



## Research Article

## Roe deer summer habitat selection at multiple spatio-temporal scales in an Alpine environment

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### Abstract

Habitat selection is a hierarchical process that may involve different patterns depending on the spatial and temporal scales of investigation. We studied habitat selection by European roe deer (*Capreolus capreolus*) in a very diverse environment in the Italian eastern Alps, during summer. We sampled both coarse-grained habitat variables (topographic variables, habitat types and cover) and fine-grained habitat variables (forage components of habitat) in used and available locations along the movement trajectories of 14 adult roe deer equipped with GPS telemetry collars. We used conventional logistic regression to assess roe deer habitat selection at the seasonal home range scale, and conditional logistic regression to take into account the temporal aspect of habitat selection on a weekly basis. Our results indicate that topographic variables were not significant predictors for summer roe deer habitat selection. Roe deer strongly selected dense canopy cover, probably to avoid heat stress during warm summer days. In accordance with previous observations, roe deer preferred young forest stands dominated by pioneer species such as ash (*Fraxinus* spp.) and hazel (*Corylus avellana*) over climax environments. Roe deer positively selected shrubs (in particular *Fraxinus* spp., *Erica herbacea*, *Rhododendron* spp. and *Vaccinium* spp.) throughout the study period, whereas selection for grasses and sedges emerged only at the weekly scale. Habitat selection was clearly related to vegetation phenology, since roe deer selected plants in the most nutritive phenological stages, i.e., shrubs with buds, new leaves and fruits, and newly emergent grasses and sedges. Finally, we found stronger and more significant regression coefficients for forage components of habitat and habitat types at the weekly scale, indicating that matching spatial and temporal scales may improve our understanding of ecological patterns driving habitat selection. Conversely, selection patterns for canopy cover did not change across scales, indicating that this variable likely drives habitat selection in a similar way throughout the entire season.

## Introduction

Within Hutchinson's ecological theatre, where the evolutionary play is performed (Hutchinson, 1965), the field of habitat ecology represents one of the main acts. Considering its niche-based definition, habitat is the ensemble of resources and conditions present in an area producing occupancy and determining the survival and reproduction of organisms (Hall et al., 1997; Hirzel and Le Lay, 2008). Habitat selection in particular is defined as the multi-scale process by which an animal chooses resources (Johnson, 1980). Because habitat selection directly acts on the survival and reproductive success of individuals, it indirectly affects population dynamics and species distributions (Holt, 2003; Gaillard et al., 2010). Habitat selection may be influenced by a variety of factors, such as nutrition, behavior, competition, predation, but also the scale of selection and can be recognized as a hierarchical process in space and time (Johnson, 1980; Senft et al., 1987; Wiens, 1989; Manly et al., 2002; Hirzel and Le Lay, 2008).

Scales in space and time have been long recognized as central themes in ecology (e.g., Hutchinson, 1965; Gaillard et al., 2010). For example, the activities animals undertake to meet their needs, such as feeding, reproducing, moving, occur at different spatial scales. For the field of habitat ecology, Johnson (1980) provided an intuitive framework in which selection scales are nested. He defined the first order selection

scale as the distribution range. At the second order animals should select home ranges. At the third order, resources within the home range should be selected and finally, at the fourth order scale, small site specific resources such as nests or den sites or specific foraging items should be selected. While these levels of selection are only broad categorizations along a continuum of spatial selection scales from very coarse to very fine (Gaillard et al., 2010), they provide useful guidelines for the study of habitat selection.

Next, Wiens (1989) pointed out that ecological processes are bounded by the relationships between the spatial and temporal scale of variation (i.e., processes taking place at small spatial scales will also be defined by small temporal scales). Thus, as spatial scaling increases in ecological systems, temporal scaling increases concurrently. Defining the spatial scale at which habitat selection is defined also leads to defining the temporal scale along a continuum of spatio-temporal dimensions (Gaillard et al., 2010). For example, decisions animals make at different temporal scales may include bites taken at very short time intervals within seconds, minutes or hours (Senft et al., 1987; Nathan et al., 2008). In contrast, at the spatial scale of home range occupancy intervals between decisions may last hours, days, months and years. At the broadest scale, spatio-temporal dynamics at the species level are subject to processes over hundreds of square kilometers during millions of years. While intuitive, the concept of temporal scaling has rarely been recognized and incorporated into evaluating the role of scaling in habitat selection studies, although habitat selection can be variable

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in time due to changes in resource quantity and quality. Mismatching space-time scaling may mask ecological relationships and average out fine-scale habitat selection patterns (Wiens, 1989).

The European roe deer (*Capreolus capreolus*) is one of the most common ungulate species in Europe (Melis et al., 2009), where it can occupy a diversity of habitat, including deciduous and coniferous continental forests, Mediterranean scrublands, agricultural plains, but also high latitudes and altitudes, where harsh winters and a short growing season limit population distribution and abundance (Jepsen and Topping, 2004). At the latitudinal and altitudinal extremes of its distribution range, variable seasonal habitat selection patterns including seasonal migration, allow roe deer to adapt to changes in habitat suitability in space and time (Mysterud, 1999; Ramanzin et al., 2007; Cagnacci et al., 2011). However, while being a generalist species with a large fundamental niche, roe deer favor heterogeneous or mixed habitat, providing a combination of concealment cover for protection from predators and humans and high quality forage (Cederlund et al., 1998; Duncan et al., 1998; Mysterud and Ostbye, 1999; Said and Servanty, 2005; Said et al., 2005). Being a small concentrate selector, roe deer generally prefer highly palatable browse vegetation, such as early phenological stages of forbs and shrubs, with high nutritional protein and low fiber contents (Demment and van Soest, 1985; Gill et al., 1996; Tufto et al., 1996). At the same time, food habits of roe deer are plastic and may change rapidly (Tixier and Duncan, 1996; Cornelis et al., 1999) in response to changes in the spatial and temporal availability of food items, leading to a strong seasonal diet specialization (Duncan et al., 1998).

In general, research seems to indicate that roe deer show a high degree of ecological plasticity, but they are very selective at small micro-habitat scales, such as foraging and seeking protective cover. However, most studies on fine-scale habitat composition, including forage plants, were conducted in optimal roe deer habitat, such as central Europe (e.g., Maillard et al., 1989; De Jong et al., 1995) and plains (e.g., Holisova et al., 1982, 1984), or controlled conditions (Tixier et al., 1997). Unfortunately, in more extreme and highly seasonal environments at the limits of their distribution range, such as alpine regions, studies that investigate how topography, canopy and plant communities affect roe deer habitat selection are rare. Indeed, alpine environments are characterized by high heterogeneity, because habitat composition changes frequently over short distances due to, e.g., extreme gradients in elevation, aspect and slope, which condition vegetation community diversity and rapid changes in phenology. Because such heterogeneity is likely to be reflected by roe deer home ranges, the alpine environment offers a unique opportunity to study how covariates at different grain sizes may affect third-order habitat selection in this small ruminant.

We aimed to study selection of habitat covariates with different grain sizes, ranging from larger grained macro-habitat covariates, such as topography or habitat type, to very fine grained micro-habitat observation units, such as plants found within sampling quadrats. Moreover, we investigated these effects at two temporal scales, seasonal and weekly. We outlined our objectives, hypotheses and predictions in Tab. 1. In general, because of their overall high ecological plasticity, but also very specialized feeding habits, we expected differing degrees of selectivity for coarse and fine grained habitat covariates (H1). First, we predicted little selectivity for coarse grained habitat variables, such as topographic covariates (P1a). Next, there is general agreement that the two major habitat requirements for roe deer are forage (Duncan et al., 1998) and cover for concealment from predators (Cederlund et al., 1998). One strategy by which roe deer may relieve heat stress and thus lower energy expenditure during summer is to use dense canopy cover for shade (e.g., Mysterud, 1996). Therefore, we expected that roe deer would show positive selection for dense canopy cover (P1b). Next, because roe deer are considered concentrate selectors (Van Soest, 1994), we expected their third-order habitat selection to be driven also by habitat providing highly nutritious plants. Thus, we predicted early successional habitats to be preferred, because they provide more browse and hiding cover (P1c). As roe deer show high energy and nutrient requirements and preference for the richest parts of the consumed plant species (Tixier and Duncan, 1996), we expected to find a positive se-

lection for fine-grained microhabitat covariates indicating high-quality food resources, such as shrubs and forbs in their earlier phenological stages (P1d; Albon and Langvatn, 1992; Van der Wal et al., 2000; Mysterud et al., 2001; Hebblewhite et al., 2008).

To detect patterns of environmental heterogeneity at specific spatial scales we must also match them with appropriate temporal scales within the same domain (Wiens, 1989). Finding the appropriate units for both space and time remains a fundamental challenge in habitat selection studies (Gaillard et al., 2010). For our second objective, we aimed to fill this gap by comparing used versus available animal locations in a matched-case design along a temporal continuum throughout the summer season. Specifically, we hypothesized to improve our analysis for dynamic covariates when comparing used and available roe deer locations matched for the same sampling time (H2; Compton et al., 2002), rather than averaging covariates out throughout the entire summer season. In particular, we predicted to find similar selection patterns for covariates that remain fairly static throughout one summer season (macro-habitat), since these covariates are supposed to drive habitat selection in a similar way throughout the entire season (P2a). Conversely, we predicted to find stronger or more significant regression coefficients for the fine grained covariates that change throughout the summer season, e.g., forage components (P2b).

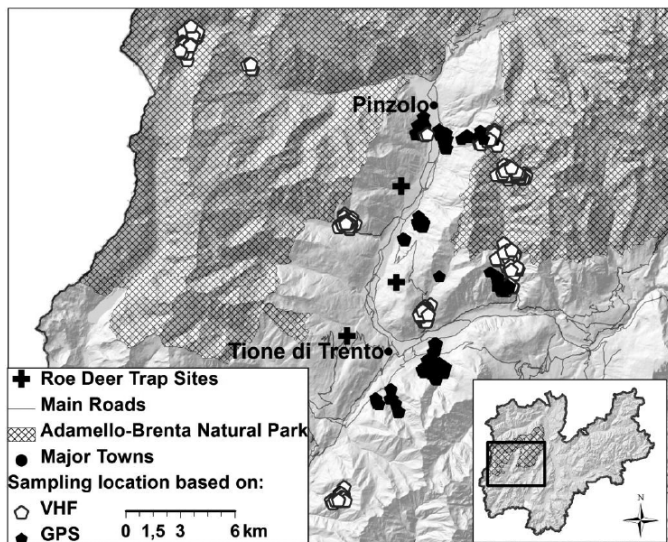
## Materials and methods

### Study area

The study area (approximately 40000 ha) is located in the Italian eastern Alps and includes the north-western part of the Autonomous Province of Trento (Val Rendena and Valli Giudicarie, Fig. 1). Elevation ranges from 400 m in the main valleys to 3500 m at the highest peaks in the Brenta and the Adamello-Presanella mountain ranges and the area is characterized by a high environmental, morphological and geological complexity. Along the valley bottoms agricultural grasslands and crops as well as deciduous forests, mainly comprised by European beech (*Fagus sylvatica*) and European ash (*Fraxinus excelsior*), predominate. Understory vegetation is patchily distributed and is dominated by common hazel (*Corylus avellana*) and brambles (genus *Rubus*). Higher elevations and the narrow lateral valleys are covered by coniferous forest, mainly comprised of Norway spruce (*Picea abies*), silver fir (*Abies alba*) and European larch (*Larix decidua*). Mountain pine (*Pinus mugo*) as well as shrublands of rhododendron (genus *Rhododendron*) interspersed with alpine grasslands prevail above elevation of 1600 m. Ungulate species inhabiting the region include (in order of abundance): roe deer, chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus*), and ibex (*Capra ibex*). The predator community is characterized by red foxes (*Vulpes vulpes*) and reintroduced brown bears (*Ursus arctos arctos*). The human population density of approximately 31/km<sup>2</sup> is low in comparison to other parts of Italy.

### Roe deer location data

We used data from 14 radio-collared roe deer (10 females, 9 adults and 1 subadult, and 4 adult males), which were captured throughout the study area during winter of 2012/2013 using individual box traps (Schemnitz, 1994). All roe deer were fitted with Global Positioning System (GPS) collars (Vectronic Aerospace, GSM GPS Plus, Berlin, Germany). All collars were scheduled to collect one location every three hours and equipped with a very high-frequency (VHF) beacon and a drop-off mechanism programmed to release the collar after two years. Collar data were downloadable via the Global System for Mobile Communication (GSM) device (Tomkiewicz et al., 2010) that allowed daily data transfer to a server using the cellular network. In case of incomplete GSM coverage, data were transferred at successive connections with the GSM network. All animal capture and handling procedures were approved by animal care protocols of the Trento Province (Wildlife Committee of the Autonomous Province of Trento, September 11<sup>th</sup> 2011) and the University of Montana (AUP 060-12MHWB-113012).



**Figure 1** – Study area of the summer habitat selection assessment of roe deer. The area is comprised in the Val Rendena and Valli Giudicarie territory, Trentino (Autonomous Province of Trento), Italian eastern Alps.

**Sampling design**

We studied fine-scale roe deer habitat selection by comparing used locations to random available locations between April and October 2013. The study time frame is ecologically important for roe deer, since it corresponds to the reproductive season, comprehending the establishment and defense of territories, natal dispersal, births and the rutting period (Linnell et al., 1998). Moreover, in our study area, where partial migration was observed (Ramanzin et al., 2007), the time interval we chose includes both the migration during spring from winter to summer ranges, as well as the start of the fall migration, from summer to winter ranges (Cagnacci et al., 2011). Due to an incomplete GSM coverage throughout the study area, we employed two different methods to determine used and available locations. First, for animals for which we received GPS locations via GSM network in the previous 8 days, we projected a 50 m grid over the location data of animals and selected the grid cell with the highest number of animal locations. Within this cell we selected the most recent GPS location as our used loca-

tion. We paired each used location with one random available location in the closest cell without GPS locations. Although GPS collars can collect large amounts of locations compared to previously existing technologies such as VHF devices (Cagnacci et al., 2010), we aimed at balancing our ground-based sampling effort across individuals. Thus, we selected one pair of used-available locations/animal/week for all collared roe deer (28 sampling locations/week). All spatial analyses for the selection of sampling locations were conducted in Quantum GIS (1.8.0). Next, for animals for which GSM coverage was not available in the previous eight days, we determined used locations using VHF-triangulation to maintain a consistent weekly sampling schedule for all individuals. We recorded  $\geq 3$  bearings within approximately 30 min to avoid larger movements by the animal (Millspaugh et al., 2012). To account for VHF triangulation error, and the only periodic assessment of the animal position as compared to the GPS method, we validated roe deer presence at triangulated roe deer used locations by searching for recent signs of roe deer presence, such as fresh tracks, faeces and bed sites. In this case, we determined available locations in a random direction at a distance of 150 m from the used locations. As a further validation, we assessed how the presence of VHF data could have affected our sampling design. Normally, GPS locations were eventually rescued from the collars, via later GSM transmission or from dropped-off collars. We therefore calculated a VHF error, in terms of distance (m) between a given VHF triangulation and the corresponding GPS used location which we would have sampled in presence of GSM coverage at the time of sampling. The average distance was found to be  $386 \pm 302$  m. Moreover, we tested for the effect of the method to determine the sampling locations on our predictions (see Statistical analyses below).

In used and available locations we estimated several macro-habitat covariates, including topography, habitat types, cover (Myysterud and Ostbye, 1999) and micro-habitat components, i.e., vegetation composition and phenology (Hebblewhite et al., 2008). In particular, we recorded the macro-habitat covariates at the point location or grid cell scale, whereas we measured the micro-habitat covariates within sampling subunits, i.e., 2 adjacent quadrats of  $1 \text{ m}^2$  for vegetation. We decided to sample shrubs, that we defined as dicotyledons with a woody stem  $< 7$  cm diameter, both in the vegetation sampling quadrats, and in an additional larger area ( $7 \text{ m}^2$  quarter circle centered on the quadrats) given the predicted importance of this highly nutritious plants/vegetative stage for roe deer (Duncan et al., 1998). For a detailed description

**Table 1** – Objectives, hypotheses and predictions for summer habitat selection by roe deer, *Capreolus capreolus*, in Italian eastern Alps (Autonomous Province of Trento).

Objectives	Hypotheses	Predictions
1) Roe deer habitat selection at the <i>seasonal</i> home range scale.	<b>H1:</b> Roe deer show a high ecological plasticity for coarse grained habitat covariates, but selectivity increases in response to specific requirements and for finer grained micro-habitat covariates, such as forage items.	<b>P1a:</b> Topographic variables (macro-habitat), such as elevation, aspect and slope, will not be significant predictors for roe deer habitat selection. <b>P1b:</b> Roe deer will use habitat according to its cover value (macro-habitat). In particular, roe deer will select for increased canopy closure and hiding cover (horizontal and vertical cover). <b>P1c:</b> Roe deer will use habitat according to its overall browsing value (macro-habitat). In particular, roe deer will use habitats with higher browse availability (i.e., shrubs) and early successional forest stages (such as shrub-habitats). <b>P1d:</b> Finer grained (micro-habitat) variables will be selected, according to their forage quality value. Roe deer will select for areas rich in forbs and shrubs in early phenological stages.
2) Roe deer habitat selection at the spatially and temporally matched ( <i>weekly</i> ) scale.	<b>H2:</b> Matching the domain of spatial and temporal scaling will improve our understanding of ecological patterns.	<b>P2a:</b> Selection patterns for topographic covariates, habitat classes and cover (macro-habitat) will be similar to those observed at the seasonal home range scale, since these covariates are expected to drive habitat selection in a similar way throughout the same season. <b>P2b:</b> Regression coefficients for forage items (micro-habitat) will be stronger and more significant when matching used and available locations on a temporally (i.e., on a weekly) scale.

of all habitat covariates, and their sampling scale, please see Supplemental Table S1.

## Statistical analyses

To address our research objectives, we classified our predictor variables into three datasets: “topography and cover” (macro-habitat), all plant composition and phenology within sampling quadrats (“plants”, micro-habitat) and shrub composition and phenology within sampling quarter circles (“shrubs”, micro-habitat) present at the sampling sites. We transformed proportional data included in the “plants” and “shrubs” datasets by an arcsin square-root transformation. Finally, because we found little evidence for sex-specific differences during data explorations, we pooled data from females ( $n=10$ ) and males ( $n=4$ ). All statistical analyses were conducted in R, version 3.2.0 (R Core Team, 2013).

In an initial phase we conducted exploratory analyses within each dataset using principal component analysis (PCA) using the FactoMineR library in R (Husson et al., 2015). In the following modeling phase of our analyses, we screened the positively or negatively associated covariates in the biplots, i.e., with similar vector components or opposite vector directions, respectively. In general, we retained only those covariates with the highest absolute PCA loading score (Zuur et al., 2010), unless we found an ecological explanation for such association (see below for example “shrubs” dataset). Moreover, we also used an a priori criterion to select covariates relevant to test the working hypotheses, especially when the number of covariates was very high (e.g., “plants” dataset). We then derived an a-priori full additive model for each dataset, combining all variables that we considered relevant on the basis of the aforementioned exploratory criteria.

To estimate roe deer resource selection, we built Generalized Linear Models (GLMs; Guisan et al., 1998; Hosmer and Lemeshow, 2000). We used conventional logistic regression (Hosmer and Lemeshow, 2000) to model habitat selection by roe deer throughout the duration of the summer (Objective 1; Tab. 1). Next, to address our second objective (Tab. 1), we modeled each spatially and temporally matched pair of used and available locations (see above, Sampling design) by means of conditional logistic regression (matched-case control design; Compton et al., 2002). We thus accounted for the temporal variation in habitat use, at a weekly scale (survival R package, Therneau, 2014). We used a natural average method to obtain robust parameter estimates (multi-model inference; Burnham and Anderson, 2002). This procedure implies calculating a weighted average of parameter estimates, so that parameter estimates from models that provide little information about the variation of the response variable are given little weight (Arnold, 2010). We first performed a model selection on models with all possible combinations of covariates included in the full model for each dataset by means of Akaike Information Criterion (AIC; Burnham and Anderson, 2002). We then decided to retain only the top models ( $\Delta AIC \leq 2$ ) for the model averaging approach (MuMIn R package, Barton, 2014). In addition, to provide a measure of the goodness-of-fit, we computed the  $R^2$  of the corresponding GLM including the fixed effects predictors with weight = 1 in the averaged model (Tab. 2 and Tab. 3). Lastly, we added to such model (conventional logistics models only) individual animal and method to identify used locations as random effects (GLMMs), to account for variation between individuals in habitat selection patterns (Rabe-Hesketh et al., 2004) and test the influence of different sampling procedures on data fitting (lme4 R package, Bates et al., 2014).

## Results

### Roe deer sampling locations

During spring and summer 2013 we sampled a total of 583 roe deer locations (Supplemental Table S2; Fig. 1). Of these locations, 251 (43.05%) were obtained from GPS collar data, whereas the remaining 332 (56.95%) were obtained through VHF telemetry. The proportion of GPS and VHF data used in the analyses was not equally distributed between animals. Indeed, some animals ( $n = 6$ ) occupied areas without GSM coverage during the entire study period. In contrast, some animals

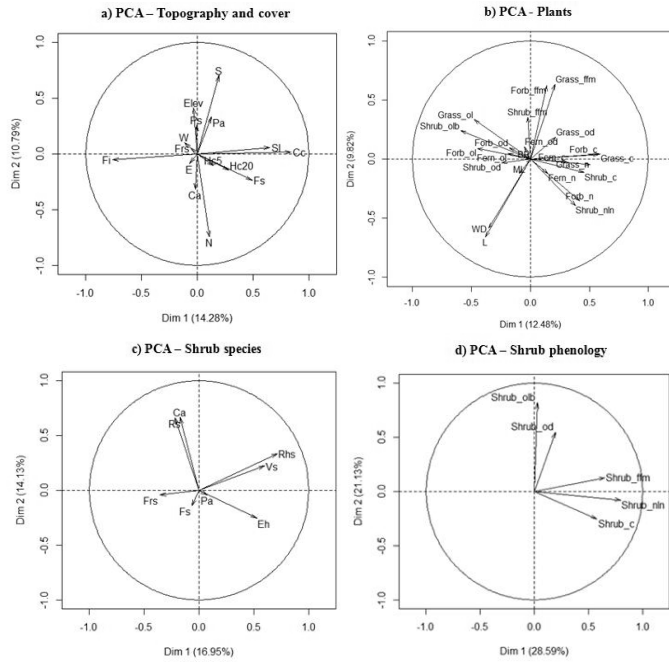
were sampled based on GPS locations ( $n = 3$ ) only. The majority of roe deer were sampled based on a mixture of VHF and GPS derived locations, because animals moved between areas with and without GSM coverage. Despite this mixture of GPS and VHF derived locations, the total number of sampling locations was balanced between animals, as we succeeded to sample all animals weekly during most of the study period. In few cases we did not sample plots at triangulated VHF locations, because we were not able to reliably validate them (i.e., we did not find any recent signs of roe deer presence).

### Exploratory phase and covariate selection

In the “topography and cover” dataset (Supplemental Table S1) we recorded the following dominant tree/shrub species during the survey: *Corylus avellana*, *Fagus sylvatica*, *Fraxinus* spp., *Picea abies*, *Pinus sylvestris*, plus open fields. As a final set of covariates for subsequent resource selection function modeling, we selected aspect, elevation, canopy cover, hiding cover at 20 m, *Corylus avellana* and *Fraxinus* spp. based on the results of PCA analyses (Fig. 2a; for all PCA loadings see Supplemental Table S3). In particular, hiding cover at 20 m, and hiding cover at 5 m and slope showed similar vector directions, but we retained only the first covariate, which had the highest absolute PCA loading. Moreover, *Fagus sylvatica* and canopy cover showed similar vector directions, as well as *Picea abies* and elevation. In the first case, we retained only canopy cover, based on PCA loadings (PCA loading<sub>*Fagus sylvatica*</sub>=0.33 vs. PCA loading<sub>canopy cover</sub>=0.77). Conversely, as we considered elevation more relevant to test the working hypotheses, we decided to retain this covariate instead of *Picea abies*, although the second covariate showed a higher PCA loading (PCA loading<sub>elevation</sub>=0.01 vs. PCA loading<sub>*Picea abies*</sub>=0.18). Finally, we found opposite directions for canopy cover and open fields, but we retained only the first covariate, based on PCA loading (PCA loading<sub>canopy cover</sub>=0.77 vs. PCA loading<sub>open fields</sub>=-0.74).

Next, we selected the covariates to formulate the full model for the “plants” dataset. This dataset potentially included all possible combinations of plant classes and phenological stages (Supplemental Table S1). Therefore, besides PCA, we also used a priori criteria based on working hypotheses to reduce the number of predictors. First, we generally found similar vector direction, but in opposite quadrants, for new plants and old alive plants, which is understandable, given that new sprouts emerge on old alive plants (e.g., forbs and old alive forbs; new shrubs and old alive shrubs; see Fig. 2b). We decided to select new plants, for consistency with the working hypotheses, although old alive plants had sometimes a stronger PCA loading (Supplemental Table S3). For similar reason, i.e., coherence with the hypotheses, we decided to exclude cured plants, old dead plants, and ferns. The full model for plants therefore included: forbs, grasses/sedges and shrubs associated with two phenological stages: newly emergent (or new/old alive with new leaves for shrubs) and flowering/fruitlet/mature.

In the “shrubs” dataset, we recorded the following species during the survey: *Corylus avellana*, *Erica herbacea*, *Fagus sylvatica*, *Fraxinus* spp., *Picea abies*, *Rhododendron* spp., *Rubus* spp. and *Vaccinium* spp. (Supplemental Table S1). With respect to shrubs species presence, we found associations that we considered ecologically meaningful, and specifically: 1) *Corylus avellana* and *Rubus* spp.; 2) *Rhododendron* spp. and *Erica herbacea* and 3) *Rhododendron* spp. and *Vaccinium* spp., as shown in Fig. 2c. Thus, we decided to add these shrub species in two groups: group 1 (*Corylus avellana*/*Rubus* spp.; G1) and group 2 (*Rhododendron* spp./*Erica herbacea*/*Vaccinium* spp.; G2). When referring to shrub phenology, new/old alive with new leaves, flowering/fruitlet/mature and cured phenological stages showed similar vector directions, as well as old alive/old alive with buds and old dead stages (Fig. 2d). In both cases, we retained only the covariate with the highest PCA loading, i.e., new/old alive with new leaves and old alive/old alive with buds (see Table A3 for PCA loadings). Thus, the full model for this dataset included *Fraxinus* spp., group 1 and group 2 associated with two phenological stages: new/old alive with new leaves and old alive/old alive with buds.



**Figure 2** – a) PCA biplot for all covariates of the “topography and cover” dataset; Ca = *Corylus avellana*, Cc = canopy cover, E = east, Elev = elevation, Fs = *Fagus sylvatica*, Fi = field, Frs = *Fraxinus* spp., Hc5 = hiding cover at 5 m, Hc20 = hiding cover at 20 m, N = north, Pa = *Picea abies*, Ps = *Pinus sylvestris*, S = south, Sl = slope, W = west; b) PCA biplot for all covariates of the “plants” dataset; BR = bare and rocks, c = cured, ffm = flowering/fruited/mature, L = litter, ML = mosses and lichens, n = newly emergent, nln = newly emergent/old alive with new leaves, ol = old alive, olb = old alive/old alive with buds, od = old dead, WD = woody debris; c) PCA biplot for shrub species covariates of the “shrubs” dataset; Ca = *Corylus avellana*, Eh = *Erica herbacea*, Fs = *Fagus sylvatica*, Frs = *Fraxinus* spp., Pa = *Picea abies*, Rhs = *Rubus* spp., Rhs = *Rhododendron* spp., Vs = *Vaccinium* spp.; d) PCA biplot for phenological stage covariates of the “shrubs” dataset; c = cured, ffm = flowering/fruited/mature, nln = new/old alive with new leaves, olb = old alive/old alive with buds, od = old dead. In all cases, the proportion of variance explained by the first (horizontal) and second (vertical) canonical dimension is reported.

**Roe deer habitat selection at the seasonal home-range scale**

For “topography and cover”, the model selection according to AIC yielded three top models with  $\Delta AIC \leq 2$  (Supplemental Table S4a). The averaged model obtained with multi-model inference included three main predictors: canopy cover, *Corylus avellana* and *Fraxinus* spp. (Tab. 2: predictor weight = 1). When we fitted a GLM to these main predictors, we obtained  $R^2=0.24$ . The addition of random effects, i.e., individual roe deer and method used to define used locations, did not improve the fit to the data of such model (proportion of variance explained =  $1.427 \times 10^{-11}$ , and  $1.0 \times 10^{-12}$ , respectively). According to these results, our first prediction (P1a) was confirmed: neither aspect nor elevation were main factors of the roe deer summer selection model. Our results also partially confirmed our second prediction (P1b), indicating that roe deer positively selected dense canopy cover, whereas hiding cover only marginally contributed to habitat selection ( $\beta=0.012$ ,  $p=0.077$ ). As expected, roe deer preferred young forest stands with abundant understory (P1c), as shown by the strong selection for the two shrub habitat types dominated by *Corylus avellana* and *Fraxinus* spp.

With respect to the “plants” dataset, we obtained eight top models with  $\Delta AIC \leq 2$  (Supplemental Table S5a), that when averaged included only one top predictor (weight = 1), i.e., shrubs with emerging new leaves. The GLM including this predictor alone reached  $R^2 = 0.50$ . The addition of random effects to such model, i.e., individual roe deer and method used to define used locations, did not improve the fit to the data (proportion of variance explained =  $1.0 \times 10^{-12}$  for both random effects). Therefore, we partly confirmed our prediction (P1d), since roe deer positively selected shrubs in the most nutritive phenological stages throughout summer, especially with new emerging leaves. Shrubs with flowers and fruits only marginally contributed to habitat selection ( $\beta=0.200$ ,  $p=0.072$ ). All other averaged coefficients were not

**Table 2** – Coefficients and standard errors obtained by averaging the top logistic regression models for seasonal habitat selection by roe deer (see Supplemental Tables S4a, S5a, S6a; averaged models:  $\Delta AIC \leq 2$ ). The predictor’s weight and  $p$ -value of each term are provided. Legend: n = new, nln = new/old alive with new leaves, ffm = flowering/fruited/mature, olb = old alive/old alive with buds, G1 = *Corylus avellana*/*Rubus* spp., G2 = *Erica herbacea*/*Rhododendron* spp./*Vaccinium* spp..

Covariate	Averaged Coefficient	Std. Error	p-value	Pred. weight
<b>Topography and cover</b>				
Canopy cover	0.041	0.011	<0.001	1
<i>Corylus avellana</i>	1.069	0.357	0.003	1
<i>Fraxinus</i> spp.	1.205	0.393	0.002	1
Hiding cover at 20 m	0.012	0.007	0.077	0.75
Elevation	$3 \times 10^{-4}$	$2 \times 10^{-4}$	0.284	0.29
<b>Plants</b>				
Shrub_nln	0.091	0.036	0.013	1
Shrub_ffm	0.200	0.111	0.072	0.80
Grass_n	0.055	0.044	0.210	0.38
Grass_ffm	0.029	0.080	0.712	0.09
Forb_n	0.003	0.051	0.950	0.08
Forb_ffm	-0.068	0.067	0.313	0.24
<b>Shrubs</b>				
<i>Fraxinus_nln</i>	0.255	0.063	<0.001	1
<i>Fraxinus_olb</i>	0.194	0.251	0.441	0.21
G1_nln	0.037	0.052	0.476	0.19
G1_olb	0.091	0.134	0.490	0.19
G2_nln	1.101	0.040	0.011	1
G2_olb	0.277	0.121	0.023	1

significant, and especially we did not find a selection for forbs in any phenological stage, contrary to what expected (P1d).

Lastly, for the “shrubs” dataset, we obtained four top models (Supplemental Table S6a), that when averaged included three top predictors (weight = 1): *Fraxinus* spp. with emerging new leaves, and the three associated species G2 (*Erica herbacea*, *Rhododendron* spp. and *Vaccinium* spp.) in both new/old alive with new leaves and old alive/old alive with buds phenological stages. The GLM included such predictors yielded a goodness-of-fit with  $R^2=0.24$ . The addition of random effects to the same model, i.e., individual roe deer and method used to define used locations, did not improve the model fit to the data (proportion of variance explained =  $1.427 \times 10^{-11}$ , and  $1.0 \times 10^{-12}$ , respectively). These results further highlighted that the most nutritive phenological stages (i.e., buds and new leaves) of shrubs are strongly selected by roe deer during summer (prediction P1d), at all altitudes. Typically, *Fraxinus* spp. can be mainly found in the valley bottoms, whereas the species in G2 represent a vegetation community characteristic of high altitudes. Other phenological stages did not present significant coefficients.

**Roe deer habitat selection at the spatially and temporally matched scale**

The conditional logistics model selection for “topography and cover” provided the same top models obtained in the conventional logistic regression analysis (Supplemental Table S4b), that when averaged yielded the same top predictors, i.e., canopy cover, *Corylus avellana* and *Fraxinus* spp. (Tab. 3). The GLM including such variables led to  $R^2=0.30$ . For canopy cover, we observed a similar selection pattern at the weekly scale than at the seasonal scale (Tab. 2 and Tab. 3:  $\beta_{log}=0.041$ ,  $p<0.001$ ;  $\beta_{c-log}=0.050$ ,  $p<0.001$ ), indicating that this variable likely drive habitat selection by roe deer in a similar way throughout the season (P2a). Conversely, we found a relatively stronger selection for the coarse-grained habitat variables (*Corylus avellana* and *Fraxinus* spp.) at the weekly scale than at the seasonal scale (Tab. 2 and Tab. 3: *Corylus avellana*:  $\beta_{log}=1.069$ ,  $p=0.003$  vs.  $\beta_{c-log}=1.800$ ,  $p=0.001$ ; *Fraxinus* spp.:  $\beta_{log}=1.205$ ,  $p=0.002$  vs.  $\beta_{c-log}=1.550$ ,  $p=0.007$ ), in contrast to our prediction (P2a).

**Table 3** – Coefficients and standard errors obtained by averaging the top conditional logistic regression models for weekly habitat selection of roe deer (see Supplemental Tables S4b, S5b, S6b; averaged models:  $\Delta AIC \leq 2$ ). The predictor's weight and *p*-value of each term are provided. Legend: n = new, nln = new/old alive with new leaves, ffm = flowering/fruitlet/mature, olb = old alive/old alive with buds, G1 = *Corylus avellana*/*Rubus* spp., G2 = *Erica herbacea*/*Rhododendron* spp./*Vaccinium* spp..

Covariate	Averaged Coefficient	Std. Error	<i>p</i> -value	Pred. weight
<b>Topography and cover</b>				
Canopy cover	0.050	0.015	<0.001	1
<i>Corylus avellana</i>	1.800	0.560	0.001	1
<i>Fraxinus</i> spp.	1.550	0.568	0.006	1
Hiding cover at 20 m	0.013	0.007	0.065	0.76
Elevation	-0.003	0.003	0.374	0.27
<b>Plants</b>				
Shrub_nln	0.124	0.042	0.003	1
Shrub_ffm	0.211	0.112	0.060	0.80
Grass_n	0.105	0.052	0.044	1
Forb_ffm	-0.090	0.072	0.214	0.35
<b>Shrubs</b>				
<i>Fraxinus_nln</i>	0.283	0.074	<0.001	1
<i>Fraxinus_olb</i>	0.148	0.251	0.556	0.19
G1_nln	0.017	0.052	0.743	0.17
G1_olb	0.093	0.140	0.505	0.20
G2_nln	0.128	0.049	0.009	1
G2_olb	0.321	0.147	0.031	1

The conditional logistics model selection for “plants” provided three top models (Supplemental Table S5b), that when averaged included two top predictors (Tab. 3): new/new leaves shrubs (also a top predictor at the seasonal scale), and newly emergent grasses/sedges (not included in the seasonal model). The GLM fitted with these fixed effect showed a similar goodness-of-fit than the seasonal model ( $R^2=0.48$ ). Thus, we confirmed our prediction that the selection for forage items would be stronger at a weekly scale (P2b).

Lastly, the top models for selection of “shrubs” at the weekly scale (Supplemental Table S6b) provided the same results than those obtained with conventional logistic regression at the seasonal scale, with *Fraxinus* spp. with new emergent leaves and the associates species of G2 in both new/old alive with new leaves and old alive/old alive with buds phenological stages as top predictors when averaged (Tab. 3). When fitted alone in a GLM, these covariates led to an  $R^2=0.31$ . Supporting our prediction (P2b), the averaged coefficients suggested a stronger selection at the weekly scale than at the seasonal scale, for all classes.

## Discussion

Six main results emerged from our study: 1) as expected, topographic variables (elevation, aspect and slope) did not emerge as significant predictors for habitat selection by roe deer (P1a); 2) as predicted, roe deer strongly selected dense canopy closure, probably to avoid heat stress during warm summer days, but contrary to our prediction, hiding cover had only a marginal effect on habitat selection (P1b); 3) as expected, roe deer preferred young forest stands with abundant understory rather than climax environments (P1c); 4) in agreement with our prediction, roe deer positively selected shrubs in the most nutritive phenological stages (especially buds and new leaves) throughout summer (P1d); conversely, we did not find a selection for forbs in any phenological stage; 5) when looking at the weekly scale, we observed similar selection patterns (i.e., regression coefficients and their significance) for canopy cover, indicating that this variable likely drive habitat selection by roe deer in a similar way throughout the entire season; conversely, regression coefficients were higher for the two preferred habitat types, *Corylus avellana* and *Fraxinus* spp., indicating a relatively stronger selection for this coarse-grained habitat variables at a weekly scale (P2a); 6) we generally found stronger regression coefficients for forage items, when matching used and available locations on a weekly scale; in par-

ticular, we observed a positive selection for newly emergent grasses and sedges at a weekly scale (P2b).

## Roe deer habitat selection at the seasonal home-range scale

Using an individual-based approach, we assessed habitat selection by roe deer in a very diverse environment in the Italian Alps during summer. The environmental heterogeneity that characterizes the study area allowed us to match coarse grained habitat variables, such as topography and cover, and fine grained habitat variables, such as food items, in a comprehensive analysis of third-order habitat selection in this small ungulate. The presence of a high ecological plasticity was expected from previous research (e.g., Jepsen and Topping, 2004) and was further confirmed by our results. Indeed, roe deer in our study area occupied a wide altitudinal range from 457 m to 1916 m a.s.l. Moreover, roe deer were found not to select habitat with respect to aspect but preferred habitat diversity. Aspect is generally regarded as a topographic covariate involved in habitat selection by temperate ungulates given its effect on food resources availability and quality. For example, Albon and Langvatn (1992) reported that the protein content of grasses and herbs was higher on north-facing slopes compared with south-facing slopes during spring in Norway. However, Mysterud et al. (2001) found that body weight of migratory red deer (*Cervus elaphus*) was positively correlated with access to diversity of aspects and variable topography rather than with the availability of a particular aspect or altitudinal class in Norway. Our results are consistent to these findings and may be related to the rapid changing in aspect gradients that characterizes our study area.

Canopy cover emerged as a strong driver of summer habitat selection by roe deer amongst macro-habitat covariates. Numerous studies have documented how cervids selectively use canopy cover to avoid adverse weather conditions, including studies on white-tailed deer (*Odocoileus virginianus*; Gates and Harmann, 1980), mule deer (*Odocoileus hemionus*; e.g., Wood, 1988), red deer (*Cervus elaphus*; Staines, 1976), moose (*Alces alces*; e.g., Demarchi and Bunnell, 1995) and roe deer (*Capreolus capreolus*; e.g., Mysterud and Ostbye, 1995; Mysterud, 1998). Use of canopy cover relates to extreme temperatures, radiation and wind speed (Mysterud and Ostbye, 1999). As our study was conducted during spring and summer, roe deer probably selected dense canopy cover to lower energy expenditures due to heat stress. Similarly, Mysterud (1996) observed that roe deer prefer to bed down below dense canopy cover during warm summer days in southern Norway. While the use of canopy cover mainly relates to thermoregulation, hiding cover is usually connected to predation risk, which is low in our study area. Indeed, the predator community is characterized by red foxes (*Vulpes vulpes*), that have been reported to prey mainly on roe deer fawns during the first two months of life (Aanes et al., 1998) and re-introduced brown bears (*Ursus arctos arctos*) at low densities, that have been shown to rarely prey on roe deer, also in the study area (Frassoni, 2002). Even if Tufto et al. (1996) observed that roe deer continue to prefer habitat with high concealment cover also in the absence of predators, our results show that hiding cover marginally contributed to roe deer habitat selection in our study. One hypothesis to explain such observation is that forest habitat characteristic of our study area provide a lower perception of risk per se than open habitat, due to lower visibility, and the possibility to quickly escape for an agile species such as roe deer (Mysterud and Ostbye, 1999). Further, other research showed that roe deer in open areas have a very high vigilance, and compensate the high visibility with specific tactics, such as grouping behavior (Mrlik, 1991; Gerard et al., 1995; Bonnot et al., 2015).

Structural components of habitats, such as canopy and the habitat type, are likely to affect both food quality and cover availability (Said et al., 2005). Being an ecotonal species generally related to early successional habitats, roe deer in our study population strongly preferred two habitat types, which were dominated by two understory species, hazel (*Corylus avellana*) and ash (*Fraxinus* spp.). These species are generally found in young forest stands in the alpine environment, before being replaced by beech (*Fagus sylvatica*) or spruce (*Picea abies*)



forests (Bernetti, 1995) and can develop dense patches of woodland thanks to their high vegetative regeneration rate. These thick habitats provide an optimal combination of high quality forage and concealment cover, and can therefore optimize the food and cover trade-off in this small concentrate selector.

Since roe deer are herbivores, the selection for a particular habitat type is expected to reflect foraging strategies and thus to overlap with the selection of feeding sites (e.g., Andersen et al., 1998; Pettorelli et al., 2001). Indeed, our results of shrub-habitat selection may be suggestive for the selection of shrubs as potentially major foraging items throughout summer. In particular, roe deer selected for habitat patches rich in *Fraxinus* spp., *Erica herbacea*, *Rhododendron* spp. and *Vaccinium* spp. The selection for *Rhododendron* spp. is remarkable, since it is generally considered a toxic plant (Caloni et al., 2013) due to the presence of terpenes in all plant parts. However, Mussa et al. (2003) already found this shrub species in the summer diet of roe deer in an Alpine environment, by means of faecal analysis method. Interestingly, roe deer are able to ingest plants which are protected by chemical defenses (Duncan et al., 1998), which might be the case for rhododendron, too. Alternatively, the selection for rhododendron might be a consequence of its association with other forage species, such as bilberry (*Vaccinium myrtillus*), which has been reported to be one of the main food resources selected by roe deer in Norway during winter (Mysterud et al., 1997). As expected, shrubs were selected in the most nutritive phenological stages, i.e., buds and new leaves. We did not find a selection for forbs, although roe deer are generally known to feed on them, especially during spring and summer (e.g., Mysterud, 1996). The strong selection for shrubs and absence of selection for forbs are in contrast with what reported by Mussa et al. (2003), who found that the summer diet of roe in the western Alps was mainly composed by herbaceous species (dicotyledons) and to a lesser extent by tree or shrub leaves. In general, reviews of studies of roe deer feeding habits (Tixier and Duncan, 1996; Cornelis et al., 1999; Gebert and Verheyden-Tixier, 2001) revealed that its diet composition is mainly explained by the environments in which they forage (Duncan et al., 1998). Thus, conclusions about food selection drawn in a particular study area will rarely be relevant to other areas (Storms et al., 2008). Furthermore, while we did not assess diet composition through direct observations or fecal analysis, i.e., fourth-order habitat selection, our findings further support roe deer dependence on specific plant typology and phenology stages, which can be explained by the comparatively high nutritional requirements of this small browser with low fat storages (Duncan et al., 1998).

### Roe deer habitat selection at the spatially and temporally matched scale

By analyzing the same datasets with two different statistical approaches, i.e., conventional and conditional logistic regression, we assessed the presence of temporal variation in third-order habitat selection by roe deer during summer. The choice to use a multiple-scale approach in habitat selection studies is a central issue, since habitat selection patterns are not necessarily congruent across spatial and temporal scales (Morin et al., 2005). The positive selection for newly emergent grasses and sedges we observed at the weekly scale, but not at the seasonal home range scale, is an example of how mismatching space-time relationships may mask fine-scale habitat selection patterns. Our result is consistent with what observed by Cornelis et al. (1999), which found that during spring and summer roe deer can double their exploitation of the graminoids typical of open pastures compared to the annual average.

Spatio-temporal heterogeneity of trade-offs between different limiting factors will shape habitat selection decision by individual animals and populations (Gaillard et al., 2010). According to classical theories of foraging (e.g., optimal foraging theory; Charnov, 1976) and habitat selection (Rosenzweig, 1981), animals are supposed to spend most time in those habitats richest in food, and habitat selection is expected to reflect food availability (Mysterud et al., 1999). However, it is then implicitly assumed that there is no trade-off between feeding sites

selection and other ecological processes, such as predator avoidance and intra- and inter-specific competition that instead may be important determinants of habitat selection. In particular, the effect of some of these additional elements might emerge at a one specific scale of analysis, thus originating differential habitat selection patterns at different temporal and spatial scales (DeCesare et al., 2013). For large herbivores, selection is commonly driven by the balance between forage quantity and quality and the presence of cover that decreases predation risk and offers protection from adverse weather conditions (Fryxell et al., 1988; Mysterud and Ostbye, 1999; Rettie and Messier, 2000). It is generally hypothesized that ungulates respond to “risk-forage” trade-offs in a hierarchical fashion (Senft et al., 1987), and may select habitats that reduce risk of predation at coarser scales and maximize forage intake at smaller scales (Rettie and Messier, 2000; Johnson et al., 2001; Hebblewhite and Merrill, 2009). Therefore, these trade-offs should be assessed at different spatio-temporal scales. In our study area, where the predation risk is low, intra- and inter-specific competition likely represent the most limiting factors for roe deer habitat selection. The positive selection for newly emergent grasses and sedges we observed only at a weekly scale might be the result of micro-site selection to avoid competition with sympatric competing species, e.g., red deer (*Cervus elaphus*). Besides inter-specific competition, intra-specific competition and population density represent other factors affecting habitat selection (Fretwell and Lucas, 1970; Fretwell, 1972). For example, Kie and Bowyer (1999) found that in white-tailed deer females with young made a greater use than males of chaparral-mixed grass habitats with dense canopy cover at moderate densities, whereas at high densities males that otherwise used more open habitats increased their use of the chaparral-mixed grass as levels of intra-specific competition increased. According to preliminary results of an extensive survey carried out in the area in the same years, the roe deer density was very low (indirect distance sampling with pellet group count: less than 3 deer/km<sup>2</sup>; Cagnacci, personal communication). However, the population density of other sympatric species, like red deer, is unknown. Thus, this remains a future line of research.

Another expected consequence of the analysis based on a “paired design” are stronger covariate effects. Indeed, regression coefficients for food items in our models were higher when using conditional logistic regression. On the one side, a matched analysis does not “average out” effects across a wide temporal scale. In particular, though, the increased coefficients for dynamic micro-habitat variables we observed may reflect the temporal variation in availability of those components. This may be particularly evident during spring and summer, when temperate ungulates are supposed to follow the “green wave” of the vegetation phenological cycle (Bischof et al., 2012). For example, flowering/fruitleting/mature shrubs only marginally affected roe deer habitat selection in the matched-paired design. The marginal significance of this covariate, that refers to phenological stages with highly nutritious portions of the plants (flowers and fruits), might be due to the fact that the flowering and fruiting phases of vegetation phenology are shorter compared to the longer leaf-growth stage. Lastly, the temporal variation in habitat selection patterns we observed for some micro-habitat variables did not emerge when referring to certain macro-habitat variables, such as canopy cover, but it did for specific habitat types, such as forest with dominant ash and hazel, also providing browsing availability. Overall, our findings highlighted the importance of considering the spatio-temporal resolution in habitat selection studies to define dynamic habitat selection drivers (e.g., plant phenology), especially when habitat covariates are collected at fine spatial scales. Roe deer represented a perfect case study for such approach, thanks to their well-established “picky” nature when selecting micro-habitat components (e.g., food items).

### Conclusions

Our results partially confirmed early observations on roe deer habitat selection, by using state-of-the-art habitat selection techniques. In particular, we highlighted the dependence on specific plant typology and phenology stages, which can be explained by the comparatively high

nutritional requirements of this small browser with low fat storages (Duncan et al., 1998).

Despite its high ecological plasticity with respect to coarse-grained habitat variables, roe deer might be directly affected by the alteration of fine-grained habitat characteristics, such as the availability of high-quality forage. Land use practices (esp. forest management of mature forests) and the variation of the vegetation growing season due to climate change are therefore potential factors affecting future distribution and abundance of roe deer throughout Europe. For example, a range contraction could be expected at the southern end of the distribution due to the increasing frequency of prolonged drought periods. In contrast, an expansion might be possible at northern latitudes or at intermediate altitudes in the alpine range due to lower snow depths and shorter duration of snow cover, and therefore earlier and prolonged vegetation growing season (e.g., Myrsterud and Sæther, 2011). Future studies might for example assess the effect of likely future changes in vegetation communities in mountainous areas, which are already considered sub-optimal environments for this species. ☞

## References

- Aanes R., Linnell J.D.C., Perzanowski K., Karlsen J., Odden J., 1998. Roe deer as prey. In: Andersen R., Duncan P., Linnell J.D.C. (Eds.). The European roe deer: the biology of success. Scandinavian Univ. Press, Oslo pp. 139–157.
- Albon S.D., Langvatn R., 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65: 502–513.
- Andersen R., Gaillard J.M., Liberg O., San José C., 1998. Variation in life-history parameters. In: Andersen R., Duncan P., Linnell J.D.C. (Eds.). The European roe deer: the biology of success. Scandinavian Univ. Press, Oslo pp. 285–306.
- Arnold T.W., 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *J. Wildl. Manage.* 74(6): 1175–1178.
- Barton K., 2014. MuMIn: Multi-model inference. R package version 1.10.5. <http://CRAN.R-project.org/package=MuMIn>
- Bates D. M., Mächler M., Bolker B.M., Walker S.C., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- Bernetti G., 1995. *Selvicultura speciale*. Unione Tipografico-Editrice Torinese, Torino.
- Bischof R., Loe L.E., Meisinger E.L., Zimmermann B., Van Moorter B., Myrsterud A., 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? *Am. Nat.* 180(4): 407–424.
- Bonnot N., Verheyden H., Blanchard P., Cote J., Debeffe L., Cargnelutti B., Klein F., Hewison A.J.M., Morellet N., 2015. Inter-individual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behav. Ecol.* 26(1): 105–114.
- Burnham K.P., Anderson C.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- Cagnacci F., Boitani L., Powell R.A., Boyce M.S., 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos. Trans. R. Soc. B* 365: 2157–2162.
- Cagnacci F., Focardi S., Heurich M., Stache A., Hewison A.J.M., Morellet N., Kjellander P., Linnell J.D.C., Myrsterud A., Neteler M., Delucchi L., Ossi F., Urbano F., 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos* 120: 1790–1802.
- Caloni F., Cortinovis C., Rivolta M., Alonge S., Davanzo F., 2013. Plant poisoning in domestic animals: epidemiological data from an Italian survey (2000–2011). *Vet. Rec.* 172(22): 1–4.
- Cederlund G., Bergqvist J., Kjellander P., Gill R., Gaillard J.M., Boisubert B., Ballon P., Duncan P., 1998. Managing roe deer and their impact on the environment: maximising the net benefits to society. In: Andersen R., Duncan P., Linnell J.D.C. (Eds.). The European roe deer: the biology of success. Scandinavian Univ. Press, Oslo pp. 337–372.
- Charnov E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9: 129–136.
- Compton B.W., Rhymer J.M., McCollough M., 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired. logistic regression. *Ecology* 83(3): 833–843.
- Cornelis J., Casar J., Hermyet M., 1999. Impact of season, habitat and research techniques on diet composition of roe deer (*Capreolus capreolus*): a review. *J. Zool.* 248: 195–207.
- De Jong C.B., Gill R.M.A., Van Wieren S.E., Burlton F.W., 1995. Diet selection by roe deer *Capreolus capreolus* in Kielder Forest in relation to plant cover. *For. Ecol. Manage.* 79: 91–97.
- DeCesare N.J., Hebblewhite M., Bradley M., Hervieux D., Neufeld L., Musiani M., 2013. Linking habitat selection and predation risk to spatial variation in survival. *J. Anim. Ecol.* 83(2): 343–352.
- Demarchi M.W., Bunnell E.L., 1995. Forest cover selection and activity of cow moose in summer. *Acta Theriol.* 40: 23–36.
- Demment M.W., van Soest P.J., 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am. Nat.* 125: 641–672.
- Duncan P., Tixier H., Hoffman R.R., Lechner-Doll M., 1998. Feeding strategies and the physiology of digestion in roe deer. In: Andersen R., Duncan P. and Linnell J.D.C. (Eds.). The European roe deer: the biology of success. Scandinavian Univ. Press, Oslo pp. 91–116.
- Frasconi P., 2002. L'alimentazione dell'orso bruno (*Ursus Arctos*, Linneo 1758) del Trentino, nell'ambito del progetto di reintroduzione "Life Ursus". Tesi di Laurea, Università degli Studi di Padova.
- Fretwell S.D., 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, NJ.
- Fretwell S.D., Lucas H.L. Jr., 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* 14: 16–36.
- Fryxell J.M., Greever J., Sinclair A.R.E., 1988. Why are migratory ungulates so abundant? *Am. Nat.* 131(6): 781–798.
- Gaillard J., Hebblewhite M., Loison A., Fuller M., Powell R., Basille M., Van Moorter B., 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. *Philos. Trans. R. Soc. B* 365: 2255–2265.
- Gates J.E., Harmann D.M., 1980. White-tailed deer wintering area in a hemlock-northern hardwood forest. *Can. Field Nat.* 94: 259–268.
- Gebert C., Verheyden-Tixier H., 2001. Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. *Mamm. Rev.* 31: 189–201.
- Gerard J.F., Le Pendu Y., Maublanc M.L., Vincent J.P., Poule M.L., Cibien C., 1995. Large group formation in European roe deer: an adaptive feature? *Rev. Ecol. Terre Vie* 50: 391–401.
- Gill R.M.A., Johnson A.L., Francis A., Hiscocks K., Peace A.J., 1996. Changes in roe deer (*Capreolus capreolus*) population density in response to forest habitat succession. *For. Ecol. Manage.* 88: 31–41.
- Guisan A., Theurillat J.-P., Kienast F., 1998. Predicting the potential distribution of plant species in an alpine environment. *J. Veg. Sci.* 9(1): 65–74.
- Hall L.S., Krausman P.R., Morrison M.L., 1997. The habitat concept and a plea for standard terminology. *Wildl. Soc. Bull.* 25: 173–182.
- Hebblewhite M., Merrill E.H., 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90(12): 3445–3454.
- Hebblewhite M., Merrill E., McDermid G., 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monogr.* 78: 141–166.
- Hirzel A.H., Le Lay G., 2008. Habitat suitability modelling and niche theory. *J. Appl. Ecol.* 45: 1372–1381.
- Holisova V., Obrtel R., Kozena I., 1982. The winter diet of roe deer (*Capreolus capreolus*) in the southern Moravian agricultural landscape. *Folia Zool.* 31: 209–225.
- Holisova V., Kozena I., Obrtel R., 1984. The summer diet of field roe bucks (*Capreolus capreolus*) in southern Moravia. *Folia Zool.* 33: 193–208.
- Holt R.D., 2003. On the evolutionary ecology of species' ranges. *Evol. Ecol. Res.* 5: 159–178.
- Hosmer D.W., Lemeshow S., 2000. Applied Logistic Regression. John Wiley and Sons, New York.
- Husson F., Josse J., Le S., Mazet J., 2015. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining. R package version 1.31.4. <http://CRAN.R-project.org/package=FactoMineR>
- Hutchinson G.E., 1965. The Ecological Theater and the Evolutionary Play. Yale Univ. Press, New Haven, CT.
- Jepsen J.U., Topping C.J., 2004. Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover. *Can. J. Zool.* 82: 1528–1541.
- Johnson D.H., 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61(1): 65–71.
- Johnson C.J., Parker K.L., Heard D.C., 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia* 127(4): 590–602.
- Kie J.G., Bowyer R.T., 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection and dietary niche. *J. Mamm.* 80(3): 1004–1020.
- Linnell J.D.C., Duncan P., Andersen R., 1998. The European roe deer: A portrait of a successful species. In: Andersen R., Duncan P., Linnell J.D.C. (Eds.). The European roe deer: the biology of success. Scandinavian Univ. Press, Oslo pp. 11–21.
- Maillard D., Picard J.F., Noel M.L., 1989. Le regime alimentaire estival du chevreuil dans une hêtre calcicole, déterminé par l'analyse des contenus stomacaux. *Bull. Off. Nat. Chasse* 139: 29–32.
- Manly B.F.J., McDonald L.L., Thomas D.L., Erickson W.P., 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London.
- Melis C., Jedrzejewska B., Apollonio M., Barton K.A., Jedrzejewski W., Linnell J.D.C., Kojala I., Kusak J., Adamic M., Ciuti S., Delehan I., Dykyy I., Krapine K., Mattioli L., Sagaydak A., Samchuk N., Schmidt K., Shkvyrya M., Sidorovich V.E., Zawadzka B., Zhyla S., 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Glob. Ecol. Biogeogr.* 18: 724–734.
- Millsbaugh J.J., Kesler D.C., Kays R., Glitzen R.A., Schulz J.H., Rota C.T., Bodinof C.M., Belant J.L., Keller B.J., 2012. Wildlife Radiotelemetry and Remote Monitoring. In: Silvy N.J. (Ed.). The Wildlife Techniques Manual - Management (Volume 2, 7th Edition). The Johns Hopkins Univ. Press, Baltimore, MD pp. 258–283.
- Morin P., Berteaux D., Klavana I., 2005. Hierarchical habitat selection by North American porcupines in southern boreal forest. *Can. J. Zool.* 83: 1333–1342.
- Mrlík V., 1991. Active protective behaviour of roe deer (*Capreolus capreolus*) in an open habitat during the winter season. *Folia Zool.* 40: 13–24.
- Mussa P., Aceto P., Abba C., Sterpone L., Meineri G., 2003. Preliminary study on the feeding habits of roe deer (*Capreolus capreolus*) in the western Alps. *J. Anim. Physiol. Anim. Nutr.* 87: 105–108.
- Myrsterud A., 1996. Bed-site selection by adult roe deer *Capreolus capreolus* in southeastern Norway during summer. *Wildl. Biol.* 2: 101–106.
- Myrsterud A., 1998. Habitat selection by roe deer relative to resource distribution and spatiotemporal scale. Dissertation, Univ. of Oslo.
- Myrsterud A., 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *J. Zool.* 247: 479–486.
- Myrsterud A., Ostbye E., 1995. Bed-Site Selection by European Roe Deer (*Capreolus Capreolus*) in Southern Norway during winter. *Can. J. Zool.* 73: 924–932.
- Myrsterud A., Ostbye E., 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildl. Soc. Bull.* 27(2): 385–394.
- Myrsterud A., Sæther B.E., 2011. Climate change and implications for the future distribution and management of ungulates in Europe. In: Putman R., Apollonio M., Andersen R. (Eds.). Ungulate management in Europe. Problems and practices. Cambridge Univ. Press, Cambridge pp. 349–375.
- Myrsterud A., Bjørnsten B.H., Ostbye E., 1997. Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* in an altitudinal gradient in south-central Norway. *Wildl. Biol.* 3: 27–33.
- Myrsterud A., Larsen P.K., Ims R.A., Østbye E., 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? *Can. J. Zool.* 77: 776–783.



- Mysterud A., Langvatn R., Yoccoz N.G., Stenseth N.C., 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *J. Anim. Ecol.* 70: 915–923.
- Nathan R., Getz W.M., Revilla E., Holyoak M., Kadmon R., Saltz D., Smouse P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. USA.* 105(49): 19052–19059.
- Pettorelli N., Gaillard J.-M., Duncan P., Ouellet J.-P., Van Laere G., 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* 128(3): 400–405.
- R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rabe-Hesketh S., Skrondal A., Pickles A., 2004. Generalized multilevel structural equation modeling. *Psychometrika* 69: 167–190.
- Ramanzin M., Sturaro E., Zanon D., 2007. Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. *Can. J. Zool.* 85: 280–289.
- Rettie W.J., Messier F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23: 466–478.
- Rosenzweig M.L., 1981. A theory of habitat selection. *Ecology* 62(2): 327–335.
- Said S., Servanty S., 2005. The influence of landscape structure on female roe deer home range size. *Landscape Ecol.* 20: 1003–1012.
- Said S., Gaillard J.M., Duncan P., Guillon N., Guillon N., Servanty S., Pellerin M., Le-feuvre K., Martin C., Van Laere G., 2005. Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *J. Zool.* 267: 301–308.
- Schemnitz S.D., 1994. Capturing and handling wild animals. In: Bookhout T.A. (Ed.). Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, MD pp. 370–418.
- Senft R.L., et al., 1987. Large Herbivore Foraging and Ecological Hierarchies. *BioScience* 37(11): 789–799.
- Staines B.W., 1976. The use of natural shelter by red deer (*Cervus elaphus*) in relation to weather in north-east Scotland. *J. Zool.* 18: 1–8.
- Storms D., Aubry P., Hamann J.-L., Said S., Fritz H., Saint-Andrieux C., Klein F., 2008. Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildl. Biol.* 14(2): 237–250.
- Therneau T., 2014. A Package for Survival Analysis in S. R package version 2.37-7. <http://CRAN.R-project.org/package=survival>
- Tixier H., Duncan P., 1996. Are European roe deer browsers? A review of variations in the composition of their diets. *Rev. Ecol. Terre Vie* 51: 3–17.
- Tixier H., Duncan P., Seehovic J., Yant A., Gleizes M., Lila M., 1997. Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. *J. Zool.* 242(2): 229–245.
- Tomkiewicz S.M., Fuller M.R., Kie J.G., Bates K.K., 2010. Global positioning system and associated technologies in animal behaviour and ecological research. *Philos. Trans. R. Soc. B* 365: 2163–2176.
- Tufto J., Andersen R., Linnell J., 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *J. Anim. Ecol.* 65: 715–724.
- Van der Wal R., Madan N., van Lieshout S., Dormann C., Langvatn R., Albon S.D., 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia* 123: 108–155.
- Van Soest P., 1994. The nutritional ecology of the ruminant. O&B Books Inc., Corvallis, Oregon.
- Wiens J.A., 1989. Spatial Scaling in Ecology. *Funct. Ecol.* 3(4): 385–397.
- Wood A.K., 1988. Use of shelter by mule deer during winter. *Prairie Nat.* 20: 15–22.
- Zuur A.F., Ieno E.N., Elphick C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1: 3–14.

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Table S1** Habitat covariates sampled by the used and available locations along the movement trajectories of roe deers.

**Table S2** Number of locations and relative percentage of GPS/VHF sampling sites.

**Table S3** PCA loadings (horizontal dimension) of habitat covariates.

**Table S4** AIC,  $\Delta$ AIC and AIC weights for the top models ( $\Delta$ AIC $\leq$ 2) for “topography and cover”.

**Table S5** AIC,  $\Delta$ AIC and AIC weights for the top models ( $\Delta$ AIC $\leq$ 2) for “plants”.

**Table S6** AIC,  $\Delta$ AIC and AIC weights for the top models ( $\Delta$ AIC $\leq$ 2) for “shrubs”.