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ORIGINAL PAPER

Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer

Federico Ossi · Jean-Michel Gaillard · Mark Hebblewhite · Francesca Cagnacci

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Abstract In alpine environments, snow typically reduces the accessibility of herbivores to food during winter and may hamper survival in those species with poor adaptation to move in deep snow. Supplemental feeding systems compensate for food limitation, but modify resource distribution and potentially affect individual space use. We investigated the importance of snow cover and supplemental feeding in shaping winter habitat use and selection of the European roe deer (*Capreolus capreolus*), a small deer species not specifically adapted to snow. We applied a used/available experimental design to assess the effects of snow cover on roe deer distribution at a fine scale and compared this approach with remotely sensed satellite data, available at moderate spatial resolution (snow MODIS). Based on this, we developed a resource selection function. We found a strong selection for habitat spots covered by forest where snow sinking depth was less pronounced, likely providing thermal and hiding protection on the one side and minimising the effect of snow on locomotion on the other. Roe deer showed only a minor preference for sites in proximity to feeding stations, possibly compensating the costs of access to these sites by means of a 'trail-making' behaviour. Snow cover assessed by moderate resolution satellite was not proportional to roe deer probability of use, highlighting the importance of local information on snow quality and distribution to complement remotely sensed data.

Keywords Roe deer · Winter resource selection · Snow sinking depth · Supplemental feeding · Resource selection function · Snow MODIS

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F. Ossi (✉) · J.-M. Gaillard
UUMR CNRS 5558 Biométrie et Biologie Évolutive, Université Claude Bernard Lyon 1, Bat G. Mendel 43 Bd du 11 Novembre 1918, 69622 Villeurbanne Cedex, France
e-mail: federico.ossi@gmail.com

F. Ossi · F. Cagnacci
Biodiversity and Molecular Ecology Department, IASMA Research and Innovation Centre, Fondazione Edmund Mach, Via Mach 1, 38010 San Michele all'Adige, TN, Italy

M. Hebblewhite
Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT, USA

M. Hebblewhite
Molecular Ecology Department, IASMA Research and Innovation Centre, Fondazione Edmund Mach, Via Mach 1, 38010 San Michele all'Adige, TN, Italy

Introduction

Snow cover is one of the environmental factors that are more affected by the current worldwide global change, especially in terms of timing and amount of average and extreme snowfalls (O'Gorman 2014), number of days with snow cover and quality of snow on the ground (Steger et al. 2013). In temperate and boreal regions, snow is a critical factor for survival of large herbivores over the winter (Telfer and Kelsall 1984), although it has a positive effect on body condition recovering in late spring and summer (Serrano et al. 2011). In many of these areas (Alps, Scandinavia, Central and Eastern Europe) supplemental feeding is a widespread management approach to compensate for resource scarcity and enhance overwinter survival of large herbivores (Putman and Staines 2004). Snow cover and presence of feeding stations are likely important factors potentially conditioning movement, resource selection and distribution of large herbivores. As such, the influence of these factors on the ecology of large herbivores has to be taken into account, both for a better understanding of the use of space by the target species and for conservation and management purposes (Lundmark 2008).

Snow can hamper individual survival of herbivores by limiting resource acquisition in two ways. First, snow leads to decrease resource availability by burying food items (Hovey and Harestad 1992). Grazers are especially sensitive to snow (Robinson and Merrill 2012), whilst mixed-feeders (e.g. grazing and browsing) often show shifts in food selection, as reported in mountain caribou (*Rangifer tarandus caribou*) (Kinley et al. 2007). Second, the hardness and density of the snow cover influence the sinking depth of the animals in the snow (Lundmark and Ball 2008), increasing the energetic cost of walking (Parker et al. 1984; Bunnell et al. 1990) and ultimately leading herbivores to decrease mobility and overall activity (Rivrud et al. 2010), especially in small and medium species (Telfer and Kelsall 1984; Mysterud et al. 1999).

The effect of snow on survival of large herbivores varies among species and depends from morphological or physiological adaptations to snow of the species. Formozov (1946) classified species as 'chionophobes' ('snow haters'), 'chioneuphores' ('snow tolerators') or 'chionophiles' ('snow lovers'), according to the way the animals cope with the limitations imposed by a snowy environment. Those species that did not develop particular adaptations to snow (i.e. 'chionophobes') can compensate by exhibiting behavioural responses to snow presence, which can take place at multiple spatiotemporal scales (Telfer and Kelsall 1984; Holand et al. 1998). For instance, seasonal migrations from summer to winter ranges are often triggered by the first snowstorms (e.g. white-tailed deer *Odocoileus virginianus*: Fieberg et al. 2008; moose *Alces alces*: Ball et al. 2001; roe deer: Mysterud 1999; Cagnacci et al. 2011). However, since seasonal migration does not always allow animals to escape snow during winter (Lundmark 2008), winter survival often depends on resource selection at a finer spatiotemporal scale, i.e. third-order resource selection sensu Johnson (1980). Between-patches selection within winter ranges (Lundmark 2008; Telfer and Kelsall 1984) enables individuals to maximise energy intake whilst minimising energy expenditure (Schmitz 1991). Selection of shallow snow locations for wintering such as steep slopes where snow usually blows off (Reitan 1988), or trail-making behaviour, with animals following well-defined trails where snow is harder and sinking is reduced (Crête and Larivière 2003; Lundmark and Ball 2008), provides examples of behavioural responses associated to such fine-scale resource selection.

The occurrence of supplemental resources as the ones provided with artificial feeding management is likely to alter individual movements and resource selection by providing attractive spots (see, e.g. moose: van Beest et al. 2010; roe deer: Guillet et al. 1996). Often, the presence of snow cover and availability of feeding stations coexist in space and time, for the aforementioned management practice. Thus, considering the interplay between the presence of a snow cover and its physical features (i.e. thickness, hardness, density) and wildlife management practices aimed to mitigate the harshness of mountain or northern climate is particularly relevant to investigate movement and resource selection by animals in winter.

Assessing the influence of snow on winter resource selection is not a trivial task and requires accurate snow data. At the local scale, snow thickness measurements have been recorded either directly in the study site (Ramanzin et al. 2007) or by meteorological stations located nearby (Mysterud et al. 1997; van Beest et al. 2011). At a large spatial scale, index of the presence of snow cover (but not snow thickness) has usually been derived from remotely sensed Moderate Resolution Imaging Spectroradiometer data (MODIS) (e.g. Cagnacci et al. 2011). However, the critical snow parameter of large herbivores for winter resource selection is the snow sinking depth, which affects the energetic cost of locomotion more than snow thickness by itself (Parker et al. 1984; Telfer and Kelsall 1984; Crête and Larivière 2003) and is likely to be more influential on resource selection (Lundmark 2008). Sinking depth of ungulates has been related to some kind of measurements of snow quality (e.g. hardness and density: Bunnell et al. 1990; Lundmark and Ball 2008), but to our knowledge, no direct comparative analysis of the performance of different snow metrics has been so far attempted to predict reliably resource selection.

We aimed here to fill this biological and methodological gap by quantifying the relative importance of a remotely derived index of snow cover presence (as derived by MODIS) and empirically collected snow measurements in an alpine population of European roe deer (*Capreolus capreolus*). Among the several characteristics of a snow layer (see Pruitt 2005 for an extended review), we focused here on snow thickness, defined as the total height of the snow layer from ground to surface, and snow sinking depth, i.e. a direct measurement of the height at which an individual sinks in the snow, that strongly depends on the hardness and density of the layer as well as on the locomotion and anatomy of the animal.

In this paper, we use roe deer as a suitable model species. Roe deer are a small cervid whose geographic distribution covers most of Europe. Roe deer exhibit a high ecological and behavioural plasticity, which allows them to adapt to a wide range of environments (Andersen et al. 1998), including northern countries and mountainous areas where winter conditions are particularly severe (Holand et al. 1998). However, roe deer are morphologically not adapted to move in deep snow, because of foot loading and low brisket height, with an energy expenditure for walking that becomes important when snow exceeds 50–60 cm (Holand et al. 1998). Moreover, fat and protein reserves in roe deer only cover at most 20 % of total energy expenditure (Mysterud et al. 2001), which makes roe deer dependent on continuous access to high-quality food

(Holand 1992). Roe deer are thus particularly sensitive to snow ('chionophobes' sensu Formozov 1946), with negative effects on population dynamics (see Gaillard et al. 1998 for a review). Consequently, roe deer are likely to be especially dependent on supplemental feeding during severe winters (Guillet et al. 1996), which provides high-quality food provided ad libitum during the critical season (Putman and Staines 2004).

In such a context, the interplay between thickness of the snow cover, its sinking depth and presence of feeding stations is expected to drive winter resource selection by roe deer in areas where severe winters occur. In roe deer, winter resource selection at the home range scale should be principally driven by the maximisation of net energy gain (e.g. Said et al. 2009). Indeed, other space use-conditioning physiological and behavioural phases, like territoriality and reproduction, exert their effects mainly in spring-summer (Hewison et al. 1998). Despite the expected influence of the presence of a snow layer and supplemental feeding on winter resource selection by large herbivores in alpine and northern environments, only few studies have been performed to date on that topic. In northern environments, roe deer in winter have been reported to select spots with less snow by exploiting local habitat types and topographical features (Holand et al. 1998). A selection for bedding sites under dense forest canopy where snow accumulation is limited (Mysterud et al. 1999) and thermal shelter reduces energetic requirements (Mysterud and Østbye 1995) has also been reported in roe deer.

We evaluated the effect of snow on roe deer winter resource selection in an alpine environment, using a tool expressly calibrated to evaluate roe deer sinking depth in the snow. We then assessed whether snow cover data derived from MODIS composite models importantly accounted for observed winter resource selection by roe deer. In this way, we aimed to evaluate whether an empirical assessment of snow conditions is more powerful than model-based predictions from MODIS data in explaining roe deer movements in winter, as discussed in other studies (Brennan et al. 2013). We expected roe deer to avoid areas with thick and high sinking snow because their short shoulder height prevents them to move in snow, as already reported in Scandinavia (prediction 1) (Mysterud et al. 1997; Ratikainen et al. 2007). We also expected no effect of MODIS snow data on roe deer winter resource selection in an alpine area because these data only provide qualitative information about the presence of snow in a given area, without any indication on the characteristics of the snow layer that are expected to shape individual winter resource selection (prediction 2). Moreover, the coarse spatial (500 m) and temporal (8 day periods) scale of these data may not satisfactorily fit the high local spatiotemporal heterogeneity of the alpine environment.

Since variation in thickness and sinking depth of the snow layer is affected by several environmental biotic and abiotic factors, we evaluated their importance in shaping roe deer winter resource selection. In particular, we investigated the effect of terrain slope, which influences snow persistency over time; forest canopy, since snow is thicker in open areas than under closed canopy (Lundmark and Ball 2008); and global solar radiation, an accurate measurement of the sun cumulated radiation that affects snow melting and surface hardness modification (Warren 1982), influencing therefore the snow layer thickness and sinking depth. We expected roe deer to select woody steep areas with high solar radiation to limit both the thickness and persistence of snow (prediction 3) (Mysterud et al. 1999; Lapena and Martz 1996). We also evaluated the effects of supplemental feeding on winter resource selection by roe deer. Following previous studies (Cederlund 1982; Guillet et al. 1996), we expected roe deer to select feeding stations by ranging close to these attractive points (prediction 4).

Materials and methods

Study area and sampling animals

The study was conducted in a 40,000 ha mountainous area in north-eastern Italian Alps (Val Rendena and Valli Giudicarie; Autonomous Province of Trento, Italy; Fig. 1). Eighteen adult roe deer (4 males and 14 females) were captured during a field campaign in winter 2012–2013. Animals were captured with wooden box traps, baited with pellets of cereals and corn, and placed in the proximity of feeding stations filled up ad libitum throughout the winter. Capture sessions lasted a few days each, during which access to the food in the feeding stations was prevented in order to drive the roe deer into the box traps. Captured roe deer were marked and equipped with GPS-GSM radio collars (VECTRONIC Aerospace GmbH, GPS plus 3D collars) programmed to collect fixes at 3 h intervals. The study area is typically alpine, characterised by craggy terrain with elevations ranging from 400 m in the main valley bottoms to 3500 m at the highest peaks. The climate is continental in the valleys, whilst it is strongly alpine above tree line. Based on data from 1990 to 2013, average yearly rainfall in the area is around 1100 mm, whilst average monthly temperature ranges from −1 °C in December to 18 °C in July. During winter, snow layer thickness is generally shallow (<20 cm) at the lowest elevation, whilst it is deeper than 1 m above 1600–1700 m where it might persist from December to April (data source: www.meteotrentino.it). The area is covered to about 40 % by forest, both coniferous and deciduous; vegetation composition ranges from mixed deciduous trees mostly made of common beech (*Fagus sylvatica*), mixed with larch (*Larix* spp.) and pine (*Pinus* spp.), to conifer forests composed of pine and spruce (*Picea* spp.). Above tree line (about 1800 m), mountain pines (*Pinus mugo*) dominate, whilst open habitats are

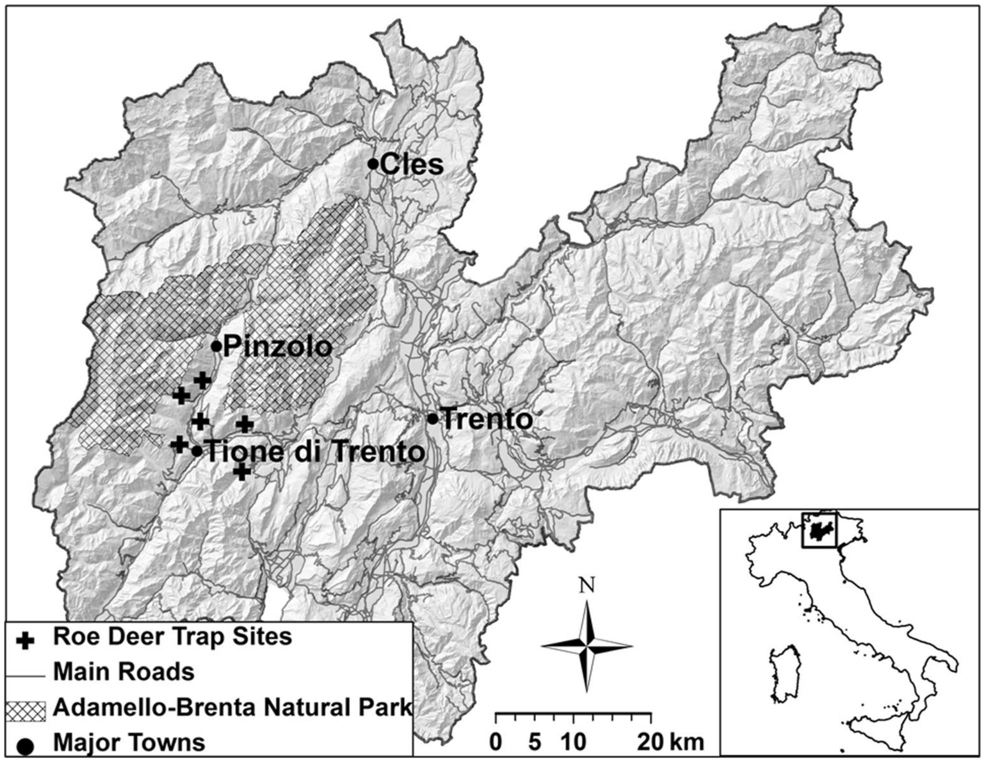

Fig. 1 The study area set in the western portion of Trentino, Italy, in the Eastern Alps

covered by alpine herbaceous species. Roe deer is present in the area with a density of 4.5–7.0 ind/100 ha, according to the estimate by means of pellet-group count distance sampling method (Marques et al. 2001; Acevedo et al. 2010) obtained in a previous research performed in an adjacent area with similar characteristics (Cagnacci F., personal communication). Other large herbivores include chamois (*Rupricapra rupricapra*), red deer (*Cervus elaphus*), mouflon (*Ovis musimon*) and ibex (*Capra ibex*). A reintroduced population of brown bear *Ursus arctos* of a minimum number of 40–44 individuals also occupies the area, along with red fox (*Vulpes vulpes*). Roe deer are hunted with selective quotas from September to the end of December, but adult males are customarily all killed within the first 2 weeks of September. In 2012, in the study area, more than 300 roe deer have been shot, mainly fawns and young adults (less than 3 years old); in the same period, about 100 red deer, 70 mouflons and more than 1000 chamois have been hunted in the same area, whilst ibex is not hunted.

Field data collection and processing

We investigated roe deer resource selection by performing a field campaign during winter 2012/2013. We applied a used versus available but unused empirical design to assess resource selection by individual roe deer (Manly et al. 2002). The identification of the used and available sites for sampling included several steps. First, we overlapped a grid of 50 m size cells with the GPS relocations of the previous 8 day period, and we determined the cell that included the biggest number of GPS relocations. We then identified the 'used site' for each individual during an 8 day period as the barycentre of the relocations falling in the most used cell. At this stage, we determined the 'available site' as a random location that fell in a not used cell, within a 300 m radius buffer centred on the 'used site' (Fig. 2). Thus, empirical measures were paired at both used and available sites (Thomas and Taylor 2006). In some cases, GPS locations were not transmitted on time through the GSM system, due to low coverage. Thus, the used location was assessed by triangulation with the Very High Frequency (VHF) beacon; the available site was determined by a combination of two random numbers, the first indicating an angle to get a direction from the used site (number between 0 and 359) and the second indicating the distance (in meters) from the used site in that direction (number between 150 and 300). In each site, used or available, we firstly recorded the 'index of snow cover patchiness', i.e. a qualitative indicator of snow layer cover patchiness (three classes: uniform, patchy or absent). Then, when snow was present, we measured its thickness with a rigid meter. We then assessed snow sinking depth with a snow battage probe (provided by company 'Obiettivo neve', www.obiettivoneve.it). This tool is commonly used to measure the hardness of the snow layer (see Appendix 1 for full details). We calibrated the snow probe to roe deer by applying the distal portion of a roe deer hind leg to the tip of the probe to measure more accurately the effective snow sinking depth of roe deer. With an equal distribution of

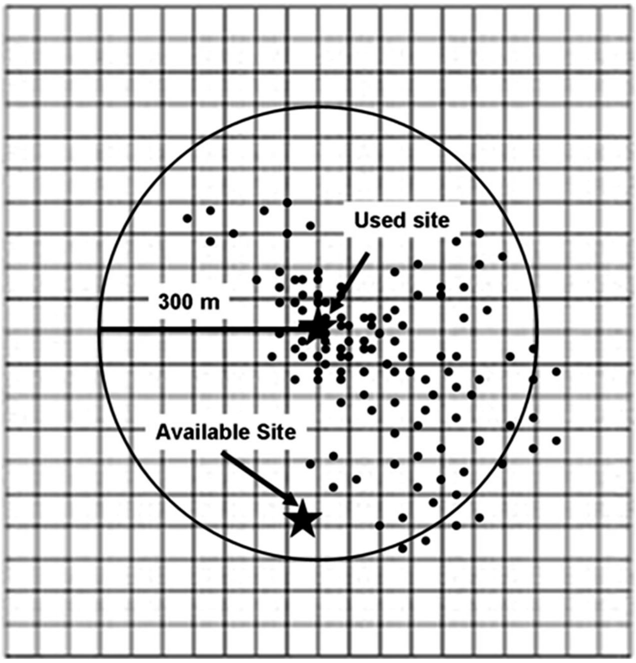

Fig. 2 Scheme of the determination of the used and available sites for empirical snow sampling assessment. The size of the buffer is indicated. *Filled circles* represent GPS locations

the mass on the three legs stepping on the ground during a walking locomotion mode, the weight that each leg exerts on the snow surface is:

$$F = (m/3) * g$$

when assuming that roe deer walking motion can be simplified by a static assessment. Thus, given the average roe deer body mass in the area (20±1.6 kg; Autonomous Province of Trento 2010), we provided the probe with additional mass so that the overall weight exerted by the probe was equal to 70 N. We performed the snow sinking measurements by gently releasing the probe in the snow and measuring the reached depth with a rigid meter. At each site where snow assessment was performed, we did multiple randomised trials to take into account local variation in snow conditions. Then, we computed the average and standard deviation of those multiple measures for both snow thickness and sinking depth. Lastly, we recorded the presence and the type of forest canopy (three classes: open spots, coniferous trees and broad-leaved trees) both at 'used' and 'available' sites.

We then processed the collected data in Quantum GIS (QGIS Development Team 2013) software to join the environmental variables to 'used' and 'available' sites. A digital elevation model (DEM) at 10 m resolution was used to estimate terrain slope and 3D distances to feeding stations. We elaborated in ArcMap 9.2 (ESRI 2009) a model to compute the solar radiation in each pixel, based on a combination of a digital terrain model and sky view with default values for diffuse radiation. We used remotely sensed MODIS (MODIS10A2) on 8 day intervals at 500 m resolution to get 'Snow MODIS', i.e. a remote index of snow cover presence (a binary variable) each week in a given pixel (Hall et al. 2002). Data sources and processing and the complete list of covariates are reported in Table 1. We evaluated the accuracy of the empirical forest canopy classification by matching it with the data derived from a reclassified CORINE IV level layer (CLC) at a resolution of 25 m (CORINE Land Cover level IV; Commission of the European Communities 2006). We individually analysed each case of mismatch by projecting them on an orto-photo raster at a resolution of 10 m and decided onto a final classification.

Modelling and statistical analysis

We selected an a priori list of covariates based on biological knowledge. We checked for possible collinearity problems by fitting bivariate regressions (Zuur et al. 2010) and accounted for them either by retaining only one covariate for each collinear group of variables or by fitting the collinear terms in interaction. Moreover, we controlled for temporal autocorrelation by fitting a smoothed effect of time (week) based on cyclic splines. We thus obtained a 'full' a priori model (for a detailed description of the procedure: Appendix 2). We checked for outliers in the distribution of the retained covariates by visual observation. For further confirmation, we took into account this aspect also after fitting the final model, by means of analysis of hat values, i.e. the effect that each observed value has on each fitted value (the Hat Matrix, Hoaglin and Welsch 1978).

We investigated the winter use by roe deer of each habitat covariate by means of descriptive statistics (average±standard deviation for continuous variables; percentage of use for dummy and categorical variables). We assessed the winter resource selection of roe deer by fitting a logistic regression within a generalised linear mixed model (GLMM) framework (Hosmer and Lemeshow 2000). In these models, the dependent variable took values 1 (when the site was used) or 0 (when the site was available but unused) (Boyce and McDonald 1999). We estimated the coefficients for the exponential approximation to the logistic discriminant function, which yields a relative probability that roe deer select a given location (on a logit scale) as a function of uncorrelated a priori covariates (Lele et al. 2013). The response variable was modelled for dependence on predictor variables in the context of the GLMMs framework to accommodate autocorrelation and variation in sampling intensity, by fitting individual as random effect (Gillies et al. 2006). Since this effect was negligible (see "Results" and Table 4), we removed it from the model, thus resuming to a generalised linear model framework (GLMs) to perform the analyses. We performed a model selection on all possible models derived from the full model obtained after the exploratory analyses, based on Akaike

Table 1 Climatic and geographic covariates computed for used and available roe deer sites

Variable	Source and website (optional)	Type, resolution	Elaboration and tools
Canopy cover	• Corine Landcover (CLC) V level 2006 • http://www.sinanet.isprambiente.it/Members/mais/Corine/clc2006_IVliv_ita_/view	Vector, 25 m	• Reclassification to 5 classes (not available; open; conifer woods, but not larch; larch woods; broad-leaved woods) • Tool: v.reclass within QGIS Sextante toolbox
Slope (0–90°)	• Digital Terrain Model for the Autonomous Province of Trento	Raster, 5 m	• None • None
Distance from closest feeding site	• Digital Terrain Model for the Autonomous Province of Trento • Coordinates Feeding Sites from Local Hunters Association	Raster, 5 m	• Elaboration in ESRI ArcGIS 9.2 • Tool: Path Distance within Spatial Analyst toolbox
Solar radiation (kWh/m^2/month)	• Digital Terrain Model for the Autonomous Province of Trento	Raster, 20 m	• Elaboration in ESRI ArcGIS 9.2, UNIFORM_SKY model for diffuse radiation • Default values for diffuse proportion (0.3) and transmissivity (0.5) • Tool: solar analyst toolbox (ESRI ArcGIS 9.2)
Snow MODIS (presence/8 days)	• NASA-MODIS snow • http://modis-snow-ice-gsfc.nasa.gov/MOD10A2.html	Raster, 500 m	• None • None

information criterion (AIC) scores (Burnham and Anderson 2002). We retained those models with ΔAIC<2, on which we computed the predictors' weight. In compliance with the multi-model inference theoretical framework, we obtained a final model by averaging weighted coefficients and standard errors across retained models (Burnham and Anderson 2002). In parallel, we obtained a simplified version of the model by selecting only those covariates included in all models with ΔAIC<2 (i.e. predictor's weight=1), in compliance with the principle of parsimony. This model allowed us to operate model validation techniques as in the classic Resource Selection Analysis framework (Boyce et al. 2002). On this model, we therefore performed goodness-of-fit tests using *R*-squared test, Hosmer-Lemeshow test, classification tables and receiving operating characteristics (ROC) (Boyce et al. 2002; Hosmer and Lemeshow 2000). Moreover, a *K*-fold cross-validation (Boyce et al. 2002; *K*=5) was applied to assess the robustness of the model. Finally, we checked for multicollinearity of the retained model calculating variance inflation factors (VIF) (Graham 2003). All the analyses were performed in R (version 3.0.2 The R Foundation Core Team 2013; lme4 R package: Bates et al. 2014; MuMIn package: Barton 2013).

Results

During the winter 2012/2013, 252 used and available matching sites were assessed for local variables. Among those used/available sites, 104 cases were identified by means of the triangulation with the VHF beacon. Empirical snow assessment was performed at 139 sites (62 used and 77 available), whereas snow was absent in the remaining 113 sites (64 used and 49 available). Forest canopy was misclassified compared to CORINE IV data in 82 sites (33 %). An analysis with orto-photo raster at a resolution of 10 m indicated that misclassification occurred because the coarse spatial resolution of CORINE layers did not allow identifying habitat differences at a very small spatial scale. In such cases, we used our empirical classification of forest canopy to model the resource selection function.

A strong collinearity occurred between average snow thickness and sinking depth (r=0.89) and between these metrics and their standard deviations (see Table 2 for a comprehensive correlation matrix). Since snow sinking depth more than thickness is directly related to ungulate ability to move in snow (Parker et al. 1984), we retained only average sinking depth measurements in the following analyses. The a posteriori screening for outliers based on analysis of hat values (computed on the simplified final model, see below) led to the identification of two outliers. The putative outliers were a used location and its paired available site, which referred to a roe deer migrating out of its winter range. We excluded these data from the analysis, since our objective was to consider winter behaviour, before spring migration.

When we looked at the environmental characteristics at sites used by roe deer (Table 3), we found that roe deer used mainly steep sites (29.06±9.47°) under forest canopy (99.98 % of the sites), whilst the sites varied widely both for incidence of solar radiation (75.53±32.39 kWh/m^2) and distance from the closest feeding station (228.89±203.22 m). Data derived from MODIS indicated that snow cover was present in 54 % of the cases. Our empirical survey partially supported this result from remote sensing: snow layer was complete in 32 % of the visited used sites and patchy in 29 %

Table 2 Correlation matrix for the a priori set of covariates, chosen for their biological meaning

	AST	ASSD	SDST	SDSSD	SM	SC	DFS	Sl	SR	CP	Sex
AST	1.00	0.89*	0.61*	0.59*	0.05	0.14	−0.05	−0.32	−0.14	0.28	0.12
ASSD	0.89*	1.00	0.70*	0.75*	0.09	0.19	−0.02	−0.24	−0.21	0.19	0.11
SDST	0.61*	0.70*	1.00	0.85*	0.06	0.29	−0.01	−0.12	−0.20	0.05	0.04
SDSSD	0.59*	0.75*	0.85*	1.00	0.11	0.33	0.00	−0.16	−0.20	0.05	0.04
SM	0.05	0.09	0.06	0.11	1.00	0.09	0.11	−0.01	−0.13	0.12	0.10
SC	0.14	0.19	0.29	0.33	0.09	1.00	0.11	−0.02	−0.11	0.08	0.01
DFS	−0.05	−0.02	−0.01	0.00	0.11	0.11	1.00	0.30	0.01	0.02	0.32
Sl	−0.32	−0.24	−0.12	−0.16	−0.01	−0.02	0.30	1.00	−0.03	−0.40*	0.13
SR	−0.14	−0.21	−0.20	−0.20	−0.13	−0.11	0.01	−0.03	1.00	0.13	0.08
CP	0.28	0.19	0.05	0.05	0.12	0.08	0.02	−0.40	0.13	1.00	0.00
Sex	0.12	0.11	0.04	0.04	0.10	0.01	0.32	0.13	0.08	0.00	1.00

Relevant correlations are indicated by a star

AST average snow thickness, *ASSD* average snow sinking depth, *SDST* standard deviation of snow thickness, *SDSSD* standard deviation of snow sinking depth, *SM* snow from MODIS, *SC* index of snow cover patchiness, *DFS* distance from the closest feeding station, *Sl* slope, *SR* solar radiation, *CP* canopy presence

of the cases, whilst it was absent in the remaining 39 %. In those cases where a snow layer was present, the snow sinking depth was on average shallow (8.86±5.19 cm).

On the basis of our hypotheses and the aforementioned exploratory analysis, we evaluated the relative probability that roe deer selected a given site (on a logit scale) as a function of the following full model: average of snow sinking depth, index of snow cover patchiness, snow MODIS, a two-way interaction between slope and canopy presence, solar radiation, distance from the closest feeding station and sex. The equation of the full model was the following:

$$\mathrm{Logit}(P) = \frac{\exp\left(\widehat{\beta}_1\left(ns(W) + \widehat{\beta}_2(\mathrm{DFS}) + \widehat{\beta}_3(\mathrm{ASSD}) + \widehat{\beta}_4(\mathrm{SM}) + \widehat{\beta}_5(\mathrm{CP} * \mathrm{Sl}) + \widehat{\beta}_6(\mathrm{SR}) + \widehat{\beta}_7(\mathrm{Sex}) + \widehat{\beta}_8(\mathrm{SC}) + \widehat{\beta}_9(\mathrm{RI})\right.\right.}{\left(1 + \exp\left(\widehat{\beta}_1\left(ns(W) + \widehat{\beta}_2(\mathrm{DFS}) + \widehat{\beta}_3(\mathrm{ASSD}) + \widehat{\beta}_4(\mathrm{SM}) + \widehat{\beta}_5(\mathrm{CP} * \mathrm{Sl}) + \widehat{\beta}_6(\mathrm{SR}) + \widehat{\beta}_7(\mathrm{Sex}) + \widehat{\beta}_8(\mathrm{SC}) + \widehat{\beta}_9(\mathrm{RI})\right)\right.\right.}$$

where Logit(P)=relative probability that roe deer selected a given location (on a logit scale) as a function of the covariates x_n, where n is the coefficient for each x covariate estimated from logistic regression (Manly et al. 2002; Lele et al. 2013); W = observation week; DFS = distance from the closest feeding station; ASSD = average of snow sinking depth; SM = snow derived from MODIS; CP = canopy presence; Sl = slope; SR = solar radiation; Sex =

Table 3 Environmental characteristics at sites used by roe deer. For continuous variables, we computed the average and standard deviation, whilst for categorical ones, we determined the percentage of occurrence for any specific category (n=250)

Variable	Average	Standard deviation
Distance to closest feeding site (m)	228.89	203.22
Slope (°)	29.06	9.47
Solar radiation (kWh/m^2)	75.53	32.39
Average snow sink depth (cm)	8.86	5.19
Variable	Number occurrences	Percentage
Canopy closure ‘present’	123	99.98
Canopy closure ‘absent’	2	0.02
Snow MODIS ‘present’	68	0.54
Snow MODIS ‘absent’	57	0.46
Snow cover ‘complete’	48	0.39
Snow cover ‘patchy’	36	0.29
Snow cover ‘absent’	41	0.32

sex of the individual; SC = index of snow cover patchiness; and RI = random effect of the individual. Adding individual roe deer identity as a random factor did not substantially improve the goodness-of-fit of the model (Table 4; proportion of variance explained 3.15 e-13). The averaged model by means of multi-model inference (see Appendix 2 and Tables 5 and 6) indicated that roe deer strongly avoided sites without forest canopy (s=−5.208±3.612; w_i=1), characterised by high snow sinking depth (s=−0.053±0.023; w_i=1) and far from the closest feeding station (s=−0.003±0.001; w_i=1). Other averaged coefficients, such as snow derived from MODIS or slope, did not differ from 0 (s=0.162±0.292; w_i=0.097 and s=0.011±0.016; w_i=0.653, respectively).

The final simplified model based only on covariates with w_i=1, included forest canopy (β=−3.088±0.747) (Fig. 3), snow sinking depth (β=−0.055±0.022) (Fig. 4a) and closeness to feeding station (β=−0.003±0.001) (Fig. 4b). These effects do not change sign nor magnitude with respect to the averaged coefficients shown above.

Goodness-of-fit of the simplified model using Hosmer-Lemeshow test was satisfactory (χ^2=9.72; p=0.29). The integral of ROC (Fig. 5) was equal to 0.74, which indicates a statistically significant difference between the fitted model and the null one. Consistently, when we derived a classification table (with a cut-point of 0.5), we correctly classified 67 % of the data, with a specificity equal to 0.792 and a sensitivity equal to 0.52. Lastly, the K-fold cross-validation estimate of accuracy was equal to 0.76 (p=0.02), showing the robustness of the fitted model. Variance inflation factors did not show any evidence of collinearity in the final simplified model (canopy presence 1.0008; distance from the closest feeding station 1.002; average snow sinking depth 1.001). All these statistics clearly indicate that the model we selected provided a satisfactory representation of the data.

Discussion

In this work, we examined the winter habitat use and selection of individual European roe deer living in an alpine environment, by testing the effect of a series of biotic and abiotic factors on movement tactics of these individuals. In particular, we were able to quantitatively measure the effect of snow as a limiting factor on roe deer habitat use and selection by combining a robust matched case experimental design with a tool to measure snow sinking depth. Although the direct effect of snow on resource availability is expected to be more pronounced in intermediate feeders and grazers (Van Beest et al. 2011) than in browsers, our results demonstrate that the presence of snow does limit resource accessibility in browsers that are not adapted to move in deep snow like roe deer (Holand et al. 1998; Mysterud et al. 1997; Ratikainen et al. 2007). Our findings therefore support that roe deer should be classified as 'chionophobe' (Formozov 1946; prediction 1). Conversely, we only partly supported the expected relevance of supplemental feeding in shaping roe deer local distribution (prediction 4). Roe deer are dependent on continuous access to high energetic food, given their low ability to rely on fat and energy accumulation (Mysterud et al. 2001). We might therefore expect an intense use of feeding stations, representing a high-quality food source, under food scarcity and low accessibility due to snow cover. Feeding stations may therefore act as central feeding places where individuals tend to converge (Van Beest et al. 2010). Indeed, the quality and the quantity of

Table 5 List of the models retained by AIC model selection (ΔAIC<2). Details are provided in Appendix 2

Candidate models (ΔAIC<2)	AIC
Used_Avail~Sex+ASSD+DFS+CP*Sl	297.8
Used_Avail~ASSD+DFS+CP*Sl	298.1
Used_Avail~Sex+ASSD+DFS+CP	298.2
Used_Avail~ASSD+DFS+CP	298.3
Used_Avail~ASSD+DFS+SR+CP*Sl	298.5
Used_Avail~Sex+ASSD+DFS+SR+CP*Sl	298.5
Used_Avail~ASSD+DFS+SR+CP	298.8
Used_Avail~Sex+ASSD+DFS+SR+CP	298.9
Used_Avail~ASSD+DFS+CP+Sl	299.5
Used_Avail~Sex+ASSD+DFS+CP+Sl	299.5
Used_Avail~Sex+SM+ASSD+DFS+CP*Sl	299.6
Used_Avail~SM+ASSD+DFS+CP*Sl	299.7
Used_Avail~ASSD+DFS+SR+CP+Sl	299.8

DFS distance from the closest feeding station, *ASSD* average of snow sinking depth, *SM* snow derived from MODIS, *CP* canopy presence, *Sl* slope, *SR* solar radiation, *Sex* sex of the individual

Table 4 Comparison between a full model including a random effect of the individual and the same model without the random component

Model	Res. dev.	% variation random
Model random: Logit(P)~W+DFS+ASSD+SM+CP*Sl+CP+Sl+SR+Sex+SC+RI	278.8	PVR=3.16e-13
Model fixed: Logit(P)~W+DFS+ASSD+SM+CP*Sl+CP+Sl+SR+Sex+SC	278.86	

The percentage of variation explained by the random effect of the individual (PVR) is presented. Details are explained in Appendix 2

W observation week, *DFS* distance from the closest feeding station, *ASSD* average of snow sinking depth, *SM* snow derived from MODIS, *CP* canopy presence, *Sl* slope, *SR* solar radiation, *Sex* sex of the individual, *SC* index of snow cover patchiness, *RI* random effect of the individual

Table 6 (a) Model averaged coefficients and standard errors of the covariates included in the 13 models retained by means of AIC model selection (see Table 5). The predictor's weight of each term is provided. (b) Coefficients and standard errors of the covariates of a simplified version of the final model

Covariate	Averaged estimate	Std. error	Pred. weight
(a) Model averaging			
ASSD	−0.0531	0.0227	1
DFS	−0.0027	0.0008	1
CP	−5.2081	3.6114	1
SexM	0.5066	0.3568	0.486
Sl	0.0111	0.0164	0.653
CP*Sl	0.2071	0.1389	0.5
SR	0.0059	0.0049	0.368
SM	0.1615	0.2919	0.097
(b) Simplified model			
ASSD	−0.0549	0.0216	
DFS	−0.0023	0.0007	
CP	−3.0871	0.7465	

Details are provided in Appendix 2

DFS distance from the closest feeding station, *ASSD* average of snow sinking depth, *SM* snow derived from MODIS, *CP* canopy presence, *Sl* slope, *SR* solar radiation, *Sex* sex of the individual

food provided in feeding stations are higher than those of any forest plant in harsh winter, thus justifying the expectation of intense use (Guillet et al. 1996). However, the distribution of snow cover patches, rather than that of feeding stations, seemed to drive roe deer habitat use in winter, at a fine scale.

Our study typically addressed a third-order resource selection question (sensu Johnson 1980). Roe deer has been described as a species with a high behavioural and ecological plasticity (Andersen et al. 1998). In our sampled population, most individuals were able to survive over winter in an environment for which they are neither morphologically nor physiologically adapted (Holand et al. 1998), by adjusting their movements to select favourable patches within the home range. The heterogeneous distribution of snow cover at fine spatial scale, which is typical of mountain environments at

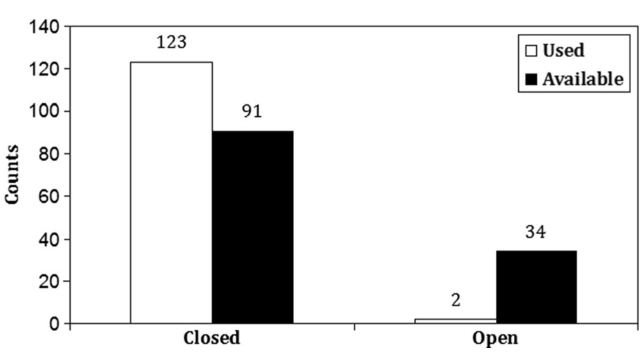

Fig. 3 Distribution of used versus available plots of roe deer in open and closed habitats

intermediate elevations, allowed roe deer to prefer spots with the absence or shallow snow (see also Guillet et al. 1996), even in the presence of heavy snowfalls in the area. In areas with a more uniform snowpack across the landscape like observed in Northern Europe, the proximity to feeding stations might hold a stronger effect on roe deer habitat use. As an anecdotal observation supporting our interpretation, five individuals died within a month for late heavy snowfalls (March 2013), that brought a thick, continuous and slushy layer of snow, even at low altitudes. Most animals showed signs of starvation and very low fat content.

In our case study, all roe deer could potentially use the feeding stations because they were captured in their proximity. On average, roe deer did select for locations close to feeding stations, but the selection coefficient was not as strong as expected. However, in several cases, we could observe a clear trail-making behaviour (F. Ossi, personal communication). Trail-making can be considered another fine-scale behavioural adaptation to snow, on top of preference for shallow snow patches within the home ranges. Trail-making has been observed for the majority of species dwelling in snowy environments, for the obvious advantages of limiting energetic expenditure of locomotion and increasing velocity of movements (e.g. white-tailed deer *O. virginianus*: Telfer and Kelsall 1984; coyote *Canis latrans*: Crête and Larivière 2003). Therefore, roe deer might rely on feeding stations as opportunistic food sources, but those may not necessarily result in central feeding places. This outcome has profound consequences on the management of such practice. We suggest to consider supplemental feeding for roe deer only in areas that record abundant snow precipitation and permanence of snow cover on the ground for extended periods of time throughout winter, i.e. where snow truly represents a limiting factor for these browsers. We also indicate that feeding station placement should take into account the trade-off between energy expenditure for locomotion in snow, connectivity to refuge resting areas and energy gain by forage. In fact, our study showed that roe deer are more sensitive to snow sinking depth, which increases locomotion cost, than to the proximity to feeding stations, which animals can access quite easily using trails. Hence, managers should place feeding stations in specific sites that can be accessed relatively more easily than others, even in the worst weather conditions. Since roe deer showed a great preference for local sites under forest canopy, where snow is shallower and thermal protection can be found (see below), feeding stations may be placed in forested areas. This way, animals should be able to accede them reducing locomotion costs whilst improving thermoregulation and finding hiding shelters.

Indeed, the main driver of roe deer habitat use was the presence of canopy cover, not snow presence or distribution of feeding stations. Topographic factors, such as terrain steepness and solar radiation, were instead not retained in the

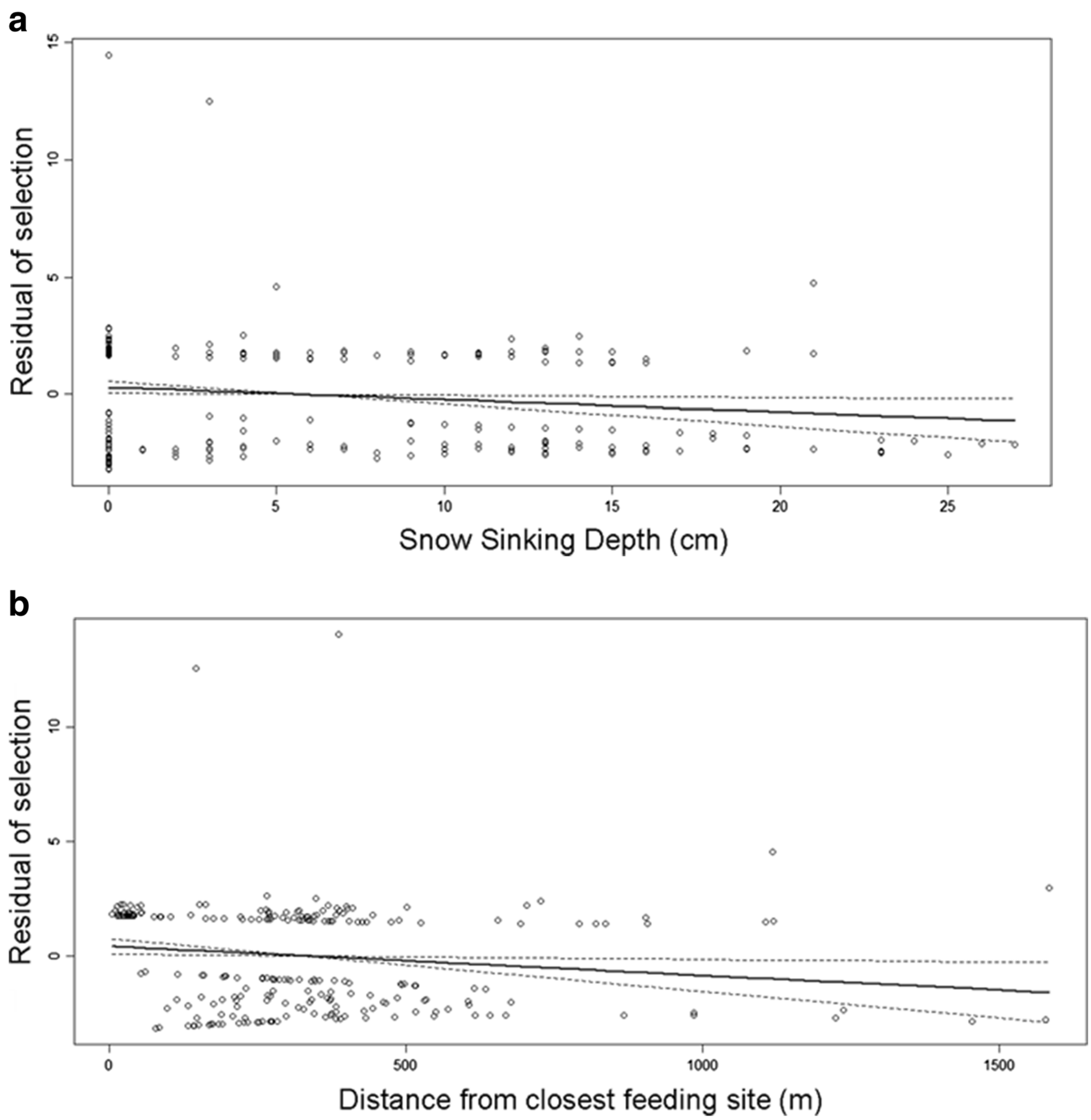

Fig. 4 Partial residual plots showing the effects of average snow sinking depth (**a**) and distance from the closest feeding station (**b**) on winter resource selection in roe deer, after controlling for the effects of all other covariates in the simplified version of the model (Table 6). A partial residual plot is a plot of $r_i+b_k\times i_k$ versus x_{ik}, where r_i is the ordinary residual for the *i*th observation, x_{ik} is the *i*th observation of the *k*th predictor and b_k is the regression coefficient estimate for the *k*th predictor. The *regression line* indicates the partial fit, the *dashed lines* indicate the standard error

models (prediction 3). Snow is consistently deeper in open areas than under closed woods (Lundmark and Ball 2008), because the forest canopy intercepts snow and induces structural changes to snow cover on the ground (Mysterud et al. 1999). In addition, canopy also provides thermal cover and offers an efficient refuge to avoid wetting of pelage and thereby maintain body temperature (Mysterud and Østbye 1995). This issue is particularly relevant in a small-sized species like roe deer, which is susceptible to cold stress given the small surface-volume ratio (Holand et al. 1998). Lastly, canopy offers an excellent hiding shelter. Cagnacci et al. (2011) previously found that in heterogeneous landscapes, roe deer tend to spend the least time in open areas, by crossing them rapidly during migration events. We therefore argue that woody areas in winter time represent the most preferred habitat for all aforementioned factors combined. Contrary to our prediction, we did not detect a clear effect of slope on roe deer use. Whilst slanting ground generally diminish the permanence of snow, by increasing the sliding factor (Lapena and Martz 1996) and thus representing a potentially favourable factor to roe deer presence, this trades-off with the higher energy requirements for moving on steep terrain (Lachica et al. 1997). Moreover, the effect of canopy cover on snow persistence on the ground might prevail on that of sloping

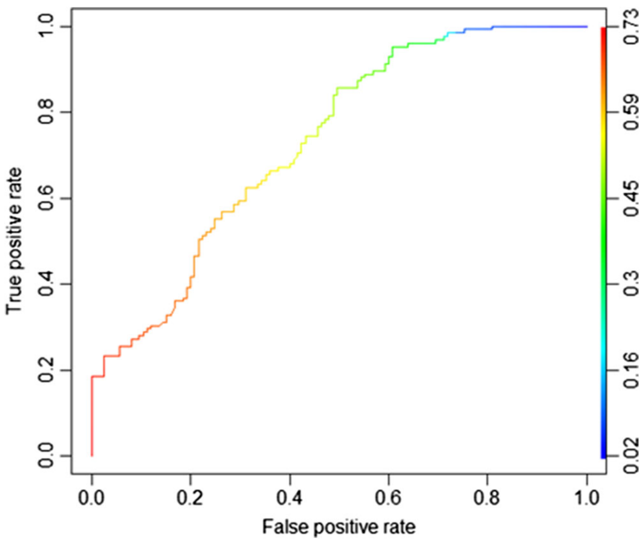

Fig. 5 The receiver operating characteristics (ROC) curve from the best model fit. ROC curves compare sensitivity (false negative rate) versus specificity (true positive rate) across a range of values (cut offs) for the ability to predict a dichotomous outcome. The more the specificity increases, the more sensitivity decreases (i.e. false positive rate increases). The more the curve displays an asymptotic shape, the bigger is the area under the ROC curve, and the better is the fit of the model

terrain. The absence of any effect of solar radiation is more surprising. The index of solar radiation combines information from the digital terrain models, the height of sun on the horizon and the sky view from a given location. Therefore, solar radiation should provide a synthetic measure of the influence of sun heat on snow presence and melting. A strong effect on winter resource selection by roe deer could be expected hence. However, the spatial scale at which we assessed roe deer used and available sites might have been too fine to evidence any effect of such a complex topographic variable. The available location was randomly chosen within a buffer of 300 m centred on the used location. Within such a limited spatial extent, solar radiation is not expected to change abruptly and thus cannot capture the differences in snow condition that are instead seized by a local empirical measure.

The index most often used to assess snow cover effect in resource selection studies, MODIS snow (Profitt et al. 2013), was not retained as a main effect in our models (prediction 2). Conversely, the snow measures taken with the snow probe were an important driver of roe deer winter habitat selection, clearly showing that our technique is promising to evaluate the effects of snow on fine-scale roe deer movement patterns. Data from MODIS or similar models with low spatial accuracy should be preferred for large-scale studies where an empirical assessment for the same type of data is unpractical (e.g. Cagnacci et al. 2011). Local measurements of snow should be undertaken when the spatiotemporal scale of analysis is finer than the one of the predictive models (Brennan et al. 2013), as in our case study. Indeed, measuring the effective animal sinking depth is not trivial (Parker et al. 1984). We agree with Lundmark (2008) that one should measure snow consistency by mimicking animals' locomotion effect on the snow layer as closely as possible to get reliable results. In general, we suggest wildlife managers to consider fine-scale snow assessment if the objective is to evaluate resilience of populations to snow at medium and small spatial scales. The calibrated penetrometer that we used represents a valid tool for doing that. One aspect we noticed was that the measurements of the snow probe and the global thickness of the snow layer were strongly correlated. We argue that this correlation might have occurred because of slush snow consistency, given the relatively low elevation range where roe deer dwelled and snow was sampled (elevation range from 700 to 1400 m a.s.l.). This pattern could also have occurred because we performed the sampling only during daily hours, when sun heat leads the snow cover to approach the melting temperature (Lundmark and Ball 2008). However, roe deer have been recently shown to be more active in winter during daylight than during night (Pagon et al. 2013), indicating that our sampling likely represents conditions that roe deer face when moving. Ideally, the time of the day in which the snow sampling is performed should be adjusted to that of animals' main activity and movements.

The use of supplemental feeding has been traditionally associated to increase of winter survival and better quality of summer trophies, although robust supporting evidence is still controversial (Putman and Staines 2004). However, aggregation of individuals at feeding stations has also undesired side effects, such as the risk of contamination and disease transmission in wild populations (Navarro-González et al. 2013; Sorensen et al. 2014). In general, the management choice for supplemental feeding should be seen as a trade-off, in an attentive cost-benefit assessment. In particular, climate change may decrease abundance and persistence of snow at intermediate latitudes and low-medium altitudes (Steger et al. 2013). Therefore, the use of supplemental feeding for species ranging in such environmental context may not find much justification.

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Ethical standards The authors declare that animal handling practice, such as captures and collar marking, complies with the current Italian laws on animal welfare and has been approved by the Wildlife Committee of the Autonomous Province of Trento on 11th of September 2011.

Appendix 1

Tool for empirical assessment of snow sinking depth

The battage probe (Fig. S1) is a percussional tool made of tubular elements marked with a centimeter scale. A driving pole is put above these elements, whose number depends on the overall thickness of the snow layer. An additional weight with a central hole is placed on the top of the driving pole and released.

Tests of the hardness of snow layers are performed as follows:

- The probe without any additional weight (i.e. tubolar elements + driving pole) is placed on the snow surface, and its sinking is measured.
- The additional weight is added to the whole tool, without releasing it (i.e. at the bottom of the driving pole); the sinking depth is measured.
- The additional weight is released from points at increased height on the driving pole and this operation is repeated a certain number of times for each height. The procedure goes on until the probe has entirely entered into the snow layer. The hardness of the layer is defined as

$$R = P * n * H * D^{-1} + P + A$$

where P = additional weight (N); n = number of times the weight is dropped at a certain height H; H = dropping height (m); D = sinking height of the probe (m); and A = weight of the tubolar elements (N). This operation is repeated each time the snow probe encounters a new layer, until the ground.

In our experiment, we calibrated this tool to evaluate the pressure that a roe deer exerts on the snow surface and consequently to get a realistic estimate of its sinking in the snow. We provided the tubular elements of two further additional weights of mass equal to 2.5 kg each (Fig. S2a). Then, the overall mass of the probe was equal to 7 kg (2.5*2+2 kg of the tubular elements and the additional weight provided with the probe). The resulting weight of 70 N approximates the force exerted by the leg of a 20 kg roe deer during a walking mode, under the assumption that roe deer walking motion can be simplified by a static assessment and that at each step the pressure is equally distributed on all the three legs in contact with the ground. Moreover, we substituted the steel tip of the probe with the distal part of a roe deer hindleg (Fig. S2b) to mimic more accurately the impact of roe deer on the snow. The snow sinking measurements were performed by gently releasing the probe in the snow and measuring the reached depth with a rigid meter, without assessing the specific hardness of the snow layer.

Appendix 2

Procedure to identify the initial full model and for model selection

We identified a set of potentially biologically meaningful covariates to analyse roe deer winter resource selection and specifically: a spline of the week to take into account the time autocorrelation; the distance from the closest feeding station; remote index of snow cover presence derived from MODIS; empirically recorded index of snow cover patchiness; average snow sinking depth; average snow thickness; canopy presence, terrain slope and solar radiation; individual sex; and identity of the individual.

Based on the collinearity analysis (Table 2), we retained average snow sinking depth but not average snow thickness in the full model. Moreover, we also fitted a two-way interaction between canopy presence and terrain slope.

Thus, the final set of covariates to fit in a model included a spline of the week; the distance from the closest feeding station; snow cover presence derived from MODIS; average snow sinking depth; index of snow cover patchiness; a two-way interaction between canopy presence and slope; solar radiation; sex; and the identity of the individual fitted as random effect.

The procedure of model selection we used involved several steps. First, we assessed the importance of the contribution of the random effect of the individual to determine the goodness-of-fit of the initial full model (Table 4). We fitted a GLMM including the terms above mentioned (model random, AIC=312.9), as well as a GLM with the same framework but not the random effect (model fixed, AIC=310.86). We computed the percentage of variation explained by the random effect of the individual as the ratio between (i) the difference between the deviance of the model with random effect and the model without it and (ii) the deviance of the null model. We found that this value was very low (3.15e-13); therefore, we decided to remove the random effect, to perform the rest of the analyses using generalised linear models.

We used an AIC-based model selection (Burnham and Anderson 2002) to determine the models which better explained the variation of the response variable (ΔAIC<2). We thus retained 13 models (Table 5), neither of which included the spline of the week or the index of snow cover. We computed the predictors' weight on the retained models. We then proceeded with two parallel approaches to obtain the final models. First, in compliance with the multi-model inference theoretical framework, we performed model averaging on these models. We obtained a final averaged model with weighted coefficients and standard errors (Table 6). Moreover, in compliance with the principle of parsimony, we obtained a simplified version of the model by retaining only those covariates included in all models with ΔAIC<2, i.e. with predictor's weight=1. Thus, this version of the final model included the canopy presence, the distance from the closest feeding station and the average snow sinking depth (Table 6). The estimated model was validated according to the classic Resource Selection Analysis framework (Boyce et al. 2002).

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