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Plastic response by a small cervid to supplemental feeding in winter across a wide environmental gradient

Federico Ossi,[1,2,]† Jean-Michel Gaillard,[2] Mark Hebblewhite,[1,3] Nicolas Morellet,[4] Nathan Ranc,[1,5] Robin Sandfort,[6] Max Kroeschel,[7] Petter Kjellander,[8] Atle Mysterud,[9] John D. C. Linnell,[10] Marco Heurich,[11,12] Leif Soennichsen,[13] Pavel Sustr,[14] Anne Berger,[15] Michele Rocca,[16] Ferdinando Urbano,[17] and Francesca Cagnacci[1,5]

[1]*Biodiversity and Molecular Ecology Department, IASMA Research and Innovation Centre, Fondazione Edmund Mach, Via Mach 1, 38010 San Michele all'Adige, Trentino, Italy*
[2]*UMR CNRS 5558 "Biometrie et Biologie Evolutive", Université Claude Bernard Lyon1, Bat G. Mendel 43 Bd du 11 Novembre 1918, 69622 Villeurbanne Cedex, France*
[3]*Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, Montana 59812 USA*
[4]*UR35 Comportement et Écologie de la Faune Sauvage, Institut National de la Recherche Agronomique (INRA), B.P. 52627, F-31326 Castanet-Tolosan, France*
[5]*Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138 USA*
[6]*Department of Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences Vienna, Gregor-Mendel Straße 33, A-1180 Vienna, Austria*
[7]*Chair of Wildlife Ecology and Wildlife Management, University of Freiburg, Fahnenbergplatz, 79085 Freiburg, Germany and Forest Research Institute of Baden-Wuerttemberg, Wonnhaldestraße 4, 79100 Freiburg, Germany*
[8]*Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Science (SLU), SE-73091 Riddarhyttan, Sweden*
[9]*Department of Bioscience, Centre for Ecological and Evolutionary Synthesis, University of Oslo, P.O. Box 1066, Blindern, NO-0316 Oslo, Norway*
[10]*Norwegian Institute for Nature Research (NINA), P.O. Box 5685, Sluppen, NO-7485 Trondheim, Norway*
[11]*Department of Conservation and Research, Bavarian Forest National Park, Freyunger Straße 2, 94481 Grafenau, Germany*
[12]*Chair of Wildlife Biology Ecology and Wildlife Management, University of Freiburg, Fahnenbergplatz, 79085 Freiburg, Germany*
[13]*Mammal Research Institute, Waszkiewicza 1, 17-230 Bialowieza, Poland*
[14]*Department of Biodiversity Research, Global Change Research Centre, Belidla 986/4a, Brno, 60300 Czech Republic*
[15]*Leibniz-Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Straße 17, 10315 Berlin, Germany*
[16]*Trentino Hunting Association, Via Guardini 41, 38121 Trento, Italy*
[17]*IUAV University, Santa Croce 191, 30135 Venice, Italy*

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Abstract. Supplemental feeding for ungulates is a widespread practice in many human-dominated landscapes across Europe and North America, mainly intended to seasonally support populations. Surprisingly, little consideration was given so far to the effect of supplemental feeding on ungulate spatial ecology at a large scale, in management and conservation studies. Analyses of the main ecological drivers influencing the use of supplemental feeding sites by ungulates across a gradient of abiotic and biotic factors are currently lacking. We conducted a large-scale assessment of ecological and management drivers of use of feeding station sites in roe deer (*Capreolus capreolus*), a small cervid widely distributed across Europe that is particularly sensitive to winter severity. We tested four competing hypotheses by comparing the time spent at feeding station sites by 180 individual Global Positioning System-collared roe deer from nine populations spanning a wide latitudinal and altitudinal gradient. We found that roe deer used feeding station sites highly opportunistically in response to winter severity across its range. The harshest weather conditions at the northern range limit or the highest elevations provoked an intense use of feeding station sites, which typically peaked at the end of winter, in accordance with the adverse weather and nutritional condition hypotheses. Consistently, milder winters corresponded to a reduced and/or more homogeneous use of supplemental feeding. In general, intensively used feeding station sites heavily conditioned spatial

behavior of roe deer. Importantly, biotic factors such as the presence of competitors decreased roe deer use of supplemental feeding station sites. Our results emphasize the importance of this human-induced alteration to resource distribution, especially in the context of the rapidly occurring climate change that is modifying resource availability for ungulate populations.

Key words: artificial feeding; climate behavioral responses; climate change; roe deer; winter severity, ungulate management.

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† **E-mail:** federico.ossi@fmach.it

Introduction

The spatiotemporal variation of resources, which is typical of seasonal environments, is a key factor affecting large herbivore space-use patterns at multiple spatiotemporal scales (Fretwell and Lucas 1970, Tufto et al. 1996, Owen-Smith et al. 2010). In temperate environments, and particularly at high latitudes or mountain areas, resources are scarce in winter because vegetation stops growing (Kreyling 2010) and snow cover renders food inaccessible (Hovey and Harestad 1992). The scarcity of resources in winter, combined with high thermoregulation costs (Moen 1978, Holand et al. 1998) and high costs of movement in deep snow (Parker et al. 1984, Lundmark and Ball 2008), constitutes a key limiting factor for survival (Telfer and Kelsall 1984) and represents a major determinant of population dynamics of large herbivores (e.g., Delgiudice et al. 2006).

The provisioning of winter supplemental feeding, which is a widespread management practice in the northern and mountain areas of Europe and North America (see reviews in Putman and Staines 2004, Milner et al. 2014), evidently alters the natural system. The establishment of feeding stations, which are often provided with human-prepared food (usually highly concentrated cereals in pellets), constitutes an alternative resource in winter that causes modifications of individual space-use patterns such as a reduction in migratory behavior (Möst et al. 2015), spatiotemporal alteration of the migration pattern (Sahlsten et al. 2010, Jones et al. 2014), shifts in home range core areas utilization (Kilpatrick and Stober 2002, Cooper et al. 2006), and reduction in home range size (Guillet et al. 1996). In particular, feeding stations can act as attractive places toward which individuals tend to move (Guillet et al. 1996, van Beest et al. 2010, Jerina 2012) and concentrate (Sahlsten et al. 2010). Thus, the potential or effective benefits of winter supplemental feeding management (e.g., enhanced overwinter survival: Peterson and Messmer 2007, better trophy quality: Putman and Staines 2004, increased population density: Peek et al. 2002, forest damage prevention: Gundersen et al. 2004) may trade off with the negative consequences of this practice (enhancement of disease transmission risk at feeding station sites: Sorensen et al. 2014, competitive feeding behavior and derived stress: Ceacero et al. 2012, increment of browsing pressure in feeding station sites surroundings: Mathisen et al. 2014, alteration of natural selection patterns: Mysterud 2010, and rumen acidosis: Ritz et al. 2013). Fundamental to whether the effects of supplemental feeding might be positive or negative on large herbivores is the degree to which this practice alters their spatial distribution.

While the consequences of supplemental feeding station sites on space-use tactics have been already documented at local scales (e.g., Guillet et al. 1996, van Beest et al. 2010), understanding the proximate factors affecting their use by individuals has received much less attention. If feeding stations represent an alternative food resource to compensate for winter constraints, their use might vary in relation to recent changes in landscape and weather conditions (Craine et al. 2010). In fact, the increase in temperatures (Jones et al. 1986) and the modification of snow cover distribution (Steger et al. 2013, O'Gorman 2014) can substantially alter plant phenology (Wipf et al. 2009), thus affecting the spatiotemporal distribution of natural resources (Post and Stenseth 1999). In this context, assessing the determinants of use of feeding

station sites across contrasting populations represents a crucial element to understand and predict variation in space-use patterns deriving from spatiotemporal alteration of food resources under different environmental conditions.

The European roe deer (*Capreolus capreolus*) is an ideal model species to investigate effects of supplemental feeding because of its distribution across a wide range of environmental conditions (Andersen et al. 1998). In particular, some populations at the edges of the distribution range (i.e., Scandinavia and high elevations in the Alps) experience harsh winter conditions, limiting the survival of a species that is not well adapted to cope with winter severity (Holand et al. 1998, Mysterud 1999, Ramanzin et al. 2007). In such contexts, supplemental feeding stations have been used as alternative food resources for roe deer (Putman and Staines 2004). Previous studies have shown that roe deer use feeding station sites intensively by concentrating in their surroundings (Guillet et al. 1996, Cederholm 2012). However, no study so far comprehensively analyzed the combination of environmental and management-related factors on the pattern of use of these anthropogenic resources by roe deer. We here filled this gap by means of a large-scale comparative analysis contrasting several roe deer populations exposed to supplemental feeding across a wide altitudinal and latitudinal gradient. We addressed this goal in the context of the collaborative project EURODEER that gathers millions Global Positioning System (GPS) locations from individual roe deer across its distribution range (4.5 million GPS locations; 1470 individuals; 31 study areas: www.eurodeer.org). Earlier EURODEER studies showed high ecological plasticity of this small cervid in spatial behavior, for example, through partial migration (Cagnacci et al. 2011) and home range size variation (Morellet et al. 2013) in dependence of climatic, weather, topographic, and land-use-specific variables. We here contributed to this large-scale picture by taking into account a major, and yet commonly neglected, alteration of ecosystems in human-dominated landscapes.

We tested four main hypotheses related to both the pattern of use of feeding station sites and the consequences of this behavior on roe deer space-use tactics. Firstly, under the "adverse weather condition hypothesis", the use of feeding station sites should vary across the year in relation to temporal variation in food resource availability and weather conditions. Accordingly, we predicted a temporal variation in feeding station sites use by roe deer across the year, in combination with the provisioning of food at the stations and an aggravation of winter conditions (presence of snow cover and low temperatures; Prediction 1). Secondly, under the "food competition hypothesis", the use of feeding station sites should depend on inter-specific competition for food. Since roe deer are inferior competitors compared to larger ungulates such as fallow deer *Dama dama* (see, e.g., Focardi et al. 2006) and red deer *Cervus elaphus* (Richard et al. 2010), we expected to observe a decrease in the use of feeding station sites when competitors had free access to the food (Prediction 2). Thirdly, under the "nutritional condition hypothesis", we expected the temporal peak of use of feeding station sites to occur at the end of the winter (Prediction 3), because of the combined effect of a deterioration of body condition (Parker et al. 2009) and increased energetic demands for late gestation (females) and preparation for territory establishment (males). Finally, under the "home range food abundance hypothesis" (Morellet et al. 2013), the intensity of use of feeding station sites should influence spatial behavior of this ungulate. In particular, home range size should decrease with increasing availability of concentrated resources (Saïd et al. 2009). Therefore, we expected individual weekly home range size to be inversely related to the intensity of use of feeding station sites by roe deer (Prediction 4).

Materials and Methods

Study areas, feeding stations, and related covariates

Our study was based on individual trajectories obtained from roe deer marked with GPS collars. We selected our study sample from the EURODEER database (www.eurodeer.org). The study period spanned all years between 2005 and 2014, but with differences across study areas (see Appendix S1 for a complete match between years and study areas). In particular, we subset the EURODEER data to select the study areas where supplemental feeding practices occurred (see Fig. 1 and Appendix S1 for details). For each study area, we collected detailed data on the distribution of feeding station sites and on feeding station

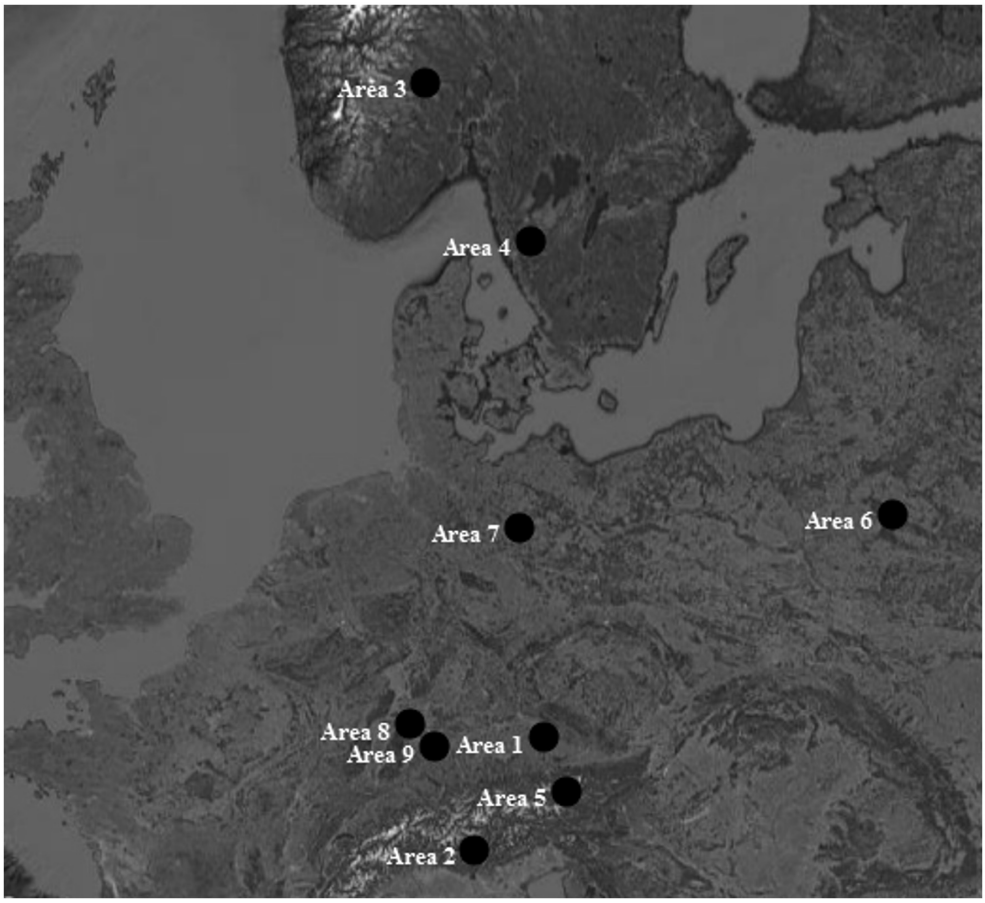


Fig. 1. Distribution of roe deer (*Capreolus capreolus*) study areas in the EURODEER network, considered in this work. Area 1: Bavarian Forest National Park and Sumava National Park; Area 2: Italian Alps; Area 3: Norway; Area 4: Sweden; Area 5: Austrian Alps; Area 6: Bialowieza Forest; Area 7: Brandenburg; Area 8: Baden-Wuerttemberg (Rhine Valley); Area 9: Baden-Wuerttemberg (Hegau).

management (Appendix S2). This information included the typology of feeding station, that is, whether a feeding site was a proper feeding station or a box trap baited with food and used to lure and capture roe deer; the *energetic quality* of the food provided, which we reclassified as low or high based on the average values of metabolizable energy (ME, MJ/kg of dry matter) of the food supplied; the potential presence of competitors for access to food, which we derived from a combination of the mere presence of competitors for food in the area (based on sightings and site-specific knowledge, e.g., issued from wildlife management plan), and the accessibility of the feeding station site for the competitor species (e.g., presence of wooden bars to prevent the use of feeding stations by species larger than roe deer); the activation status of the feeding station, which we assessed for the periods within each management year in which food was provided. Our temporal resolution in determining the activation state of feeding stations was the week. We chose to work at a weekly scale to account for the expected quick response of roe deer to changes in resource availability (Pellerin et al. 2010), and because that was the minimum temporal unit to obtain accurate and standardized information across the large spatial scale of analysis. We thus obtained for each feeding station a time series of weekly activation of the feeding station (hereafter weekly feeding stations), according to the management of that specific feeding site.

Then, we associated each weekly feeding station with data on snow cover (presence/absence), which were derived from the Moderate Resolution

Imaging Spectroradiometer (MODIS) MOD10A2 16-day composite maximum snow extent data at level V005 (data downloaded from NASA WIST, http://reverb.echo.nasa.gov/ Hall et al. 2002). We also collected weekly average minimum temperature data, which were derived from the closest meteorological station to a given feeding station site (average distance between the meteorological station and the feeding station site of 30 km; data downloaded from the European Climate Assessment & Dataset project, http://www.ecad.eu; Tank et al. 2002).

Spatiotemporal overlap between feeding stations management and roe deer movement

To address our working hypotheses, we quantified the use of feeding station sites by roe deer. Therefore, we had to spatially overlap roe deer trajectories and feeding station sites distribution while taking into account the state of activation of the feeding station. This was done through three criteria. Firstly, we included those individuals that were monitored at least 60 consecutive days in winter, defined as the period between 1st October of a given year and 30th April of the following year (i.e., excluding spring and fall migratory movements; Cagnacci et al. 2011). Secondly, we defined which feeding station sites were accessible to each roe deer, based on individual movement patterns in the winter period. Specifically, for each combination individual roe deer/winter, we used all winter GPS locations to compute a winter home range with the Kernel *href* method (UD = 90%; Worton 1989). Then, we buffered each home range using the maximum distance between the barycenter and the most distant vertex of the home range. We considered accessible feeding station sites by an individual roe deer those sites that overlapped with the "buffered" home range (Appendix S3). Thirdly, we assigned the weekly activation status to such feeding stations (see paragraph "Study areas, feeding stations, and related covariates" in section *Materials and Methods*). Thus, each individual roe deer/winter was linked to a list of individual weekly feeding station sites, for which we determined the use.

Determination of feeding station sites use

We measured the use of weekly feeding station sites by an individual roe deer based on the spatiotemporal overlap between roe deer weekly movements and a buffer area around the feeding station site. To do this, we first built weekly individual movement trajectories based on the assumption of linear interpolation between subsequent locations. Then, we performed a pilot study to identify (1) the appropriate metric to measure feeding station site use based on the individual trajectories and (2) the appropriate buffer size around feeding station sites (Appendix S4). In particular, we evaluated the effect of GPS location sampling frequency (original data were not sampled regularly; 3, 6, 9 h) and buffer size (50, 100, 200, and 400 m) on two candidate metrics, the weekly proportion of time spent by an individual within a buffer and the number of weekly GPS locations falling within the same buffer. We found that the proportion of time spent within a buffer was independent from the sampling frequency, while this was not the case for the number of GPS locations falling within the buffer (Appendix S4). Since in the original dataset the periodicity of GPS locations was not regular across study areas, we retained the proportion of time spent within a buffer as the most appropriate metric for our analyses. Moreover, since we could find only a weak effect of buffer size on the selected metric (Appendix S4), we chose a buffer of 50 m, to be consistent with previous work (e.g., Guillet et al. 1996) and to assess the use of feeding station sites by roe deer at the finest possible spatial scale (i.e., using a conservative approach). All spatial analyses were conducted in PostgreSQL 9.1 database with its spatial extension PostGIS 2.0 (http://www.postgresql.org/; http://postgis.refractions.net/), using the EURODEER database (www.eurodeer.org) as described in Cagnacci and Urbano (2008) and Urbano et al. (2010).

Statistical analysis and modeling

Determination of factors affecting use of feeding station sites (first and second predictions).—We modeled the pattern of use of feeding station sites by roe deer using generalized additive mixed models (GAMMs; Wood 2006). We fitted a used–unused logistic regression design (Hosmer and Lemeshow 2000), where the dependent covariate was a true probability of use (Manly et al. 2002). Specifically, we defined a weekly feeding station as "used" by a individual roe deer (i.e., "1"), when the individual spent more than 1% of its monitoring time in that week within the

Table 1. Model selection procedure to determine the temporal component of the model for feeding station sites use by roe deer.

Model	ΔAIC
Logit(P) ~ s(WMT, bs = "cr," by = Study area)	0
Logit(P) ~ WMT × Study area	46.38
Logit(P) ~ s(WMT, bs = "cr")	1669.42
Logit(P) ~ WMT	1826.11

Notes: ΔAIC, difference in AIC between a given model and the best one; Logit(P), logit of the probability of use of a given feeding station site; WMT, weekly minimum temperature; WMT × Study area = linear two-way interaction between the weekly minimum temperature and the study area; s(WMT, bs = "cr") = formula to fit a cubic regression spline smooth of the weekly minimum temperature; s(WMT, by = Study area) = formula to fit an interaction between the spline smooth of the weekly minimum temperature and the study area.

50-m buffer. This way, we reduced the misclassification of simply being near feeding station sites by chance as true use.

As a first step, we evaluated whether and how weekly minimum temperature influenced the overall temporal pattern of use of feeding station sites by roe deer. We fit four generalized additive models (GAMs; Wood 2006) to assess the dependence of the use of feeding station sites on the weekly minimum temperature, which we expressed either as a linear effect or as a cubic regression spline smooth, alone or in interaction with the study areas. We ran a model selection based on Akaike Information Criterion (AIC, Burnham and Anderson 2002, Table 1). In parallel, we also measured the percentage of overall temporal pattern (P_{WMT}) accounted for by the weekly minimum temperature by means of an ANODEV procedure (Skalski et al. 1993, Table 2). To achieve this second goal, we computed three generalized additive models to model the dependence of the use of feeding station sites on the study area (simplest model "S"), the cubic regression spline smooth of the weekly minimum temperature in interaction with the study area (intermediate model "I"), and the observational week in interaction with the study area (most complex model "C"). We computed P_{WMT} as:

$$P_{WMT} = 1 - \frac{(LI - LC)}{(LS - LC)} \quad (1)$$

where LI, logLikelihood of the intermediate model; LC, logLikelihood of the most complex model; LS, logLikelihood of the simplest model.

We then quantified those covariates that could explain the pattern of use of feeding station sites, based on our predictions—in particular, the activation of the feeding station (active/inactive) and the presence of snow cover (presence/absence; first prediction), the potential competition with other ungulates (second prediction). We also added covariates to control for site-specific characteristics and, in particular, the latitude and altitude of the site; the individual sex and age class (juvenile: <1 yr; yearling: between 1 and 2 yr; adult: older than 2 yr); the energetic quality of the food provided; and the typology of the feeding station (see Appendix S2 for details about these covariates). We accounted for co-linearity patterns among covariates (Graham 2003, Zuur et al. 2007) by choosing for each pair of correlated covariates the one with the highest explanatory power in univariate models (Appendix S5). Therefore, we obtained a full model that included the temporal component, the two-way interaction between latitude and altitude, and five single terms (activation of feeding station, potential competition, energetic quality of the food provided, sex and age class). The full GAMM also included the random intercepts of individual and year (Gillies et al. 2006), to account for expected variation due to individual roe deer behavior and differences in the pattern between years.

We ran a model selection procedure based on AIC scores of all 32 GAMMs resulting from the potential combinations of the terms considered in

Table 2. ANODEV procedure to determine the proportion of the overall temporal pattern explained by the spline smooth of the weekly minimum temperature (P_{WMT}).

Model	LogLik	P_{WMT}
Logit(P) ~ s(WMT, bs = "cr," by = Study area)	−7518.670	71%
Logit(P) ~ Study area	−8242.935	
Logit(P) ~ factor(week) × Study area	−7226.270	

Notes: LogLik, logarithm of the likelihood of a given model; P_{WMT}, percentage of the overall temporal pattern accounted for by the weekly minimum temperature; Logit(P), logit of the probability of use of a given feeding station site; WMT, weekly minimum temperature; s(WMT, bs = "cr") = formula to fit a cubic regression spline smooth of the weekly minimum temperature; s(WMT, by = Study area) = formula to fit an interaction between the spline smooth of the weekly minimum temperature and the study area; factor(week) × Study area = linear two-way interaction between the factorized observational week and the study area.

the full model, besides the two-way interaction between latitude and altitude of the feeding station site, the temporal component of the GAMM, and the random intercepts, which we kept in all models. We further evaluated the importance of each fixed and random term included in the best model (ΔAIC < 2) in contributing to the goodness-of-fit of the model by means of the command "ANOVA" in R (Appendix S6). Lastly, we assessed the goodness-of-fit of the final model by computing its pseudo-R^2, in the McFadden formulation:

$$\text{pseudo-}R^2 = 1 - \frac{\text{DF}}{\text{DN}} \quad (2)$$

Determination of the temporal peak of use of feeding station sites (third prediction).—We assessed the temporal peak of use of feeding station sites using a GAM (Wood 2006). Specifically, we fit the dependence of the probability of use of feeding station sites on a cyclic cubic regression spline smooth of the observational week in interaction with the study area. We used this model to estimate weekly use of feeding station sites by roe deer. Then, for each combination individual/monitoring year (e.g., roe deer 1/yr 2007; roe deer 1/yr 2008), we extracted the week of peak of use of feeding station sites, the week that corresponded to the maximum predicted value for that specific combination individual/yr. For each study area separately, we determined the top week of use of feeding station sites as the median (50th quantile) of the distribution of the week of peak of use among all combinations individual/yr. We also measured the variation in this pattern by computing the 25th and 75th quantiles of the distribution.

Effect of use of feeding station sites on roe deer spatial behavior (fourth prediction).—We computed the weekly individual home ranges using the Kernel ad hoc method (UD = 50%; see Morellet et al. 2013 for further details). Then, we joined the weekly home ranges with time spent by an individual in proximity of weekly feeding station sites (i.e., based on the combination between the individual and the weekly feeding station—see paragraph "Spatiotemporal overlap between feeding stations management and roe deer movement" in section *Materials and Methods*). We limited this analysis to those weekly feeding station sites at which the individuals spent at least 1% of their weekly monitoring time. We eventually fit a linear model to evaluate the dependence of the log-transformed weekly home range size on the amount of time spent in the proximity of the weekly feeding station sites. The R^2 provided an indication of the goodness-of-fit of the model. We performed all the analyses in R software (version 3.0.2 The R Foundation Core Team 2013; mgcv Rpackage: Wood 2006, MuMIn: Bartoń 2013).

Results

We obtained 15,265 sampling units (weekly feeding stations) to estimate the pattern of use of feeding station sites (Appendix S7), from 180 selected individuals. Sex ratio and age structure of monitored individuals were biased toward adult females (8966 sampling units for females vs. 6299 for males; 12,199 sampling units for adults vs. 2292 for sub-adults and 774 for juveniles). Almost one-third of the data (5086) were collected in one study area (Bavarian Forest National Park, study area 1).

Determination of factors affecting use of feeding station sites (first and second predictions)

Model selection identified one single best model (ΔAIC < 2) that included the spline smooth of the weekly minimum temperature in interaction with study area, the two-way interaction between latitude and altitude, the activation of feeding stations, the potential competition, the age class of individuals, and the random intercepts of individual and observational year. All these terms improved the goodness-of-fit of the model (Appendix S6). Therefore, in accordance with our first prediction, both winter severity and provisioning of food at feeding stations shaped the use of feeding station sites by roe deer. In particular, we found that the weekly minimum temperature accounted for 71% of the overall temporal pattern of use of feeding stations sites (Table 2). Accordingly, the spline smooth of the weekly minimum temperature shaped the temporal variation of use of feeding station sites by roe deer across all study areas except for study area 7 (Brandenburg Forest; Table 3). We also found that roe deer use of feeding station sites increased when they were actually provided with food ($\beta = 0.33 \pm 0.07$, $P < 0.001$; Table 4), while the effect of snow cover was negligible and as such removed from the analyses due to its high correlation with the activation status of the feeding stations (Appendix S5). As expected

Table 3. Smooth and random terms, and their statistical significance, retained in the best model.

Term	EDF	Level of significance
s(WMT) × Study area 1	5.303	***
s(WMT) × Study area 2	3.274	***
s(WMT) × Study area 3	2.493	***
s(WMT) × Study area 4	2.657	***
s(WMT) × Study area 5	5.734	***
s(WMT) × Study area 6	2.224	***
s(WMT) × Study area 7	4.886	–
s(WMT) × Study area 8	1.813	**
s(WMT) × Study area 9	1.642	***
R(year)	6.735	***
R(individual)	174.797	***

Notes: EDF, estimated degrees of freedom; s(WMT) × Study area "x", spline smooth of the weekly minimum temperature at any "x" study area; R(year), random intercept of the observational year; R(individual), random intercept of the individual.

Stars (*) denote the significance level, and specifically: $^{***}P < 0.001$; $^{**}P < 0.01$; "–", lack of significance.

based on the adverse weather condition hypothesis, the use of feeding station sites slightly increased at high altitudes in the southern part of the range considered for this analysis (i.e., on the Alps), and at low elevation at northern latitudes (i.e., in Scandinavia; $\beta = -0.0003 \pm 0.0001$, $P < 0.001$; Table 4). In compliance with our second prediction, the potential presence of competitors for food dramatically reduced the use of feeding station sites by roe deer ($\beta = -3.75 \pm 0.49$, $P < 0.001$; Table 4). Conversely, neither the typology of feeding stations nor the energetic quality of the food provided affected roe deer use of these sites. Sub-adults ($\beta = -0.69 \pm 0.17$, $P < 0.001$) and adult roe deer ($\beta = -0.96 \pm 0.19$, $P < 0.001$) used feeding station sites significantly less than juveniles (Table 4), while we could not find any sex-related difference in the pattern of use of feeding station sites. Both random intercepts of individual and observational year were retained in the best model (Table 3), although they explained a markedly different proportion of the total observed variation ($PV_{individual} = 16\%$; $PV_{year} = 0.6\%$; Appendix S6). Overall, the model fit the observed data well (pseudo-$R^2 = 0.33$).

Determination of the temporal peak of use of feeding station sites (third prediction)

We detected a temporal pattern across all the study areas, although this result was more evident in some study areas than others (especially study area 1, Bavarian Forest National Park; study area 2, Italian Alps; study area 3, Norway; study area 5, Austrian Alps; study area 9, Baden-Wuerttemberg Hegau; see also Fig. 2). In partial accordance with the third prediction, the peak of use of feeding station sites occurred from the 5th to the 11th week of the year (February–March) in six of the study areas, but not in Bialowieza Forest (study area 6, peak week: 2), Brandenburg (study area 7, peak week: 1), and Baden-Wuerttemberg Rhine Valley (study area 8, peak week: 1; Table 5). Moreover, in two study areas especially (study area 3, Norway; study area 5, Austrian Alps), roe deer used feeding station sites for a long period in winter, as revealed by the lower 25th and upper 75th percentiles of the distribution of the peak week of use with respect to the other study areas (Table 5).

Effect of use of feeding station sites on roe deer spatial behavior (fourth prediction)

We used 3974 individual weekly feeding stations to evaluate the effect of the amount of use of feeding station sites on the overall roe deer space-use patterns (172 animals represented of the total of 180 individuals). The weekly amount of use of feeding station sites spanned from 21 to 7319 min. In accordance with our fourth prediction, we found that the intensity of use of feeding station

Table 4. Parametric coefficients and standard errors of the fixed terms retained in the best model.

Term	Estimate coefficient	Standard error	Level of significance
Alt	0.0178	0.0054	**
Lat	13.3912	2.6090	***
Act (1)	0.3308	0.0701	***
Age (sub-adults)	−0.6855	0.1671	***
Age (adults)	−0.9556	0.1991	***
PC (1)	−3.7500	0.4887	***
Alt × Lat	−0.0003	0.0001	***

Notes: For categorical variables, the coefficient refers to the difference between the category in the parentheses and the reference category. For age class, the reference category is "fawns." Alt, altitude of the feeding station site; Lat, latitude of the feeding station site; Act (1), activation of feeding stations, category "activated," ref. category "not activated"; PC (1), potential competition, category "present," ref. category "absent"; the symbol "×" denotes two-way interactions between the terms.

Stars (*) denote the significance level, and specifically: $^{***}P < 0.001$; $^{**}P < 0.01$.

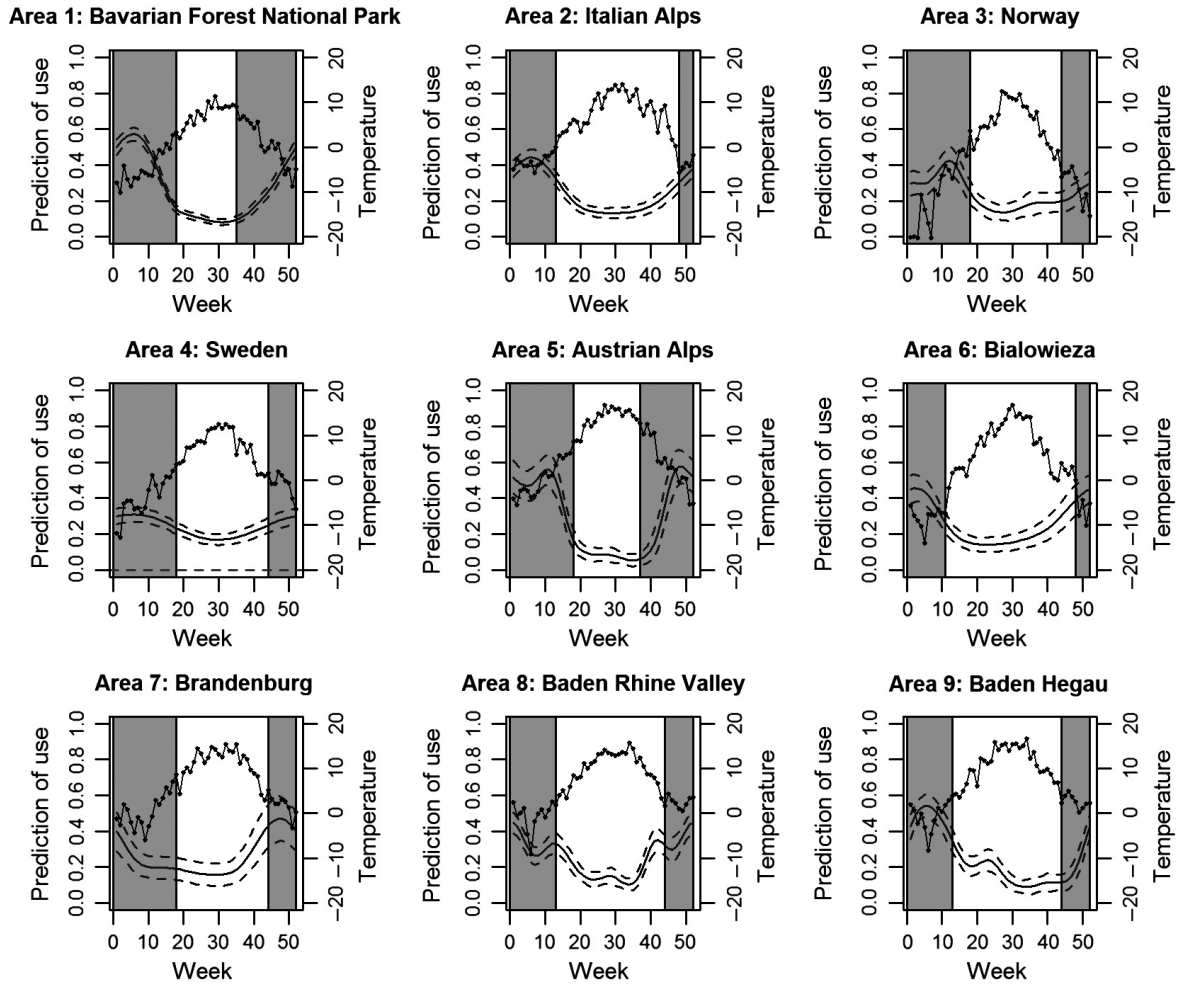


Fig. 2. Plot of the predicted probability of use of feeding station sites throughout the year (continuous thin line), with 95% confidence intervals (dashed lines), for each study area separately (left vertical axis of each plot). The dotted line indicates the pattern of variation of weekly average minimum temperature by study area (right vertical axis of each plot). Shaded areas represent the period of activation of the feeding stations. Area 1: Bavarian Forest National Park and Sumava National Park; Area 2: Italian Alps; Area 3: Norway; Area 4: Sweden; Area 5: Austrian Alps; Area 6: Bialowieza Forest; Area 7: Brandenburg; Area 8: Baden-Wuerttemberg (Rhine Valley); Area 9: Baden-Wuerttemberg (Hegau).

sites was inversely related to the home range size ($\beta = -0.002$, $P < 0.001$; $R^2 = 0.09$, Fig. 3).

Discussion

This work evidences that roe deer use supplemental feeding station sites opportunistically, as expected for a species that shows a high ecological plasticity in space-use patterns (Cagnacci et al. 2011, Morellet et al. 2013). In accordance with our first prediction, roe deer mainly used feeding station sites when environmental conditions were harsh, and only if these sites indeed represented an alternative source of food. The use of feeding station sites peaked in the second part of winter across most of the study areas, as a likely response to a prolonged lack of natural resource availability and deterioration of body condition, in compliance with our third prediction. In such context, and in agreement with our fourth prediction, an intense use of feeding station sites corresponded to reduced home range

Table 5. Summary of the week of peak of use of feeding station sites by roe deer (*Capreolus capreolus*) across the nine study areas.

Study area	25th percentile	Median	75th percentile
Bavarian Forest National Park	4	6	6
Italian Alps	6	6	6
Norway	1	10	12
Sweden	6	6	6
Austrian Alps	49*	11	11
Bialowieza National Park	52*	2	3
Brandenburg Forest	48*	1	2
Baden-Wuerttemberg (Rhine Valley)	0	1	1
Baden-Wuerttemberg (Hegau)	0	5	5

Notes: Weeks refer to the winter season as defined in the main text (1st October–30th April of the following year).

The star (*) denotes those cases when the 25th percentile occurred in the last weeks (late fall) of the previous solar year with respect to the peak of use.

size. This pattern of use of feeding station sites was also dependent on the presence of other species that may outcompete roe deer for access to food, as expected based on our second prediction. Notably, feeding station sites were used when hunters or wildlife managers filled them with food such as pellets, corn, hay, or fruit (i.e., when they were "active"). Thus, the inclusion of the activation status as a predictor of feeding station sites use confirmed that indeed we were measuring the effects of supplemental feeding (and not of other confounding factors).

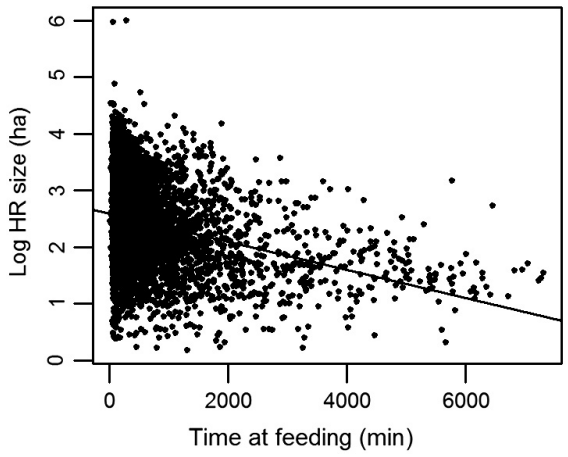


Fig. 3. Plot of the variation of natural logarithm of the weekly home range size (ha) in relation to the time spent (min) in the surroundings of the feeding station sites. The prediction of the linear model is presented in black continuous line.

Determination of the factors affecting use of feeding station sites (first and second predictions)

The use of feeding station sites by roe deer represented a clear example of the fine-scale behavioral adaptations of this ungulate to cope with severe winter conditions, strongly supporting the "adverse weather condition hypothesis". In particular, roe deer are highly sensitive to low temperatures that can critically affect their survival (e.g., Heurich et al. 2012) because of an increase in the energetic demand for thermoregulation (Mautz 1978). In such situation, roe deer energetic requirements should push the individuals to search for food intensively. The presence of feeding station sites where food is provided represents an easily accessible and concentrated source of food that can be opportunistically used under such high energetic demands. The intensive use of feeding station sites when environmental conditions were severe has been reported also in other ungulates (e.g., elk *Cervus canadensis*: Mangus 2011, wild boar *Sus scrofa*: Oja et al. 2014). Interactive effects between latitude and altitude (that we used as a factor to control for study area) also supported the adverse weather condition hypothesis. The interaction coefficient was slightly negative, indicating a more intense use of feeding station sites at high latitude and low altitude or low latitude and high altitude. Indeed, in Norway, the northernmost study area considered, supplemental feeding is deployed at the bottom of valleys (Mysterud 1999, Gundersen et al. 2004), and in the Alps, the southernmost area, supplemental feeding is deployed on mountain slopes (Ossi et al. 2014). These areas represent two extremes of the distribution range of roe deer, latitudinal and altitudinal, where winter conditions are arguably the most severe (e.g., Mysterud 1999, Ramanzin et al. 2007).

Roe deer use of feeding station sites might also be expected to depend on snow cover. Indeed, snow is an important component of winter severity that negatively affects roe deer body condition, both by increasing the energetic demand for locomotion and by reducing food availability (Holand et al. 1998, Ewald et al. 2014). Empirical local-scale studies supported this hypothesis

(Guillet et al. 1996, Cederholm 2012, Ossi et al. 2014), but here we did not find any effect of snow cover on feeding station sites use by roe deer. We argue that this result is due to the coarse spatiotemporal resolution of the snow cover index used in this study (i.e., snow MODIS, see *Materials and methods* for details) with respect to the fine-scale movements to access feeding station sites. Indeed, Ossi et al. (2014) found that empirical assessment of snow cover largely outperformed MODIS data in predicting fine-scale space-use patterns by roe deer in an Alpine area (see also Brennan et al. 2013). Thus, we recommend that future studies in this direction should benefit from advances in remote sensing research providing higher resolution snow cover, and indeed snow depth data (O'Gorman 2014).

In this study, we did not detect any effect of the energetic quality of the food provided on roe deer use of feeding station sites. Indeed, if roe deer use feeding station sites mainly to compensate for a lack of natural resources, we should have expected their dependence on feeding stations to increase with the quality of the food provided. It is true that our classification of the food provided at feeding stations was only a qualitative categorization of food types, based on metabolizable energy. At a large scale, however, it was not possible to perform a dedicated experimental manipulation of the food provided, nor a detailed assessment of natural food resources available in the surrounding of feeding sites (another potential confounding factor). Regardless of these challenges, we confirmed that diverse, clustered artificial resources affect space-use patterns of animals, independently of broad differences in the type of food provided.

If food supplied at feeding station sites compensates for winter severity, one should also expect heterogeneous responses depending on the condition of the individuals. Juveniles and old individuals (i.e., older than 7 yr; Gaillard et al. 1998, Heurich et al. 2012) are in particular expected to rely on food supplied at feeding stations sites most. As expected, we found that juveniles relied on feeding station sites more than yearlings and adults. Our results predict that use of feeding station sites should also increase in senescent individuals, leading supplemental feeding to reduce the mortality of this age class (e.g., Foley et al. 2015).

The availability of easily accessible food during winter when natural resources are lacking is clearly attractive for wildlife species in general. Roe deer are small ungulates that unsuccessfully compete with other larger species for foraging on limiting resources (fallow deer *Dama dama*: Focardi et al. 2006, red deer *Cervus elaphus*: Richard et al. 2010). As expected, we found that roe deer use of feeding station sites was reduced by the presence of competitors able to access the same feeding station sites, thus supporting the "food competition hypothesis". Our results fit with the drastic reduction in feeding station sites use by roe deer in the presence of fallow deer recently observed in Sweden (Cederholm 2012). However, in this work, we could not distinguish whether roe deer avoided the feeding stations because of a lack of food or the presence of competitors (because of aggressive inter-specific interactions among individual at feeding stations). We encourage further research on that topic, which might involve deploying camera traps at feeding station sites and then evaluating the effective use of feeding station sites by the target species.

Determination of the temporal peak of use of feeding station sites (third prediction)

The use of feeding station sites by roe deer varied throughout the year in most of our study areas. The temporal pattern in the use of feeding station sites followed winter severity, confirming the role of supplemental feeding as alternative food resources. Thus, we expected a condition-dependent response not only among individuals (e.g., in relation to age), but also for each individual throughout the season. A prolonged exposure to a lack of natural food and other winter constraints (e.g., snow depth and low temperatures) can cause a decrease in individual performance (Parker et al. 2009). Further, changes in the physiological state (e.g., linked to the reproductive cycle) can increase energetic demands and these two factors can interplay to worsen body conditions. In roe deer, energetic needs increase in late winter in response to increased energy demand of late gestation in females (Hoffmann et al. 1978) and of antler growth and territory establishment in males (Liberg et al. 1998). Accordingly, we found that roe deer used feeding station sites mainly in the second half of the winter, especially in those areas where winter conditions are harsher, thus strongly

supporting the "nutritional condition hypothesis". Indeed, in Norway and Austrian Alps, roe deer used feeding station sites for longer than in other areas where conditions are less demanding for roe deer survival and where the seasonal onset of vegetation is anticipated (Pettorelli et al. 2005), confirming previous findings in a Swedish population (Cederholm 2012).

We can thus infer the existence of an environmental-dependent temporal gradient of feeding station sites use by roe deer, driven by the combination of the intensity of winter severity and the individual physiological response. At one edge of temporal use of feeding station sites, there are those areas where winter conditions are extreme, such as the Alps and Scandinavia. At the other edge, there are those areas where winter severity is less accentuated and prolonged, leading to an earlier peak of use of feeding station sites. This is the case for Brandenburg Forest (Germany, study area 7) and the Rhine Valley (Germany, Baden-Wuerttemberg, study area 8). Unexpectedly, we also detected a similar pattern in Bialowieza Forest (Poland, study area 6), where, however, the conditions should be as limiting as in Northern and Alpine environments. We can speculate that the presence of wolves, which can prey on roe deer at feeding station sites, may explain such unexpected results, although we could not evaluate this directly. Feeding stations may thus offer a useful experimental setting to test for the effects of risk–forage trade-offs in the presence of recovering carnivores in Europe.

Effect of use of feeding station sites on roe deer spatial behavior (fourth prediction)

The use of feeding station sites by roe deer had a major effect on individual space-use patterns during winter. The more the individuals used feeding stations, the more they shrank their weekly home ranges, thus strongly supporting the "home range food abundance hypothesis". This finding is in line with the expected inverse relationship between home range size and availability of food resources, as reported by Morellet et al. (2013). The presence of a concentrated and patchy high-quality resource attracts individuals toward these places (roe deer: Guillet et al. 1996, moose *Alces alces*: van Beest et al. 2010). Consequently, individuals reduce their core areas (Guillet et al. 1996, Kilpatrick and Stober 2002, van Beest et al. 2011), especially when climatic conditions are most severe (van Oort et al. 2007). In this respect, our findings support the hypothesis of Morellet et al. (2013) in their multi-population study on roe deer spatiotemporal variation of home range sizes. In their study, they found a lack of seasonal variation in home range size at northern latitudes and in the Alps, in contrast to predictions (Morellet et al. 2013), since a home range size variation was expected in relation to the scarcity of resources in these areas, especially in winter. They hypothesized that this could be due to the presence of alternative supplemental food provided at feeding stations, in those areas. Our results support this hypothesis.

Conclusions

Our work represents one of the first large-scale assessments of feeding station sites use by an ungulate. We showed a pervasive use of feeding sites by roe deer across different European countries and landscapes. Supplemental feeding has strong effects on the winter ecology of this (and likely other) ungulate species, affecting the individual response to winter severity. Thus, supplemental feeding represents, in the most of the studied areas, an integral part of the "anthropogenic biome" (sensu Ellis and Ramankutty 2008), which needs to be taken into account when studying space-use patterns and ecological responses of roe deer and other ungulates. These findings open several research scenarios to investigate benefits and drawbacks of feeding stations as a management practice. On the one side, we call upon a careful assessment of the positive effects of different supplemental feeding regimes: (1) on roe deer performance at the individual level, for example, as measured by body mass; (2) on performance at the population level, for example, as measured by winter survival rate or juvenile recruitment (e.g., Foley et al. 2015). For example, Foley et al. (2015) showed that supplemental feeding does not enhance calf recruitment or population density in an elk population that has been fed for over 70 yr. On the other side, researchers should point at the negative effects of this practice. For example, our study proves that the practice of artificial feeding alters the ecological responses, and space-use patterns, of a wildlife species. Through artificial feeding, the carrying capacity

might be boosted, with unexpected consequences at other trophic levels (i.e., summer over-browsing; inter-specific competition). Similarly, the grouping of individuals at feeding station sites might cause intra-specific competition to establish a social dominance among individuals (Espmark 1974), which in turn can enhance stress levels (Ceacero et al. 2012) and potentially counterbalance the energetic benefit obtained by feeding on opportunistic artificial resources. Moreover, grouping may also enhance disease transmission among individuals (see Sorensen et al. 2014 for a review). Conversely, individuals might benefit from grouping at feeding station sites to reduce the individual predation risk (Belotti et al. 2014) from wolves and lynx (Melis et al. 2009). Indeed, supplemental feeding practice reduced migratory behavior (Jones et al. 2014), and feeding sites acted as foci for disease transmission of Brucellosis, increasing prevalence of Brucellosis in over 100,000 elk through the entire greater Yellowstone Ecosystem (Brennan et al. 2014). Because roe deer are the most abundant ungulates in Europe and constitute reservoirs for several zoonosis, including those with direct transmission among individuals (e.g., Carpi et al. 2009, Eggert et al. 2013), disease transmission at feeding station sites is an issue of particular relevance to be investigated.

Lastly, it is necessary to evaluate the role of supplemental feeding in light of the current fast-occurring climate change (Alley et al. 2003). If wildlife management through supplemental feeding aims at compensating the lack of natural resources in winter, climate change may modify the need for supplemental feeding (Post and Stenseth 1999). In particular, snow cover is undergoing dramatic changes (Steger et al. 2013), especially at intermediate and low elevations where it is constantly reducing (O'Gorman 2014). In these areas, the winter environment for roe deer might be less limiting for individual survival, as a combination of reduced costs of locomotion in deep snow (Ossi et al. 2014) and the permanence of natural food resources in winter. Consequently, warmer winters with shallower snow may reduce the need for supplemental food provision.

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