recherche Scientifique (J-MG, CB, AL). This study was funded by the Office National de la Chasse et de la Faune Sauvage.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Annual variation in the net squared displacement for each roe deer (*Capreolus capreolus*; *Name_Year*) in the National Game and Wildlife Reserve of Les Bauges mountain range (Savoie, France) for each year in the monitoring period (2004–2008).

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Submitted 22 August 2014. Accepted 19 February 2015.

Associate Editor was Lisa A. Shipley.