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Ecological determinants of roe deer (*Capreolus capreolus*) spatial behavior and movement in limiting conditions

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Contents

PUBLICATIONS

The following thesis is based on a series of papers at different stages of progress. Five papers have already been published on peer-reviewed journals:

- Morellet N., Bonenfant C., Börger L., **Ossi** F., Cagnacci F., Heurich M., Kjellander P., Linnell J.D.C., Nicoloso S., Sustr P., Urbano F., Mysterud A. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. Journal of Animal Ecology 82:1326–1339. doi: 10.1111/1365-2656.12105
- Cagnacci F., Focardi S., Heurich M., Stache A., Hewison A.J.M., Morellet N., Kjellander P., Linnell J., Mysterud A., Neteler M., Delucchi L., **Ossi** F., Urbano F. 2011 Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos. 120: 1790-1802.
- Marfievici R., Murphy A.L., Picco G. P., **Ossi** F., Cagnacci F. 2013. How Environmental Factors Impact Outdoor Wireless Sensor Networks: A Case Study. In: 10th IEEE International Conference on Mobile Ad-hoc and Sensor Systems (IEEE MASS 2013), Hangzhou, China, October 14-16, 2013.
- **Ossi** F., Gaillard J-M., Hebblewhite M., Cagnacci F. 2014. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. European Journal of Wildlife Research, 61(1), 111-124.
- Picco, G. P., Molteni, D., Murphy, A. L., **Ossi**, F., Cagnacci, F., Corrà, M., & Nicoloso, S. (2015, April). Geo-referenced proximity detection of wildlife with WildScope: design and characterization. In Proceedings of the 14th International Conference on Information Processing in Sensor Networks (pp. 238-249). ACM.

Four other papers currently correspond to manuscripts at different stage of preparation that will be submitted for publication in international journals:

- **Manuscript 1: Ossi** F., Gaillard J-M., Hebblewhite M., Morellet N., Kroeschel M, Kjellander P, Mysterud A., Linnell, J. D. C., Sandfort R., Heurich M., Sustr P., Berger A., Urbano F., RoccaM., Soennichsen L., Ranc N., Cagnacci F. Perturbation of food availability affects space use of large herbivores: a large scale study on roe deer. *In prep*. [**Chapter 1**]
- **Manuscript 2: Ossi** F., Focardi S., Giannini N., Picco G, Molteni D., Gaillard J-M., Cagnacci F. Connect to contacts: accounting for detection error by proximity loggers in studies of animal ecology. *In prep.* [**Chapter 3.1**]
- **Manuscript 3: Ossi** F., Guting R. H., Behr T., Cagnacci F. Spatiotemporal databases and animal tracking data: an attempt to infer spatial relationships under limiting conditions. *In prep.* [**Chapter 3.2**]
- **Manuscript 4: Ossi** F., Cordano E., Eccel E., Bianchini E., Cagnacci F. From roe deer winter resource selection to prediction of roe deer spatial distribution: challenges and proposed solutions to fill this gap. *In prep.* [**Chapter 2.2**]

ABSTRACT

For the majority of large ungulates living in temperate regions winter is the limiting season, because of the combined effects of lack of resource availability and severity of climatic conditions. Those species that did not develop any particular morphological and physiological adaptation to cope with winter severity may adopt movement and space use tactics instead (like e.g. migration). Specifically, these space use patterns may emerge at different spatiotemporal scales to allow individuals to accede the resources they need and escape unfavourable conditions, thus determining both individual fate and population dynamics. A detailed understanding of the relationship between limiting factors in wintertime, and individual movement response, is remarkable to preserve and manage wildlife successfully, especially in the context of fast-occurring climate change that induces important alterations in landscape and resource distribution (e.g. changes of snow cover patterns). The comparison of movement tactics under different environmental scenarios, e.g. by means of large-scale analysis at the species distribution range, represents a valuable approach to work in that direction and to assess the effects of landscape alteration on individual movement.

Roe deer (*Capreolus capreolus*) is an excellent model species to investigate these issues, because its distribution range covers most of Europe, thanks to its high ecological plasticity. For those populations that live in northern and mountain environments, winter is the limiting season because roe deer lack any morphological and physiological adaptations to cope with winter severity. In spite of the adoption of specific movement tactics such as partial migration from summer to winter ranges, roe deer may still face limiting conditions in some areas of the distribution range exposed to winter severity. Wildlife managers therefore have developed supplemental feeding programs to sustain roe deer (and other ungulate) populations. Regardless of the pervasiveness of this practice and the potential negative ecological

consequences (such as for example the enhanced probability of disease transmission), if and how the interplay between distribution of supplemental feeding sites and winter severity may shape roe deer spatial ecology remains mostly unknown.

During my PhD, I provided a contribution to investigate in this direction. First, I relied on the data stored and managed in the EURODEER database (www.eurodeer.org) to evaluate across a wide latitudinal and altitudinal gradient how individuals responded to the presence of these patchily distributed resources under different environmental conditions and supplemental feeding management.

The comprehensiveness of large scale datasets such as EURODEER is counterbalanced by some limitations in terms of data resolution of some potentially meaningful environmental variables, such as snow cover. To overcome these limitations, I empirically collected accurate data on snow cover and snow sinking-depth to assess the combined effect of snow and of the distribution of feeding stations on winter resource selection in an Alpine population of roe deer.

The investigation of the effect of feeding stations on individual space use tactics should go hand in hand with a proper assessment of the inter-individual relationships occurring at feeding stations, which in turn correspond to contacts btween animals. Measurements of contact rates is a relatively new ecological interest, and could be performed either by visual recording of observers, or by means of proximity loggers or, as alternative, using tracking data that permit to infer spatial relationships from individual trajectories. The latter two approaches are more practical in terms of application, but both need to be carefully calibrated to avoid biased ecological inference derived from the obtained contact measurements. In this context, I performed a detailed analysis and modelling of the factors influencing the connectivity of recently introduced proximity loggers (WSN, Wireless Sensor Network). In parallel, I explored the potential applicability of SECONDO spatiotemporal database for the investigation of spatial relationships among individuals through the more widespread GPS tracking data.

The large-scale comparative analyses I conducted along a wide latitudinal and altitudinal gradient showed that the use of feeding sites by roe deer is highly seasonal, and specifically associated to low temperatures and activation of the feeding stations, but not to snow cover. Moreover, I found some indications that winter use of feeding stations was negatively affected by the presence of competitors. Finally, I found a strong signal of the reduction of individual home range size in relation to feeding site use. Local assessment of roe deer winter resource selection partially supported these results: the main drivers of roe deer resource selection included the proximity to feeding stations (although to a lesser extent than expected) and, a more strong inverse relationship with snow sinkng depth. The main driver of roe deer habitat use was presence of forest canopy. The absence of any statistically significant effect of the index used for measuring snow at a large scale (MODIS) supported the importance of local measurements of snow to complement remotely-sensed data.

The finding that the use of feeding stations leads individuals to concentrate their movements around these sites supports the hypothesis of high contact rate between individuals at feeding sites. i.e. as they would work as attractive points. The assessment of encounters is preliminary to the evaluation of such hypothesis. I have demonstrated Wireless Sensor Network proximity loggers as tools with high potentiality for assessment of encounters. At the same time, my work has strongly indicated the need to carefully calibrate these tools before applying them for any biological investigation, and provided practical guidelines on how to proceed, including how to model the error probability. Alternatively, I laid the first technical premises to assess encounters from the more widespread GPS tracking data, by means of high-performance queries within an appropriate spatiotemporal database.

I conclude that roe deer use feeding stations, but only when winter conditions are particularly harsh (i.e. low temperature, abundant snow cover). In a context of climate change with an alteration of snow pattern distribution due to a general increase of temperatures, it would be essential to understand whether supplemental feeding management will still be a reasonable and effective tool to manage roe deer. More generally, it would be necessary to assess whether roe deer indeed need feeding stations for overwinter survival. This work clearly provides evidence that the distribution of feeding stations modifies roe deer spatial behaviour. A full understanding of the patterns of animal aggregation, derived from the correct measurement of contact rates, is thus fundamental to understand the consequences of supplemental feeding practices on animal welfare, and ecosystem consequences (e.g., disease transmission). Research in these directions would ultimately permit to understand the trade-off between benefits and costs, both for wildlife, and as a human action, of supplemental feeding practices, thus helping wildlife managers to take the right decisions.

Key words: roe deer, large-scale analysis, proximity sensors, supplemental feeding, snow conditions, snow cover, snow sinking depth, inter-individual spatio-termporal relationships.

INTRODUCTION

Movement is fundamental for life at multiple spatiotemporal scales, driving individual fates as well as population dynamics and, lastly, the evolution and the diversity of life (Nathan et al. 2008). As such, a comprehensive understanding of the relationship between the reasons for moving and the resulting movement patterns represents one of the most relevant steps for improving our ecological insights on a focal species and consequently adopt appropriate management strategies for its conservation (e.g. Jones et al. 2014). One of the most important challenges is to identify the limiting factors influencing the space use patterns of a given species (Sih and Gleeson 1995), to then analyse the movement tactics through which individuals tackle them. An effective way to work in this sense is to contrast populations of a same model species that live under different environmental conditions (Stien et al. 2010). In fact, a longitudinal comparison of individual movement response to diverse environmental pressures might permit to understand how individuals adapt to changes of the environment in which they live (Morellet et al. 2013). Insights in this direction might be particularly relevant for wildlife management and conservation, especially in a period like the present-day one of fast-occurring environmental changes due to climate change (Alley et al. 2003).

One of the most immediate outcomes of landscape and climate changes is the spatiotemporal alteration of the distribution of resources (Craine et al. 2010), which in turn affects individual movements at multiple spatiotemporal scales (Owen-Smith et al. 2010). Indeed, for most animal species, and for large ungulates in particular, the acquisition of resources is one of the main drivers of individual movement, space use and habitat selection (Fretwell and Lucas 1970). This pattern is emphasized especially in the most energetic demanding periods for individuals, which depend on a combination of lack of resources and increased costs for survival (Parker et al. 2009). For the majority of ungulates living in the northern or mountain environments, this is the typical situation of wintertime (Telfer and

Kersall 1984). In winter, food resources are limited due to the absence of vegetation regrowth (Kreyling 2010). Moreover the snow cover, i.e. the most typical element of winter (Lundmark and Ball 2008), further reduces food availability by burying food items (Hovey and Harestad 1992). This problem is of particular relevance for grazers (Robinson and Merrill 2012), while mixed-feeders (e.g., grazing and browsing) often shift selection of food resources, as reported in mountain caribou (*Rangifer tarandus caribou*) (Kinley et al. 2007). The presence of snow cover also affects resource distribution indirectly, by hampering accessibility to resources for individuals because of high energetic cost of walking (Parker et al. 1984; Bunnell et al. 1990). The physical features of the snow cover (thickness, hardness, density) influence the sinking depth of the animals in the snow (Lundmark and Ball 2008), leading individuals to decrease mobility (Rivrud et al. 2010). Another fundamental abiotic driver of winter severity is decreasing temperature, that leads to increased costs of thermoregulation (Moen 1978), an issue of particular relevance for small and medium species (Mysterud et al. 1999).

Some ungulates have developed specific adaptations to face winter severity (Telfer and Kersall 1984). These include morphological traits such as the disproportional chest height (e.g. Lundmark 2008 on moose *Alces alces*) or the particular hoof morphology to favour movements in the snow (e.g. Fancy and White 1985 on caribou *Rangifer tarandus*); physiological adaptations such as the high gut capacity to maximize the rate of forage intake (e.g. Klein 1995 on muskoxen *Ovibos moschatos*). Formozov (1946) classified these species as "chioneuphores" ("snow tolerators") or "chionophiles" ("snow lovers"). Instead, several other ungulates living in northern or mountain environments are not particularly adapted to cope with a snowy environment. Such species, classified as "chionophobes" ("snow haters") (Formozov 1946), can compensate the lack of specific fitting to snowy environments by adopting particular behavioural responses to snow presence, which can take place at multiple spatiotemporal scales (Telfer and Kersall 1984; Holand et al. 1998). One of the most evident movement responses to cope with winter adversity corresponds to seasonal migrations from summer to winter ranges. Migration, when it occurs, represents a tactic that ungulates adopt to escape unfavourable conditions in winter (e.g. white-tailed deer *Odocoileus virginianus*: Sabine et al. 2002, Fieberg et al. 2008; moose *Alces alces*: Ball et al. 2001; on mule deer *Odocoileus hemionus*: Nicholson et al. 1997; roe deer *Capreolus capreolus*: Ramanzin et al. 2007), and is often driven by seasonal changes in habitat suitability and resource distribution (Dingle and Drake 2007). Migration can be either obligatory, when it involves all the individuals of a population (Sawyer and Hauffman 2011), facultative, if animals migrate only in certain years or late in the season for a short period (Nicholson et al. 1997, Sabine et al. 2002, Fieberg et al. 2008), or partial, when one fraction of the population is migratory and the other remains resident either in the breeding or non-breeding area (see also Lundberg 1988). Migration from summer to winter ranges generally leads animals to be in areas where environmental conditions are less harsh than in summer ones during winter months (e.g. Sabine et al. 2002, Grovenburg et al. 2009). Yet such conditions are often far from being ideal for individual survival (Lundmark 2008), thus constituting a major determinant of population dynamics (e.g. DelGiudice et al. 2006). As such, animals have to select habitat even at the within-home range level, i.e. third order habitat selection *sensu* Johnson (1980), to survive to winter severity. In particular, individuals adopt specific tactics to maximise energy intake from foraging while minimising energy expenditure for moving (Schmitz 1991). These include the selection of specific snow-free patches within winter ranges (Lundmark 2008; Telfer and Kersall 1984), such as steep slopes where snow usually blows off (Reitan 1988); trail making behaviour, i.e. the following of well defined trails where snow is harder and sinking is reduced (Crête and Larivière 2003; Lundmark and Ball 2008), which allows individuals to reach even far spots to feed by reducing locomotion expenditures (e.g. Telfer and Kersall 1979 on white-tailed deer) or by snow digging for finding forage (Fortin 2003 on bison *Bison bison*). The set of such behavioural adaptations emerges in the definition of winter home ranges, whose variation is indeed affected, among other factors, by the spatiotemporal distribution of resources within the range (Tufto et al. 1996, Kjellander et al. 2004, Van Beest et al. 2011) and by morphological characteristics that can affect individual locomotion (Kie et al. 2002; Walter et al. 2009).

The ecological context so far described, and the consequent large- and fine-scale movement patterns, can be altered by a widespread human management practice, winter supplemental feeding. In most of European areas where winter is particularly severe (Alps, Scandinavia, Central and Eastern Europe) supplemental feeding, which involves the establishment of feeding stations provided with man-prepared food (usually highly concentrated cereals in pellets), is commonly practiced or even mandatory (see Table 1), with the aim to mitigate resource scarcity and favour overwinter survival of large herbivores (Putman and Staines 2004). Specifically, reasons for this practice include maintenance of high individual densities (Peek et al. 2002); the enhancement of male trophy quality for game purposes (Putman and Staines 2004); mitigation of winter starvation to meet animal welfare concerns (Grenier et al. 1999); reduction of migratory patterns from summer to winter ranges to prevent forest damages or car accidents (Sahlsten et al. 2010, Jones et al. 2014); or reduction of browsing on young forest stems (Putman and Staines 2004, Gundersen et al. 2004). The effectiveness of this practice is controversial (Putman and Staines 2004), and several drawbacks of supplemental feeding management have been identified. First, the provisioning of food in emergency situations might alter the mechanisms of natural selection (Schmidt and Hoi 2002; Mysterud 2010). Second, foraging places tend to modify strongly individual movements by acting as central attractive places (Orians and Pearson 1979), as reported for several ungulate species (red deer *Cervus elaphus*: Smith 2001, Jerina 2012; white-tailed deer *Odocoileus virginianus*: Cooper et al. 2006; moose *Alces alces*: Van Beest et al.

2010, Gundersen et al. 2004; roe deer *Capreolus capreolus*: Guillet et al. 1996; sika deer *Cervus nippon*: Masuko et al. 2011). As such, individuals might have a higher probability to gather in proximity of feeding sites (Sahlsten et al. 2010, Fagan et al. 2007, Jerina 2012; Campbell et al. 2013) with increasing competition as a result (Putman and Staines 2004), especially in animals like ungulates that are known to segregate into stable social groups with dominance hierarchies (Clutton-Brock and Guinness 1982; Jenkins and Starkey 1984; Weckerly 1999). The rise of competitive feeding behaviour (Ceacero et al. 2012), where dominant individuals exclude subordinates from productive foraging sites (Thouless 1990) can stress animals living in groups, with further consequences for population health (Vander Wal et al. 2012). Moreover, supplemental feeding practices pose serious concerns relative to the transmission of diseases among individuals (Kenkre et al. 2007, Thompson et al. 2008, Sorensen et al. 2014). Since the dynamics of wildlife diseases depend upon transmission rates, that in turn is affected by host susceptibility to diseases, host density (Rosà and Pugliese 2007) and connectance among individuals (Perkins et al. 2009), an increment of contact rates among individuals at feeding sites can dramatically modify dynamics of disease transmission.

A detailed assessment of contact rates at feeding sites is thus required to evaluate the effects of this management practice on ungulate populations. This can be achieved either by directly observing individuals at feeding sites (e.g. by means of camera images, Thompson et al. (2008)) or by fitting contact loggers to the individuals (Creech et al. 2012, Campbell et al. 2013). Such hi-tech tools, which enhance the quality and quantity of data available for individually marked animals (Cagnacci et al. 2010, Pásztor et al. 2010), have been introduced in animal ecology research quite recently (Ji et al. 2005). The main technology used to integrate proximity detection into animal devices is based on Wireless Sensor Networks, WSNs (Yich et al. 2008). WSNs, which work on Ultra High Frequency radio transmission, UHF (300 Mhz – 3 GHz), are distributed systems composed of static loggers placed in strategic spots (like feeding stations) and mobile loggers fitted on animals. Contact detection between mobile proximity loggers (mainly from Sirtrack Ltd., Havelock North, New Zealand) permits to investigate, among others ecological applications, disease transmission patterns (e.g. Ji et al. 2005; Böhm et al. 2009, Hamede et al. 2009). Contact detection between a mobile and a fixed logger, although so far largely overlooked (but see Rovero et al. 2014 for similar application of camera traps), allows instead verifying the preference of individuals for specific focal habitats. Proximity loggers are based on specific technologies, which are subject to stochastic effects and thus errors and bias in the derived measures. As such, these tools need to be accurately tested before being applied on the target species under investigation, a rare practice so far (but see Prange et al. 2006; Drewe et al. 2012; Boyland et al. 2013; Lavelle et al. 2014). Moreover, the application of proximity loggers, although constantly increasing, is currently limited to a reduced number of case studies. A potential alternative to increase the amount of data available for analysis, and consequently the robustness of the biological inferences, is to assess contacts trough Global Position System loggers (GPS) (see e.g. Schauber et al. 2007, Kjær et al. 2008, Habib et al. 2011). This solution has two drawbacks. First, the periodic nature of GPS data does not allow assessing prolonged contacts among individuals and might eventually lead to an underestimation of contact rates (Lavelle et al. 2014). Second the intrinsic position error of GPS devices (D'Eon and Delparte 2005) prevents to identify reliably fine-scale spatial patterns (i.e. contacts occurring within a range of a few meters). However, after accepting to deal with these technical limitations, GPS can constitute a valid alternative to proximity loggers. In particular, the use of specific spatiotemporal databases, which conjugate spatial and temporal information on moving objects, permits to infer specific intra-specific relationships by movement trajectories. SECONDO is a recently developed spatiotemporal database (Guting et al. 2005) that works in that direction: it analyses trajectory couples, detecting the distance between synchronous points and ultimately extrapolates spatial information on the relationships among individuals. As well as the application of proximity loggers, the use of such devices is so far extremely limited; as such it necessitates to be carefully tested by means of one or more case studies.

In winter limiting conditions, the interplay between supplemental feeding practices, when applied, and snow cover affect the spatiotemporal distribution of available resources for large ungulates, shaping in turn both individual movements tactics (Lundmark 2008) and aggregation patterns in proximity of the feeding sites. As such, a detailed analysis of the effect of this perturbation of resource availability and distribution should be performed from a double perspective, i.e. at the individual and inter-individual levels. Moreover, spatiotemporal alteration of resources is occurring because of the effects of climate change, which particularly affect the average seasonal snow cover (O'Gorman 2014), the timing and amount of snowfalls, the number of days with snow cover, and the quality of snow on the ground (Steger et al. 2013). Consequently, predicted changes of snow cover and spatiotemporal alteration of natural resources distribution imposed by climatic change might lead to the modification in the use of the feeding sites by ungulates. It is thus fundamental to investigate the response of the individuals to such changes of resources distribution under limiting conditions, which might provide useful insights to establish plans for wildlife conservation and protection. An effective way to work in that direction is to investigate these issues carrying out large-scale analyses at the inter-population level, comparing individual responses across a wide distributional gradient of conditions of availability of food resources (Morellet et al. 2013).

An excellent model species to investigate these issues is the European roe deer (*Capreolus capreolus*). Roe deer is the most common ungulate in Europe, ranging throughout the continent with few exceptions in an impressive variety of habitats and landscapes, from central plains (Danilkin and Hewison 1996), to northern latitudes (e.g., Cederlund 1982;

Mysterud and Østbye 1995), and Mediterranean environments (e.g., Melis et al. 2004). Roe deer play an important ecological role in a consistent number of ecosystems where it is present: as a middle-sized selective herbivore (Duncan et al. 1998), it influences the dynamics of plant composition and structure of ecosystems; as a prey, its re-colonisation in the second half of the 20th century has been a pre-condition for the re-establishment and sustainability of large predators, such as the lynx (Breitenmoser et al. 2000) and the wolf; as a reservoir for several zoonosis diseases, roe deer is important for its influence on dynamics of disease transmission (Carpi et al. 2008, Carpi et al. 2009, Perkins et al. 2009, Rizzoli et al. 2009); lastly, roe deer has a strong economic value, being one of the most harvested game species (more than two million roe deer/year harvested, Burbaitė and Csányi 2009). Roe deer adapt to the most diverse environmental conditions thanks to its great ecological and behavioural plasticity, which makes this ungulate an ideal species for large-scale comparative analyses (Morellet et al. 2013). This aspect can be better evaluated in those areas characterized by a higher degree of seasonality, which is typically the case of northern countries and mountainous areas (Albon and Langvatn 1992). In these areas, roe deer populations are highly sensitive to extreme winter conditions for a combination of unfavourable morphological, physiological and life-history traits (Holand et al. 1998). First, roe deer morphology is not adapted to move in deep snow, because of foot loading and low brisket height. The energy expenditure for walking becomes important when snow exceeds 50 – 60 cm (Holand et al. 1998). Second, roe deer are close to the income breeder end of the continuum of energy allocation tactic (Andersen et al. 2000). These ungulates are capable to stock fat reserves only at a limited extent (e.g. Hewison et al. 2009), covering at most 20% of total energy expenditure (Mysterud et al. 2001). Consequently roe deer are dependent on continuous access to high quality food (Holand 1992) to intake energy to meet their high energy expenditures. As such, roe deer are particularly sensitive to snow ("chionophobes" *sensu* Formozov 1946), and populations living in northern countries and in mountainous areas are expected to have impaired survival in winter (e.g. Mysterud 1999, Ramanzin et al. 2007). Indeed Gaillard et al. (1998) found that both food scarcity and winter severity negatively affect population dynamics, especially affecting fawns and old individuals. The risky period for individual survival might be particularly acute towards the end of the winter, because of the physiological cycle of roe deer. In this period of adverse environmental conditions and limited availability of food resources, males need to gain energy to prepare for territorial establishment (Liberg et al. 1998), whilst females enter in the late phase of gestation (Hoffmann et al. 1978). As a species not adapted to extreme winter conditions, roe deer have developed partial migration behaviour as a movement tactic to respond to climatic adversity (Mysterud 1999). Although it is not yet clear why only a part of the population migrates from winter to summer ranges, it is well established that winter conditions of winter ranges are less harsh than those of summer ones (Mysterud 1999, Ramanzin et al., 2007). However, conditions in winter ranges can still be limiting for roe deer winter survival. For these reasons, supplemental feeding, which provides high quality food *ad libitum* during the critical season has often been used for roe deer maintenance throughout Europe (Putman and Staines 2004). Roe deer winter habitat selection at the range level (3rd order *sensu* Johnson 1980) should thus be directed towards the maximisation of net energy gain by avoiding snowy patches and selecting spots close to supplemental feeding sites, where present. Accordingly, roe deer populations in northern environments have been reported to select shallow snow spots by exploiting local habitat types and topographical features (Holand et al. 1998). Roe deer also select for bedding sites under dense forest canopy where snow accumulation is limited (Mysterud et al. 1997) and thermal shelter reduces energetic requirements (Mysterud and Østbye 1995). Lastly, roe deer have been found to be dependent on supplemental feeding in northern countries (Guillet et al. 1996), with a tendency to reduce winter range in proximity of supplemental feeding places. Although evidence for that is still lacking, the settlement of supplementary feeding places in winter ranges might further increase the natural tendency of roe deer to aggregate in small groups in winter to look for shelter and food (e.g., Kjellander et al. 2004). Given the role of roe deer as reservoir for several zoonosis diseases, the potential consequences of aggregation at feeding stations on dynamic of disease transmission might be particularly relevant.

In this context, a detailed assessment of the interplay between supplemental feeding and snow cover on shaping roe deer space use tactics and inter-individual relationships is of uttermost importance for the preservation/management of a species of such high ecological and economical value. Quite surprisingly, research in this direction is to our knowledge rather limited, especially considering the wide diffusion of supplemental feeding practices across Europe. My thesis aims at contributing to this topic, by reconnecting roe deer individual movement patterns with their ecological drivers under limiting conditions. I set three specific objectives for doing that, which permit both to identify general patterns at the distribution range scale of analysis, and to focus on local populations to better investigate specific issues. I describe the objectives, as well as a rationale of the work carried out during the thesis, in the next section.

OBJECTIVES

1) Ecological adaptation of movement of roe deer under limiting conditions

Large-scale analyses that compare populations living under different environmental conditions along a latitudinal and altitudinal gradient can be supported by scientific cooperation and data sharing, e.g. what takes place with the EURODEER experience (www.eurodeer.org) (Cagnacci et al. 2011). The EURODEER database is an excellent example of Virtual Research Environment for good practice wildlife data management (see Urbano et al. 2010 for general considerations). Roe deer localisations (GPS and VHF) from more than 20 study areas covering a large part of roe deer distribution are hosted in a spatial database and coupled with the relevant geographic, climatic and remotely sensed datasets. In this context, both seasonal partial migrations (Cagnacci et al. 2011) and home range size variation (Morellet et al. 2013), have been investigated. These works have shown that roe deer space use tactics well represent a model of adaptations to limiting conditions, by means of a trade-off between resource acquisition and avoidance of adverse winter conditions. In particular, migratory roe deer tend to stay longer in summer ranges, and get back to winter ranges only when conditions in summer ranges are particularly harsh (see also Mysterud 1999). At the home-range scale, resource availability is one of the main drivers of range size (Morellet et al. 2013), supporting the negative relationship existing between forage availability and home range size found for large herbivores in other studies (e.g. Huston and Wolverton 2009). Contrary to the expectations, however, Morellet et al. (2013) found an unexpected restriction of home ranges in winter in the northern and mountain countries. This was probably due to the interplay between the presence of supplemental feeding and snow cover, which both tend to reduce individual movements (e.g. Guillet et al. 1996, Rivrud et al. 2010), but this hypothesis could not be tested up to now. Based on these premises, I investigated the effects of the perturbation of spatiotemporal resource distribution constituted by the supplemental feeding practice on roe deer movement ecology, across a wide latitudinal and altitudinal gradient. In particular, I looked at the ecological factors determining the different patterns of use of the feeding stations, at different temporal scales, to then focus on the consequences of feeding station use on individual space use behaviour (**Chapter 1**).

2) Local scale assessment of winter space use patterns at the altitudinal limit of roe deer range distribution

Large-scale analyses generally suffer from the limitations due to data resolution and precision. For instance, data on snow cover collected within the EURODEER database come from a remote sensed index (MODIS: Moderate Resolution Imaging Spectroradiometer) in a form of absence/presence data (Hall et al. 2002). These data have a very low temporal (one data every 15 days) and spatial (500 meters) resolution, and as such can negatively affect the predictive power of this variable in the models (Brennan et al. 2013), underestimating the importance of this factor that instead is expected to be one of the most important determinants of winter space use tactics in roe deer (e.g. Lundmark and Ball 2008). Thus, I investigated in more details the effect of snow cover and other environmental factors (like e.g. solar radiation, canopy presence and distance from feeding stations) on predicting roe deer movements during wintertime. In particular, I analysed roe deer winter resource selection at the range scale (3rd order *sensu* Johnson 1980) on a roe deer population living in the Italian Alps, at the altitudinal limit of the species distribution (**Chapter 2.1, Ossi et al. 2015**). I collected accurate data of snow cover during a field campaign in winter 2012-2013 to establish the importance of this factor on shaping roe deer winter resource selection. This work presents a drawback in the limitation of general conclusions, which are due to the modest subset of data. I tried to reinforce them by means of an external validation of the obtained model of roe deer winter resource selection. I used for this purpose the data empirically collected during a second field campaign in winter 2013-2014, in the same area. I present these results in the **Chapter 2.2,** where I also discuss the perspective of extending the analysis to evaluate the effect of forecasted variation of snow cover distribution on the predictable changes in roe deer spatial distribution.

3) **Methodological and technological perspectives to study inter-individual relationships under limiting conditions**

The assessment of spatial relationships among individuals at feeding sites, also by means of recently developed tools, should be the natural follow-up to the investigation of their use at the individual level. The first essential step to apply correctly contact loggers to wildlife investigation is the assessment of their performance. I moved in this direction, performing a detailed analysis of Wireless Sensor Network contact detection performances, from a highly controlled scenario to a semi-natural one (**Chapter 3.1**). Such work took benefit from preliminary investigation of the environmental factors affecting Wireless Sensor Network connectivity, which is presented in Marfievici et al. (2013), and from a technical assessment of Wireless Sensor Network operation on the same contact loggers used in this study (Picco et al. 2015). Moreover, I tried to overcome limitation imposed by the reduced number of contact data so far available, applying the SECONDO spatiotemporal database to infer proximity patterns by trajectory analysis (**Chapter 3.2**). In particular, I used the GPS data collected and stored within the EURODEER project to build roe deer trajectories and test the possibility to use SECONDO spatiotemporal database to investigate inter-individual spatial relationships in proximity of feeding sites. The inferred information on spatial relationships between individuals could be used in the future to investigate the environmental and feeding management factors (like e.g. snow cover or quality of food provided), which mainly contribute to shape the observed gathering pattern at feeding sites. Ultimately, the inferred contacts occurring between individuals might be used to understand whether the use of feeding sites as a management tool affects potential disease transmission patterns occurring in a wild population.

Table 1 Supplementary feeding practices across most of European countries where roe deer have been intensively monitored. Adapted from "Putman, Apollonio and Andersen (2011). Ungulate management in Europe: problems and practice. Cambridge University Press"

Feeding obligatory	Feeding common	Feeding sporadic	Feeding forbidden
Germany (part)	Germany (part)	Denmark	Netherlands
Austria	Hungary	Belgium	
Slovakia	Slovenia	Portugal	
Poland	Baltics	Spain	
Czech Republic	Switzerland	UK	
Croatia	Italy		
	Norway		
	Finland		
	Sweden		
	France		

MATERIALS AND METHODS

In this section, I describe the methods I used to perform the research described in detail in chapters 1 and 2, i.e. respectively large and local scale analysis. First, I provide a technical description of the EURODEER database, and of the policy guidelines ruling the data sharing experience of the Eurodeer scientific collaborative group. Then, I outline the technique adopted to capture roe deer in the case study I conducted in the Italian Alps, and the capture success during the field campaign.

1. Large-scale assessment: EURODEER - an example of successful collaborative scientific project

The importance of data sharing in science

Data sharing among scientists, even from different fields, can greatly enhance the quality of scientific outcomes, producing rapid research breakthroughs that otherwise would not occur (e.g. Birnholtz and Bietz 2003). Within the field of animal ecology, the recent technological advancements, such as GPS collars (Tomkiewicz et al. 2010) and activity sensors, allows researchers to obtain more data of better quality. Where these technical advances are coupled with a collaborative approach among research groups focused on different environments, enormous advantages to research can be obtained, opening the door to long-term, multi-species, large-scale studies (Carpenter et al. 2009). This approach permits to get robust inferences for complex, multi-factorial phenomena, such as meta-analyses of movement (Hebblewhite and Haydon 2010) or the effects of climate change on animal behaviour and distribution (Cagnacci et al. 2011, Morellet et al. 2013). As such, data sharing is acquiring more and more importance in the evaluation criteria of funding institutions (e.g. European Union): data collection within a specific project should be carefully planned to facilitate accessibility of the data, which should be shared to permit their interoperable use beyond the original purposes for which they were collected (Guidelines on Data Management in Horizon 2020). Last but not least, the accessibility of data is now often required from the main peer-reviewed journals (e.g. Reichman et al. 2011; Hanson et al. 2011), so to facilitate the understanding and replication of published results.

In spite of the relevance of data sharing, this practice is far from being consolidated in animal ecology compared to other scientific fields of biology (like molecular evolution or genomics), and movement ecology papers based on collaborative projects are rare (Costello

2009). This is due to both technical aspects (e.g. availability of dedicated data e-infrastructures; definition and use of data and metadata standards) and the general reluctance of ecologists towards data sharing. This negative attitude takes roots in the additional costs and time requirement that data sharing implies (Tenopir et al. 2011), and in a general lack of proper technical skills in data management.

However, something is moving in the direction of data sharing and science collaboration, and a few initiatives have already been undertaken. In the movement ecology field, the best known is probably the Movebank project (www.movebank.org), which provides a free data archiving and back-up service, promotes data-sharing, facilitates collaborative research, and aims to support live streaming of real-time data for a large set of species and monitoring technologies (e.g. ARGOS, GPS, VHF) (Wikelski and Kays 2011). Another example comes from WRAM (Wireless Remote Animal Monitoring), a project aiming at supporting collaborative research projects on multiple species across Scandinavian countries. OBIS Seamap (seamap.env.duke.edu) instead collects animal tracking data for marine mammals, seabirds, fish and turtles from more than 600 large vertebrates species around the world (Halpin et al. 2006).

EURODEER: from the motivation to management of a successful collaborative project

Why a data sharing project on roe deer?

The European roe deer (*Capreolus capreolus*) is the most widespread ungulate in Europe. Thanks to its great ecological and behavioural plasticity (Andersen et al. 1998), this well-studied species constitutes an excellent model to investigate the adaptation of individuals to ongoing landscape alterations and climatic change (e.g. Morellet et al. 2013). Therefore, an easily accessible database collecting movement data from different areas where roe deer populations have been monitored would strongly support the attempt to perform large-scale comparative analyses of roe deer biology and ecology. In particular, data sharing and collaboration might allow investigating variation in roe deer ecology along an environmental gradient, and the population responses to the natural or human induced alteration of environmental conditions.

EURODEER chronology – From first seeds to a pan-European project

Under these premises, in 2008 the EUropean ROe DEER (EURODEER) project arose, in the form of an informal collaboration between Edmund Mach Foundation (Trento, Italy) and University C. Bernard Lyon 1 (France) to share knowledge on wildlife tracking data management. The uprise of interest in the project from other research groups led to the establishment of a more formal agreement (see next paragraph), and to the setup of a common database (www.eurodeer.org). At present (autumn 2014), 29 research groups from 11 countries joined the EURODEER project, thus leading the amount of data available for analysis to increase exponentially. In detail, the project covers 25 study areas from Mediterranean area to Scandinavia (Figure 1). The most of the data are GPS (almost 4 million locations) and VHF locations, collected from 988 radio-tracked animals. Recently, more than 20 million data coming from hi-tech activity sensors have been uploaded in the database. Moreover, since one of the major goals of sharing data projects is to perform long term, multi-species, large scale higher level ecology analysis, EURODEER project recently moved in this direction opening to the collection and housing of red deer (*Cervus elaphus*) GPS data. By now, almost 800.000 GPS locations from 140 red deer monitored across three study areas are stored within the database. EURODEER members meet regularly twice a year in high profile scientific workshops, aimed at discussing ongoing research and develop new future research lines to investigate in the context of the EURODEER project.

EURODEER policy – How to rule and manage a sharing project

EURODEER is an open community based on a collaborative process of data sharing, which are available solely to the EURODEER members to produce better science by allowing answering specific scientific questions with improved data. EURODEER welcomes any researcher who is interested to contribute with his data and expertise to integrate analyses on roe deer biology and ecology. New research groups that decide to join EURODEER group have to sign a "Terms of use" document that is articulated around several points. Most importantly:

1) The EURODEER data set can be used, fully or in part, only for analyses the partners agreed upon.

2) The partners maintain the full property and control on their own data set, and they can therefore decide to withdraw their participation at any stage.

3) The partners freely agree to study a specific theme; their data set and expertise will be provided or not provided accordingly.

4) All partners or groups of partners are invited to propose questions to be addressed with the EURODEER data set and the related set of analyses; doing so, they will also promote discussion and ask the other partners for permission to use their data set for studying the proposed theme.

5) All partners who agreed upon a theme and therefore provided their own data set and expertise will be co-authors of the scientific publications deriving from the analyses.

These characteristics differentiate EURODEER from other data sharing projects in movement ecology, both in the terrestrial, marine and avian domain. First, these projects are usually more focused on data management and sharing, rather than on answering specific biological research questions. Instead, the qualifying aspect of EURODEER derives from the expertise knowledge provided by each group about the data and the analysis stage, in that local knowledge is critical for the correct interpretation of ecological data (Zimmermann 2008).

Second, most of data sharing projects have dedicated financial and institutional support, and, as a consequence, more ambitious goals in terms of interested stakeholders and species described. Conversely EURODEER has been built with a bottom up approach, as a voluntary scientific collaboration among researchers. It is a temporary and not institutional project, without (so far) specific funds for its development. The limited expenses (e.g. hosting server costs and spatial database expert assistance) are so far mainly covered by the research groups, on a free basis (i.e. there are no mandatory costs associated with participation in the project). As a very nice follow up of this low-cost/highly effective output approach, EURODEER attracted the interest of GPS collar companies, and it is officially sponsored by Vectronic Aerospace since 2012.

EURODEER: technical aspects to maintain the project

EURODEER software platform

The implementation of EURODEER project requires an adequate information system to enable effective data and knowledge sharing (Yeung and Hall 2007, Cushman and Huettmann 2009). The EURODEER information system is designed with hardware and software for data storage, access, analysis and management in a distributed, multi-user environment. Moreover, specific tools have been developed to promote collaborative science and knowledge exchange among partners (e.g. real-time multi-user document editing tools, forum, mailing list, web site), according to the limited financial resources available.

The EURODEER information system is derived from a previous local experience (ISAMUD system, Cagnacci and Urbano 2008). It is built on a spatial relational database, which is based on a modular client/server architecture (Urbano et al. 2010). Data are stored in the server database where client software applications remotely get the information and store back the results of the analysis. To limit the implementation costs, EURODEER has been implemented based on open source software, which perfectly suits the technical requirements and the collaborative nature of the project. The core of the EURODEER software platform is a PostgreSQL database with its spatial extension PostGIS, where a large set of task-oriented software products are used to manage the data flow and processing (PhpPgAdmin, PgAdmin, GRASS, R, QGIS). The server/client structure supports the connection to data by the specific software used for analysis and visualization by each research group, both open source (e.g. QGIS, R) and closed source (e.g. Esri ArcGIS, GvSIG, MS Excel, MS Access, OpenOffice Calc, OpenOffice Base).

EURODEER data management

A correct data management is a fundamental requirement to achieve reliable scientific results and long-term preservation of data (Urbano et al. 2010). This "management layer" can facilitate integration of data of single research groups with more complex networks of data repositories and knowledge sharing across different disciplines (Christensen et al. 2011). Data coming from different sources (i.e. research groups), despite deriving from the same technology, are quite often heterogeneous. Such data need to be harmonized to allow combined and comparative analyses. In the EURODEER framework, this task is accomplished by the EURODEER data managers and curators. Specifically, each research group sends to the data manager the raw data, together with the required information to correctly use, interpret and filter the original information (e.g. date of sensor deployment on the animal and date of monitoring, outlier positions). EURODEER data managers check the quality of the received data, and harmonize the data before housing them in a centralized repository. Data harmonization aims at keeping quantitative and qualitative consistency among the different EURODEER data sets. It has been established to share the basic information coming from the GPS collars (acquisition time, latitude, longitude, altitude as measured by GPS device, dilution of precision DOP - a parameter that reflects the effect of GPS satellite geometry on GPS precision, number of satellites used to estimate the position, temperature as measured by attached sensors). These informations are integrated by basic data on animals (animal identifier, sex, date of the first capture, age class at the first capture), GPS devices (GPS device identifier, seller company, model), and studies (study identifier and study area boundaries). In a second step, the GPS data are processed within the database to obtain complementary information related to a specific location that might be useful for geometric analyses like trajectory investigations (distance from the previous point, time interval from the previous point, relative and absolute angles, speed, projected coordinates in the local UTM zone, sun angle and a tag that indicates whether the position was taken during daylight or night). Lastly, the spatial extensions (PostGIS) of the database permits to join the raw GPS locations to a set of environmental factors aimed to characterize the animal locations as multi-dimensional elements (Urbano et al. 2010). To get such a result, the managers of the EURODEER project have selected environmental data sets freely and consistently available with a European coverage and with an adequate spatial and temporal resolution, extensively using remote sensing sensing data. The recent upgraded version of PostGIS 2.0, allows also to manage raster layers within the database, and therefore spatio-temporal series (Franklin 2009; Gillespie et al. 2008) (Table 1). Such integration permits to improve the quality standard of the scientific questions, i.e. to reconnect the movement paths of an individual described by the trajectory with the underpinning environmental factors that generate that movement (Nathan et al. 2008). Similar elaboration is performed to process VHF and activity data.

EURODEER is not only a repository of roe deer tracking data. Recently, several data filtering and statistical functions have been implemented, thus permitting to perform some analyses directly within the project framework. The computation of individual home ranges and the regularization or interpolation of individual trajectories represent two notable examples.

EURODEER: Scientific achievements and future perspectives

EURODEER cooperation already led to the publication of three papers in international peer-reviewed journals. Large-scale comparative analyses permitted to shed light on the environmental factors that affect the timing and occurrence of partial migration in roe deer (Cagnacci et al. 2011). Another important achievement was the investigation of the main environmental factors that shape variation in roe deer home range across a wide altitudinal and altitudinal gradient (Morellet et al. 2013). Quite recently, the first pan-European research on breeding excursion behaviour in roe deer females has been successfully achieved (Debeffe et al. 2013).

One of the most interesting aspects of such approach to roe deer ecology investigation is the continuous uprise of scientific questions that originates from the published outcomes. In this way, the interest to cover new research issues within the EURODEER project continuously enhances the quality and quantity of produced science. Thus, the EURODEER experience shows the advantages of a collaborative approach based on a specialized community built around scientific questions and inside a specific research domain, which is characterized by a high level of trust among scientists and where the common research field stimulates active collaborations. By now, almost ten topics are under investigation, from the effect of feeding stations on roe deer movement tactics (which I lead, see chapter 1 of this thesis) to the analysis of dispersal patterns of young individuals and many others. We can thus state that science production has been the motor to data sharing, as a component of knowledge sharing, and not a consequence. EURODEER benefited from the growing enthusiasm of its members in the collaborative effort to challenge the most pressing environmental issues we are calling to face, giving a further demonstration that collaboration (in terms of both data and knowledge) is a very powerful tool of scientific investigation. EURODEER was originally designed as a network of research groups based on a shared database of roe deer movement data, but the recent opening to the collection of red deer location data constitutes a leap forward, stimulating further high level, long-term and multi-species research.

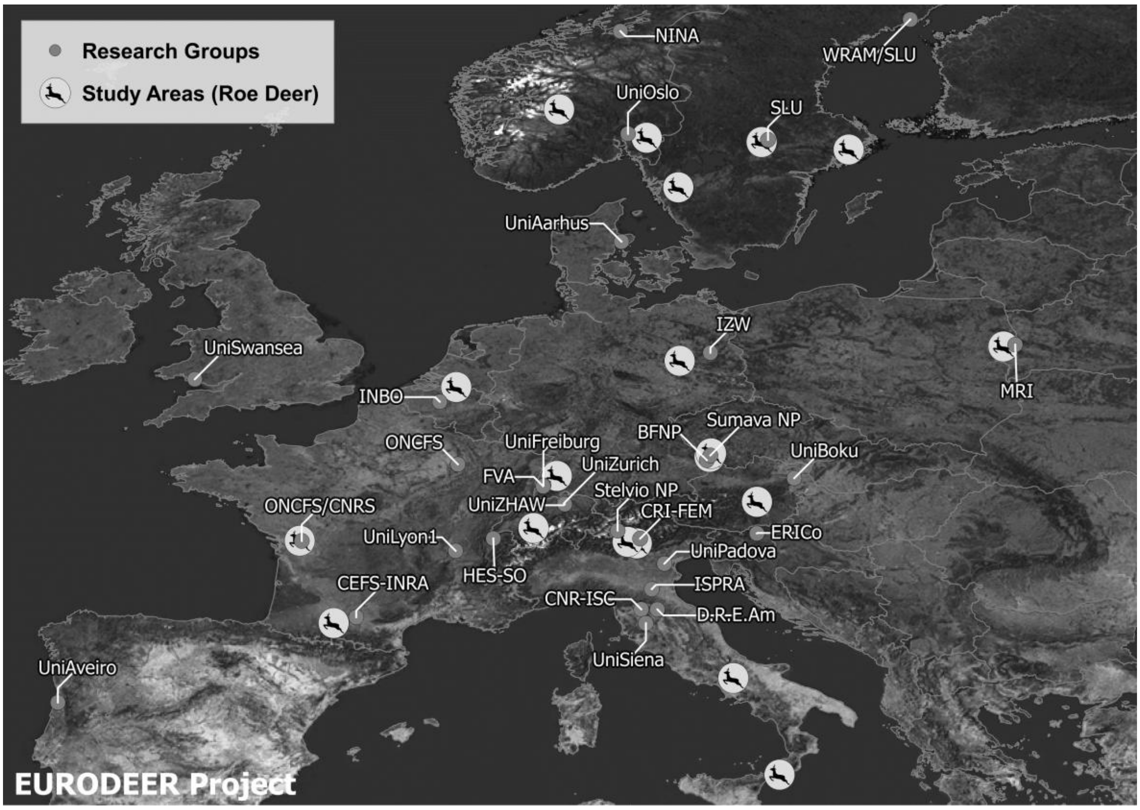
In general, the movement ecology community still suffers from the lack of definition of standards for wildlife tracking data and metadata in terms both of structure and semantics through a domain specific controlled vocabulary and ontology (Michener 2006; Madin et al. 2007; Jones et al. 2006). Some work is under development by different institutions and general references exist (e.g. OGC, Percivall 2010; Darwin Core; Ecological Metadata Language EML, Michener 2006, Fegraus et al. 2005, see also www.ecoinformatics.org), but the movement ecology community has still a long way to go for achieving and using these standards. Further support and community discussion is needed, but a science-based collaborative experience such as EURODEER represents the perfect ground for substantial improvements in this direction.

TABLES AND FIGURES

Table 1 List of the covariates and their data sources associated to each GPS location stored in the database

Variable	Data source and resolution
Altitude, slope, aspect (below 60° latitude)	Shuttle radar topographic mission, resolution 90 meters
Altitude, slope, aspect (above 60° latitude)	Aster DEM (Digital Elevation Model), resolution 30 meters
Land cover/use	Corine Land Cover (year 2006), spatial resolution 100 meters
Snow cover	Moderate Resolution Imaging Spectroradiometer (MODIS snow), spatial resolution 500 meters, temporal resolution 15 days
Normalized Difference Vegetation Index (study area level)	Spot Vegetation, spatial resolution 1000m, temporal resolution 30 days
Normalized Difference Vegetation Index (location level)	Moderate Resolution Imaging Spectroradiometer (MODIS), spatial resolution 500 meters, temporal resolution 15 days
Precipitation and Temperature (study area level)	European Centre for Medium-Range Weather Forecasts (ECMWF) operational model, spatial resolution 25 kilometres, temporal resolution 1 day
Precipitation and Temperature (detailed characterization)	Meteorological stations, spatial resolution variable, temporal resolution generally 1 day

Figure 1 Map of the study areas covered by the project.



2. Local scale assessment: Description and success rate of the capture campaign of roe deer in winter 2012/2013

INTRODUCTION

From mid-December 2012 until the end of March 2013 we performed a field campaign to capture and radio-mark roe deer in an Alpin area in Trentino, North-east Italy. In the first two months and half, we used box–traps, whilst in March 2013 we combined drop–nets.

Box traps and drop nets: technical description

Box traps are wooden boxes provided with food to attract roe deer (Figure 1). The food was provided in a small crib on the opposite side of the entrance (Figure 2). A single roe deer, attracted by food, is able to enter the box trap. As soon as it bends to feed, it touches a thin wire that makes dropping the door, thus trapping the individual. This mechanism activated a GSM modem, which was programmed to send an alert message text to the capture team. Such way, the interval from capture time to roe deer handling seldom exceeded one hour, limiting the stress for the captured individual and the risk of injury or miopathy (Beringer et al. 1990). We deployed drop nets to constitute a small fence of a few square meter size, putting some food at its centre (Figure 3). We clasped the net to clips at 2-3 meters height from ground, so that roe deer could freely enter in the fence, attracted by the food. All the clips were electronically connected and remotely commanded. We monitored the feeding site from about 50m, using a thermo–camera to minimize the disturbance for roe deer and enhance the capture success. When the individual entered in the fence, we switched on the clips mechanism, which caused the net to drop thus fencing the individual. We immediately reached the fence to block the individual in the net and perform handling operations.

Handling description

A soon as the animal was pulled out of the trap (Figure 4), handling operations started. These included ear-tagging of the individual, GPS collaring (for adults only), age assessment from tooth eruption and wear, body temperature and hind-foot measurements and sample collection of hair, faeces from the rectum and tissue biopsy by ear clipping. We could not weigh the individuals due to the difficulty to perform such handling operation on a steep and often snowy terrain. We recorded behavioural observations on roe deer stress before, during and after the handling operations, accordingly to the protocol established within the EURODEER scientific community (Table 1). Handling time never exceeded seven minutes, thus guarantying the least possible impact on roe deer welfare and survival.

Winter capture campaign

From mid-December 2012 to the end of February 2013 we opportunistically deployed four box traps in proximity of already existing feeding stations (Figure 5), which are commonly visited by roe deer during wintertime. Before any capture session, we performed an accustoming phase of a few days, where we moved the food from the proper feeding station to the crib of the box trap, and left the trapping mechanism inactive. We checked by means of camera traps and diurnal field visits the actual use of the box traps by individuals, and we activated the traps accordingly.

Globally we performed capture attempts in 16 sites in an area of ca. 30.000 ha. Capture effort at each site did not last more than a few consecutive days, after which the box trap was moved to another site. Doing so, we maximised the distribution of GPS radio-equipped roe deer across the study area. Overall the box traps were activated for 1,965 hours during the period 17 December 2012–28 February 2013.

In March 2013 we changed the capture technique in response to evolving environmental conditions. Snow melting and increase of temperature led to a decrease of use of the box traps by individuals. Indeed we often observed that when temperatures increases and snow melts, roe deer still frequent the feeding site, but seldom enter the box trap because capture fear overcompensates food attractivity. In these conditions, drop net fences represent a valid alternative to capture roe deer, which still visit the feeding sites. We performed capture attempts by means of drop nets at three of the 16 feeding sites in the area. We checked by means of camera traps that the individuals visited the selected feeding site. Then, we prepared the drop net fence during the day hours, activating it around sunset time, when roe deer generally visit the feeding stations. Every given capture attempt lasted a maximum of four hours, due to battery consumption of the thermo–camera. Globally, we performed 4 trials of drop nets capture during March 2013 in two different sites.

Capture success with box traps

Box traps were activated 82 times during winter 2012-2013. On average, time from activation of the box trap to capture event, when occurring, was equal to 24 ± 25 hours, from a minimum of 0.5 hours (indicating a capture event as soon as the trap was activated) to 144 consecutive hours of activation without any capture occurring.

In the 42% of the activation events (N = 35), a roe deer was caught, with a success rate of 1 roe deer captured per 56 hours of box trap activation. In 40% of the cases (N = 33), box traps were activated without receiving any visit by roe deer or other animals. We also captured in a few cases (16%, N = 13) other animals (badger (*Meles meles*), marten (*Martes foina*), jay (*Garrulus Glandarius*);other failures of box-trap captures were relative to malfunctioning of the trap with locking of the door due to excessive wind (N = 1); boycott of capture attempt by unauthorized refilling of the proper feeding station (N = 1); escape of the roe deer from the trap (N = 1) (Figure 6).

Among the 35 cases of roe deer capture, we recorded 25 first capture events and 10 recaptures. We captured mainly adult females (48%, N = 12) and fawn males (24%, N = 6), whilst capture success was lower for adult males (16%, N = 4) and fawn females (12%, N = 3). Recapture events affected especially fawn males (50%, N = 5) and adult females (40%, N = 4), with a single case of recapture of fawn female and no recapture of adult males (Figure 7).

Capture success with drop nets

The drop net system was active for approximatively 15 hours in total. We never succeeded in catching a roe deer with this system, although two roe deer that were approaching the centre of the fence escaped just before net dropping because of an external disturbance. The remaining times, we never detected the presence of roe deer within the fence.

Conclusions

Capture success with box traps method was high, considering the not excessive severity of the winter 2012/2013, which could potentially negatively affect the capture success rate. Captures were more successfully one or two days after a snowfall, due to a combination of low resource availability and high energetic costs of locomotion for individuals sinking in the snow (e.g. Lundmark and Ball 2008, but see also chapter 2 of this thesis for further consideration). We had no capture during snowfall events, when roe deer minimize their movements and thus do not visit the feeding sites.

Our observations with camera traps indicated that roe deer exhibit a large inter individual variation in behavioural responses to the presence of box traps. A few days (at least 2–3) of accustoming phase are important to increase the probability to catch a roe deer, but could not guarantee the success of the capture if the individuals were particularly suspicious. In particular, according to our capture rate results, it seems that adult males were less confident than adult females and fawn in getting into a box trap. A possible explanation for the lower capture success rate is due to the sex ratio imbalance in the population, with does exceeding bucks (Automomous Province of Trento, 2010). Moreover, fawns might have visited feeding sites and entered into box traps more than bucks for a combination of factors, such as a more enhanced crisis in the winter (Gaillard et al. 1998) and lack of knowledge of the potential dangers associated to feeding stations.

While box traps correspond to a well-established roe deer capture technique, drop nets were seldom tested before in a way as the one described here. Probably a mixture of human induced disturbance, unfortunate events (external disturbance) and poor weather conditions concurred to the failure of this capture technique. We might recommend to those who intend to apply a similar procedure to adjust the size of the fenced area, so to avoid escape of roe deer. In fact the noise produced from the clip mechanism immediately alarms roe deer, that immediately and very fast flush away. The time interval from the clip noise to the complete drop of the net has to be long enough to avoid roe deer escape from the fence.

TABLES AND FIGURES

Table 1 Guide to the behavioural protocol for capture of roe deer (adapted from www.eurodeer.org). The two scales in the table below are subjective measures of reaction of the roe deer during handling (left column) and immediatle after release (right column).

Points	Behavior during handling	Behavior post release
0	Calm. No resistance. No kicking with legs. No screaming.	Leaving the place slowly. Stops several times.
1	Calm. Screams not more than twice. Almost no kicking.	Run away, but stop after a short distance
2	Screaming and kicking some, but are calm between these occasions.	Runs away without stopping until it can't be seen any more.
3	Stressed out. Are screaming and kicking more, but the animal can be handled.	Falls or jumps and attempts to remove collar and/or escape from handler
4	Extremely stressed. Almost impossible to handle. Impossible to take proper measures.	Lies down, cannot stand by itself
5	Exhausted. Makes no resistance and are easy to handle. But differ from 0, in the sense that it is stressed.	

Figure 1 Box trap used for capturing roe deer. To note on the front side (i.e. the one close to the door that is shown in the image) the white box containing the modem to remotely alert the capture team.

Figure 2 Detail of the back-side of the box trap, where the crib is put and filled with food to attract the animals

Figure 3 Drop net fence to catch roe deer when winter severity decreases (i.e. less snow cover and higher temperatures)

Figure 4 Pulling the roe deer out of the box trap

Figure 5 Deployment of the box-trap in proximity of proper feeding station

Figure 6 Pie chart indicating the occurrences for each activation event.

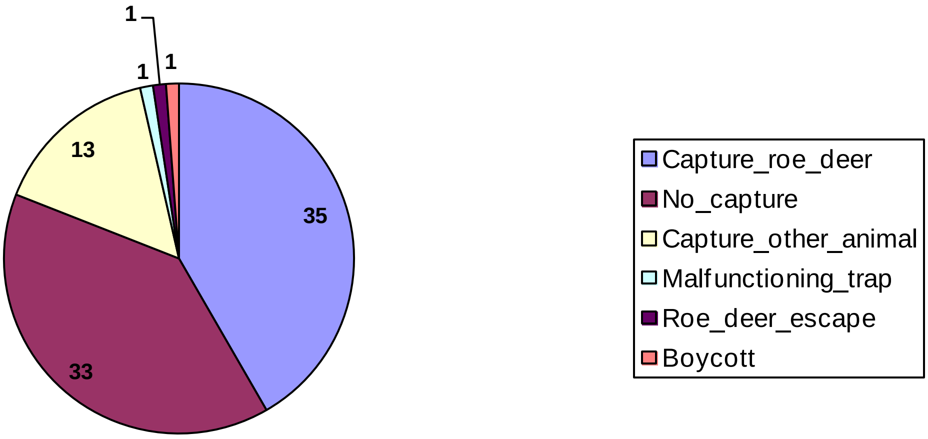
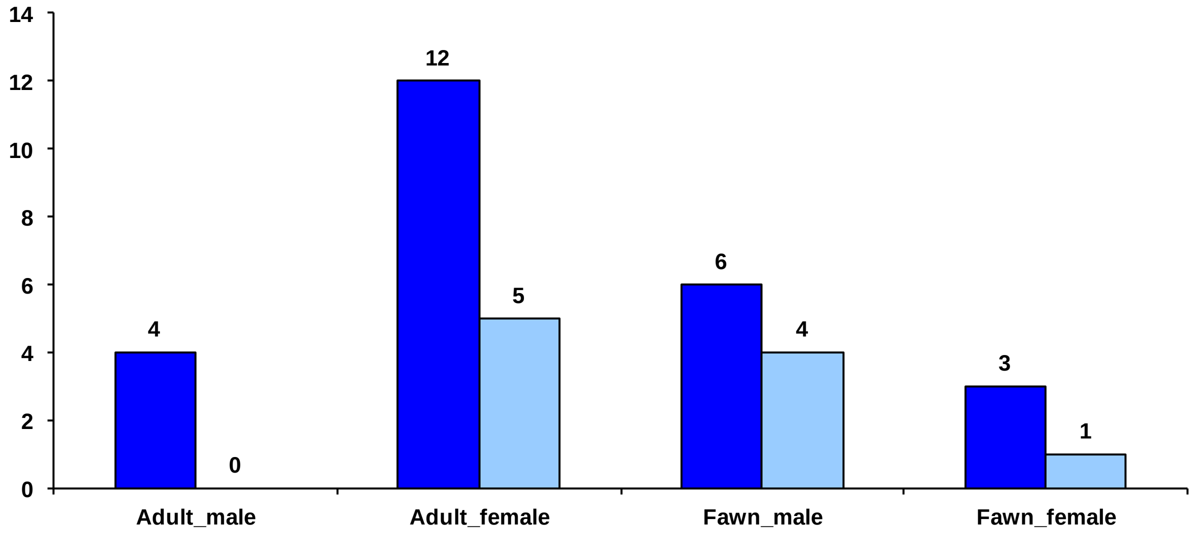


Figure 7 Histogram reporting the frequency distribution of first captures (dark blue) and recaptures (light blue) according to age and sex classes.



CHAPTER 1

Perturbation of food availability affects space use of large herbivores: a large scale study on roe deer

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ABSTRACT

Winter in mountainous and northern regions is the most critical period for the majority of ungulates, because of the combined effects of food scarcity and increased energetic costs for thermoregulation and locomotion in snow. Supplemental feeding to counter-balance the negative effects of winter on ungulates is widespread in many European countries and locally in North America, but the actual use of feeding stations by ungulates and how they influence ungulate spatial ecology has been surprisingly little studied. To fill the gap, we investigated (i) the pattern of selection of feeding sites throughout the year and (ii) the pattern of use of the selected feeding sites in winter by roe deer (*Capreolus capreolus*), a small cervid widely distributed across Europe that is particularly sensitive to winter severity. From a comparative analyses across nine populations along a wide latitudinal and altitudinal gradient, we found that selection of feeding sites by roe deer was highly seasonal and linked to the activation of feeding stations. Selection of feeding sites peaked between early January and mid-February across the observed altitudinal and latitudinal gradient. Selection was highest at low temperatures when the feeding stations were active, but was independent from snow cover. In winter, roe deer used proper feeding stations more than box traps filled with food, especially when potential competitors were absent. Increased winter use of feeding stations led to a reduction of individual home range size. Our findings demonstrate that feeding sites are an important resource that is selected and used by roe deer. The intensity of use of selected feeding sites depended on the actual benefit or easiness of access (presence of competitors, design of the feeding station). The use of supplemental feeding leads to modification of roe deer spatial behaviour, mainly through a decrease of winter home range size. Such effects have to be taken into account when defining management of conservation strategies.

Kew words: ungulates, deer, nutritional ecology, spatial behaviour, disease transmission, limiting season, General Additive Models, EURODEER.

INTRODUCTION

Resource distribution and acquisition are among the most important drivers of individual movement, space use and habitat selection in most animal species (Fretwell and Lucas 1970). In seasonal environments, resource abundance and distribution varies a lot in space and time, and thereby influences movement at multiple spatiotemporal scales (Owen-Smith et al. 2010). For instance, for the majority of large herbivores living in the northern or mountain areas, resources are scarce in winter because of both the absence of vegetation regrowth (Kreyling 2010) and the snow cover that prevents accessibility to food (Hovey and Harestad 1992). Food limitation, combined with the high energetic requirements to maintain thermoregulation at low temperatures and to move in the snow (Moen 1978; Parker et al. 1984, Lundmark and Ball 2008), makes winter time a critical period for survival (Telfer and Kersall 1984).

Ungulates have developed many adaptations to cope with winter adversities (Telfer and Kersall 1984). These include morphological traits such as the disproportional chest height (e.g. Lundmark 2008 on moose *Alces alces*) or the particular hoof morphology to favor movements in the snow (e.g. Fancy and White 1985 on caribou *Rangifer tarandus*); physiological adaptations such as the high gut capacity to maximize the rate of forage intake (e.g. Klein 1995 on muskoxen *Ovibos moschatos*); seasonal migration to escape unsuitable areas (e.g. Nicholson et al. 1997 on mule deer *Odocoileus hemionus*; Ball et al. 2001 on moose; Sabine et al. 2002 on white-tailed deer *Odocoileus virginianus*; Cagnacci et al. 2011 on roe deer *Capreolus capreolus*), trail making behaviour to decrease energy expenditures in locomotion (e.g. Telfer and Kersall 1979 on white-tailed deer), or snow digging for finding forage (Fortin 2003 on bison *Bison bison*).

Despite such adaptations, winter severity remains a critical factor for the performance of individuals, and thus constitutes a major determinant of population dynamics (e.g.

DelGiudice et al. 2006). In this context, winter supplemental feeding, which involves the establishment of feeding stations provided with human-prepared food (usually highly concentrated cereals in pellets), is a widespread management practice in the northern and mountain areas of Europe, and locally in North America. The aim for supplemental feeding varies (Putman and Staines 2004, Mysterud 2010) and can include keeping a high local population density (Peek et al. 2002); reducing winter starvation to meet animal welfare concerns (Grenier et al. 1999); enhancing the male trophy quality of males for game purposes (Putman and Staines 2004); or reducing the extent of migratory behaviour to prevent forest damages or car accidents (Sahlsten et al. 2010). However, quite surprisingly, assessing the effectiveness of supplemental feeding across a large range of environmental conditions has not yet been performed in any species of large herbivores.

The presence of feeding sites can lead animals to shift their movement patterns, as reported in several species of large herbivores (Smith 2001 on red deer *Cervus elaphus*; Cooper et al. 2006 on white-tailed deer; Van Beest et al. 2010 on moose; Guillet et al. 1996 on roe deer). Feeding sites can act as central attractive places (Orians and Pearson 1979) from which ungulates tend to move (Van Beest et al. 2010 on moose; Guillet et al. 1996 on roe deer; Jerina 2012 on red deer). This can result in local concentrations of individuals (Sahlsten et al. 2010) potentially enhancing the risk of disease transmission (e.g. Thompson et al. 2008). An in-depth investigation of the role of supplemental feeding on movement patterns is therefore essential to evaluate its actual impact and potential ecological consequences on wildlife. Our study aims at contributing to fill this gap by performing a large-scale comparative analysis across contrasting populations of a small deer species, the European roe deer.

This species provides an ideal model for such a study because roe deer are both widely distributed across a large range of environmental conditions (Andersen et al. 1998) and highly sensitive to extreme winter conditions. Roe deer are income breeders (Andersen et al.

2000) that do not stock fat reserves and mostly rely on instantaneous energy intake to meet their high energy expenditures. Moreover, roe deer are not adapted to move in deep snow (Holand et al. 1998), which may prevent them to acquire efficiently the resources they need during winter (Holand 1992). Roe deer, especially at the north and elevation extremes of their distribution range, should have impaired survival in winter (e.g. Mysterud 1999, Ramanzin et al. 2007) because both food scarcity and winter severity are two major drivers of roe deer survival, especially when they are less than 1 or more than 8 years of age (Gaillard et al. 1998). Mortality risk might be particularly high at the end of the winter, when territorial establishment in males (Liberg et al. 1998) and late gestation in females (Hoffmann et al. 1978) cause an increment of energetic demand against a still limited availability of food resources.

For these reasons, it is not surprising that supplemental feeding has often been used as a management practice of roe deer populations throughout Europe (Putman and Staines 2004). However, the effect of feeding sites in relation to roe deer movement patterns has been rarely studied (Guillet et al. 1996), although their potential role on shaping winter roe deer home ranges in northern countries was recently hypothesized (Morellet et al. 2013). A detailed investigation of the effects of feeding sites on roe deer spatial ecology is needed, because feeding sites might alter roe deer space use patterns, interactions with other individuals and lastly the dynamic of disease transmission in roe deer populations.

We addressed this overall research question using the EURODEER project (www.eurodeer.org), which includes accurate GPS movement data from several hundreds of roe deer across a wide altitudinal and latitudinal gradient (Cagnacci et al. 2011). We analysed the responses of roe deer to the presence of these artificial resources, investigating (i) the factors which influenced roe deer pattern of selection of feeding sites throughout the year and (ii) the determinants of the intensity of use of the selected feeding sites during winter. More specifically, we tested three main hypotheses regarding roe deer use and selection of feeding sites. First, under the nutritional condition hypothesis, temporal variation in selection of feeding sites throughout the year should be influenced by abiotic factors, such as food offered at feeding stations, snow distribution, and temperatures, because they determine the energetic balance of individuals (Holand et al. 1998). We thus predicted increased selection in presence of supplemental food and under severe winter conditions involving snow cover and low temperatures. Moreover, we expected selection for feeding sites to be more consistent at high elevation and northern latitudes, i.e. in those regions where winter severity is sharper and primary productivity is lower. Under the same nutritional condition hypothesis, we also expected the timing of peak of feeding to occur at the end of the winter, because of the combined effect of a deterioration of body condition (Parker et al. 2009) and increased energetic demand for late gestation (females) and preparation to territory establishment (males). Next, under the food competition hypothesis, the use of active feeding stations during winter should depend on the level of inter-specific competition for food and on the 'attractiveness' of the feeding station (that is influenced by quality of supplemental food and the typology of feeding station). We thus expected roe deer to use box traps less intensively than proper feeding stations; we also expected that the feeding stations were used more intensively in absence of competitors like fallow deer and red deer, and when the energetic content of food provided was high. Finally, under the central foraging place hypothesis (Orians and Pearson 1979), feeding stations should influence patterns of space use in roe deer, regardless of whether feeding site use was driven by winter severity or competition more. We thus expected weekly home range size in winter to be inversely related to the use of feeding stations by roe deer.

MATERIALS AND METHODS

Study areas, feeding sites and related covariates

We selected the study areas where supplemental feeding took place from the EURODEER database (see Appendix S1 and Figure 1 for details). Station-specific information (Appendix S2), included temporal variation in activation, whether the feeding station was a proper feeding site or simply a box trap used to capture roe deer; an index of the energetic content of the food provided (low vs. high); the potential competition with red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*), a composite variable between the presence/absence data of competing species in the study area, and whether managers physically hampered the access to the potentially competing species at feeding sites, e.g. by fencing the sites to permit only thin ungulates as roe deer to pass through and feed.Temporal variation in activation was measured at each feeding site on a weekly basis to account for the expected quick response of roe deer to changes in resource availability (Pellerin et al. 2010). We thus defined 'weekly feeding sites', and their state of activation.

Then, we associated each weekly feeding site with data on snow cover (presence/absence) and temperature (°C). Snow data were derived from the MODIS (define acronym here) MOD10A2 16-day composite maximum snow extent data at level V005 (data downloaded from NASA WIST, https://wist.echo.nasa.gov) (Hall et al. 2002), while temperature was obtained from the closest meteorological station (average distance between the meteorological station and the feeding station of 30 km; data downloaded from the European Climate Assessment & Dataset project, http://www.ecad.eu) (Tank et al. 2002).

Roe deer movement data and availability of feeding sites

We defined the available feeding sites to roe deer for subsequent analyses in 3 main steps. First, we excluded roe deer with too short monitoring (i.e. less than 60 consecutive days). We also removed roe deer with a monitoring overlapping active feeding station for less than 60 days. Secondly, we defined which feeding sites were available to roe deer, a critical step to determine the patterns of selection (Arthur et al. 1996). To do that, we (1) defined winter as the period starting the 40th week of a given year and ending the 16th week of the following year to allow excluding spring and autumn migratory movements (Cagnacci et al. 2011), (2) computed the winter home range with Kernel *href* method (UD = 90%) of each focal roe deer, and (3) computed a buffer around each home range, whose size was equal to the distance from the barycentre of the home range to the most distant vertex of the home range. We thus obtained a 'buffered' home range that accounted for potential out of range movements potentially leading roe deer to use feeding sites out of their main range, i.e. we used a conservative approach. We retained for the analyses those feeding sites that overlapped with the buffered home range (Appendix S3). This criterion was individual- and winter-specific, which allowed us to account for between-individual differences in movement patterns and for between-winters difference in feeding sites management, when the same individual was monitored for several winters. Third, for each combination of a roe deer and an available feeding site, we only analysed the 'weekly feeding sites' that temporally matched the roe deer monitoring period. These individual-specific weekly feeding sites represented the sample unit of our analyses.

Metrics of feeding site use

We measured the use of weekly feeding sites by a given roe deer as the spatiotemporal overlap between the location of the feeding site and the movement trajectory of the roe deer. To attain this metric, we first removed all GPS locations with less than 1 hour-interval to limit auto-correlation of data and homogenise the dataset. Then, we built weekly individual movement trajectories based on the assumption of linear interpolation between subsequent locations. We skipped the steps when the interval between locations was equal or longer than 24 hours, because of the too large uncertainty on spatial behaviour of the focal individual during such long intervals (e.g. Horne et al. 2007). We intersected the weekly trajectory of the focal roe deer with a buffer centred on each weekly feeding site (diameters= 50m, 100m, 200m and 400m). We then computed as our elective dependent variable of feeding site use, the weekly proportion of time spent by a given individual within a buffer of a given size centred on feeding sites, derived from the linear trajectory. We also computed the number of GPS locations that fell within the same buffer, as a comparative metric (see Appendix S4 for further details). We assessed whether the proportion of time spent and the number of GPS locations within a given buffer varied according to either buffer size or GPS sampling frequency of a given trajectory. The results of this sensitivity analysis (reported in Appendix S4) indicated that the proportion of time was independent from the GPS location sampling regime, whereas the number of GPS locations within the same buffer in a given week depended on the sampling regime. We therefore confirmed the proportion of time spent in buffers as the metric to indicate feeding station use. Buffer size did not strongly influence the proportion of time spent within the buffer, at least in the range of diameters we analysed. To be consistent with previous work (e.g. Guillet et al. 1996) and to assess the use of feeding sites by roe deer at the finest possible spatial scale, we performed the analyses on the proportion of time spent within a buffer with a diameter of 50 m centred on the feeding sites.

All spatial analyses were conducted in PostgreSQL 8.4.1 + PostGIS 1.5.2 (http://www.postgresql.org/; http://postgis.refractions.net/) spatial database, using the EURODEER database structure as described in Cagnacci and Urbano (2008) and Urbano et al. (2010).

Statistical analysis and modelling

Influence of abiotic factors on occurrence and timing of selection of feeding sites (1st hypothesis)

We modeled the variation in selection of feeding sites by roe deer throughout the year using the Generalized Additive Mixed Models (GAMMs) (Wood 2006). We fit a logistic regression (Hosmer and Lemeshow, 2000) with the use of available weekly feeding site as dependent variable (use=1 if the proportion of time spent within the buffer of the feeding site was equal or bigger than 0.01 vs. use=0 otherwise; percentage of time spent = 0.01 was considered as a sensible threshold to define 'feeding station use', and not random closeness to them). This resulted in a true used-unused logistic regression design where the dependent covariate was a true probability of use, not a used-available design (Manly et al. 2002). To analyze the yearly pattern of selection of feeding sites, we selected an *a priori* list of potential covariates, which included the activation of the feeding station, the snow cover (presence/absence), and the weekly minimum temperature (°C) associated to each weekly feeding site (see paragraph above for how feeding station covariates were obtained). We then fitted in the model the observational week, to estimate the seasonal pattern of feeding, as well as latitude and altitude to account for expected variation in environmental conditions across a wide latitudinal and altitudinal gradient. Before starting proper model selection, two operations were undertaken on this list of covariates: 1) we checked for co-linearity patterns between the covariates (Graham 2003, Zuur et al. 2007) (Appendix S5), accounting for them by fitting two-way interactions between the correlated covariates when necessary; 2) we ran an ANOVA based on deviance (Skalski et al. 1993) (Table 1 and Appendix S6.1) to determine the structure of the temporal variation in the model. According to the outcome of these two preliminary steps, we thus obtained a full model comprising a temporal component accounted for by the cyclic penalized cubic regression spline smooth of the week, in interaction with the study area; a fixed component including all the potential combination of two-way interactions between the weekly minimum temperature, the activation of the feeding sites and the snow cover, plus a two-way interaction between latitude and altitude; random intercepts for individual and year (Gillies et al. 2006) to account for expected variation due to individual roe deer behavior and differences in the pattern between observational years (Table S6.1). Given the complexity of model selection with generalized mixed-models (Bolker et al. 2009), we used a 'pluralistic' (Stephens et al. 2005) approach combining the best features of multiple methods to determine the most supported statistical model (Appendix S5.2), following the model selection philosophy of Harrell (2001). We firstly used a manual selection based on the AIC scores of a series of candidate models previously selected (Burnham and Anderson 2002), retaining those with difference of AIC lower than 2 (see Table S6.2). Then, we adopted a reductionist approach to evaluate whether it was possible to simplify the retained model, based on the principle of parsimony. We thus ran an ANOVA based on deviance several times (Table 2a-b and Appendix S6.2) to eventually identify the best model. We measured the proportion of time variation that was accounted for by the interaction between temperature and the activation of the feeding sites by means of an ANODEV procedure (Skalski et al. 1993) (Table 2c and Appendix S6.2). Lastly, because AIC can often select models in large datasets with poor predictive performance, we also assessed the goodness-of-fit of the best model computing its pseudo R^2, in the McFadden formulation: 1-(deviance best model/null deviance).

To test the occurrence of a peak of selection for feeding sites in the last part of the winter, we first used the best model to predict selection of feeding sites throughout the year.

Then, for each roe deer-year combination, we extracted the week in which the predicted peak of selection occurred. We fit a general linear mixed model to assess if the week of the peak of selection varied across study areas by fitting year as a random effect. We assessed the goodness-of-fit of this model by computing the pseudo R^2, as described above. Then, we identified the week of the peak of selection in each study area as the median of its distribution across all the roe deer-year of that area. We measured the amount of variation of this week among individuals by computing the 25th and 75th percentiles of the top selection week distribution, for each study area separately.

Winter use of feeding stations: influence of management related factors (2nd Hypothesis)

We focused on the winter period to test whether roe deer used feeding stations at a larger extent when these were provided with food of high energetic value and in absence of competition with related species. To concentrate on winter, we only retained the active weekly feeding sites from December 1st to March 31th, excluding the Norwegian study area (site 3), due to incompleteness of information to address this issue. We fitted a negative binomial regression with the weekly amount of time spent by a roe deer in the proximity of a given feeding station as the response variable. We removed cases when roe deer time spent was less than 1% of the total time available, to focus on ‘true’ use of the feeding station, consistently with the threshold to define used vs unused.

We selected an *a priori* list of covariates, which included the potential competition with other ungulates, the energetic quality of the food provided and the design of the feeding station. We accounted for co-linearity patterns between these covariates as described for the test of the first prediction (Appendix S5). The resulting full model after this operation included the following covariates: all combinations of two-way interactions between potential competition with other ungulates, energetic quality of food provided and feeding station design. We also controlled for individual sex and age, which we fitted as single terms; lastly, we included a random effect of the individual to account for expected variation between individuals (Table S6.1). We performed the identification of the best model (Table 3 and Appendix S6.3) and the assessment of its goodness-of-fit as done above.

Influence of feeding stations on winter home range size (3rd hypothesis)

To assess whether the intensity of use of feeding stations by roe deer led them to reduce the size of their winter weekly home range, we first computed the weekly home ranges by using the Kernel *ad hoc* method (UD = 50%) (See Morellet et al. 2013 for further details). For each combination individual-weekly feeding station, we associated the individual weekly home range size to the feeding station. We then used a linear model to test the relationship between home range size (on a log-scale) and the intensity of use of feeding stations. We assessed the goodness-of-fit of this model by computing the pseudo R-squared. We performed all the analyses in R software (version 3.0.2 The R Foundation Core Team 2013; mgcv Rpackage: Wood 2006; glmmADMB: Fournier et al. 2012).

RESULTS

Influence of abiotic factors on occurrence and timing of selection of feeding sites (1st hypothesis)

We obtained 18,376 feeding sites-animal-week to estimate the intensity of selection of feeding sites (Appendix S7), derived from a total of 389 individual-year datasets. Both the sex ratio and the age structure of roe deer monitored were biased towards adult females (10,235 weekly feeding sites for females vs. 8,141 for males and 13,770 weekly feeding sites for adults vs. 3,441 for sub-adults and for 1,165 for fawns). Almost half of the data were collected in one study site (Bavarian Forest National Park (site 1), with 9,070 feeding sites/week/animal). Data were collected in all years between 2005 and 2013, with more data in 2010 (4,980) and 2011 (4,426).

As expected, roe deer exhibited a strong seasonal pattern of selection for feeding sites across all the study areas but Sweden (site 4) and Brandenburg forest (site 7) (Figure 2). The seasonal pattern changed mostly among individuals rather than by years as shown by the relative proportion of variation explained by both these variables when added as random factors to the model (individual: 15%, $p < 0.001$; year: 0.1%, $p = 0.002$). Roe deer increased selection of feeding sites when these were active and the minimum temperatures were low (estimated slope of the interaction between temperature and activation = - 0.034; $p = 0.006$) (Figure 3). The weekly minimum temperature in interaction with the activation status of the feeding sites accounted for the 56% of the observed temporal pattern of selection of feeding sites throughout the year (Table 2c and Appendix S6.2). Conversely, snow cover did not influence the intensity of feeding site selection by roe deer, so this covariate was removed from the full model (Table 2a and Appendix S6.2). Lastly, the statistically significant and negative effect of the two-way interaction between latitude and altitude (estimated slope = - 0.0002; $p = 0.027$) (Figure 4) indicated that roe deer selected for feeding sites especially at high altitudes in the southern part of the range of this study, and at low elevation at northern latitudes. The pseudo R^2 (0.30) indicated the reasonable fit of the final model.

We investigated the timing of selection of feeding sites on a sample of 389 individual-years to determine the occurrence of peak of selection for feeding sites. Roe deer displayed a peak of selection in all populations, but the timing of this peak varied across study areas (Table 4). In Italian Alps (Site 2), Brandenburg (Site 7) and Baden-Wuerttemberg lowland (Site 8), the peak of selection occurred in the first half of January. In the Austrian Alps (Site 5), although the median resulted in the first week of January, roe deer exhibited two distinct peaks of selection for feeding sites, one around the first half of December and the other around the end of February (see Figure 2). In the remaining areas roe deer were more selective for feeding sites from early to mid-February. The top model supported the retain of the year as fixed effect, rather than as random effect, thus indicating that the seasonal pattern we report was rather consistent over years. The pseudo R^2 (0.22) supported the goodness of the fitted model.

Winter use of feeding stations: influence of management related factors

We obtained 1,605 cases of use of feeding stations by roe deer-week, whose distribution across all study areas is summarized in Appendix S8. Roe deer selected feeding stations at a different extent across study areas: the proportion of used feeding stations in winter (relative to the total available) ranged from 10 % at Brandenburg (Site 7) to 50 % in Baden-Wuerttemberg (Sites 8 and 9). The time spent at using feeding stations in a week also changed across study areas, with a minimum of 5h 20 min ± 4h 54 min in Sweden (Site 3) and a maximum of 57h 10 min ± 34h 47 min in Italian Alps (see Appendix S8).

The retained model on the pattern of use of feeding stations by roe deer poorly explained the observed variance (pseudo $R^2 = 0.026$). The use of active feeding stations in winter decreased significantly in presence of potential competitors (estimated difference = -1.05, $p < 0.001$), whilst it was not affected by the quality of food provided. Roe deer used box traps at a lesser extent than proper feeding stations (estimated difference: 0.77, $p < 0.001$). However, this was not the case when there were competitors in the area, as indicated by the positive effect of the interaction between presence of potential competitors and box traps (estimated difference: 1.19, $p < 0.001$). The use of feeding stations was not influenced by the sex and the age of individuals. The random effect of the individual accounted for the 1% of the total variation observed, i.e. more than one third of the total percentage of variation explained by the retained model (pseudo $R^2 = 0.026$), thus indicating that the extent of use of feeding stations differed consistently among individuals.

Influence of feeding stations on winter home range size

Roe deer using feeding stations in a given week had smaller home ranges (estimated coefficient = -0.002, $p < 0.001$; pseudo $R^2 = 0.07$). This is especially clear when individuals exhibited a high intensity of weekly use of feeding stations (Figure 5).

DISCUSSION

Our study demonstrates the efficiency of a large-scale analysis to ascertain the main abiotic, biotic, and management-related determinants of the selection and use of supplemental feeding in a large herbivore. Our findings show that the selection and use of feeding sites by roe deer across a wide altitudinal and latitudinal gradient were mainly driven by the energetic requirements of the animals, and only to a less extent by competition with other species or quality of food provided.

Selection of feeding sites throughout year: influence of abiotic factors and timing of selection

Roe deer selected feeding sites provided with food, but only when they had to cope with harsh environmental conditions. In northern or mountainous regions this situation is typical of winter, because of a combination of low temperature and deep snow cover that leads to increase the energetic needs of this ungulate lacking adaptations to winter conditions (e.g. Mysterud and Østbye 1995, Holand et al. 1998). In particular, we found that the combination between the activation of the feeding stations and the decrease of temperature was an important driver of the timing of the selection for feeding sites in most study areas, but none of these two factors explained by itself the pattern of selection of feeding sites. Roe deer selection of feeding sites looks therefore as an opportunistic behaviour that occurs when winter severity is particularly severe across all study areas. Roe deer do not select active feeding sites *per se*, but only when the energetic demand for thermoregulation (e.g. Mautz 1978) increases. The influence of temperature on the use of supplemental feeding has already been reported in other ungulates (e.g. Mangus (2011) on elk; Oja et al. (2014) on wild boar). Although we do not know what is the critical temperature for roe deer metabolism in winter (Weiner 1977), it is probably close to 0°C, as observed in white tailed deer (Silver et al. 1971).

This threshold was overcome in winter in all the study areas we considered, thus leading individuals to increase their selection of feeding sites. However, since this behaviour is clearly linked to the recruitment of food to compensate for increased energetic requirements, roe deer did select only those feeding sites which were refilled with food.

Although snow cover is another main determinant of energetic consumption for roe deer in winter (Holand et al. 1998), it did not influence selection of feeding sites by roe deer, in contrast to our a-priori prediction. This surprising result might have occurred because of the rough quality of the index of snow cover we used (i.e. snow MODIS, remote sensing data only providing presence-absence of a snow cover at a large spatiotemporal resolution (500 meters cell, biweekly temporal interval)). More detailed data on the thickness of the snow layer would have provided a better description of snow conditions that roe deer faced. In support, snow cover has been previously reported to be a strong determinant of selection of feeding sites by roe deer when specific data on snow thickness were available (Guillet et al. 1996; Cederholm 2012; Ossi et al., in revision). Future studies might benefit from re-examining this question using more fine-scale measures of snow depth once they become available. Across the wide latitudinal and altitudinal gradient considered in this study, harsh winter conditions occurred mostly at high altitudes and low latitudes, i.e. on the Alpine mountain range, or at high latitudes (and comparatively lower elevation) , i.e. in Scandinavia. In accordance with our prediction, we found that in these areas roe deer selected for feeding sites more, as demonstrated by the negative effect of the interaction between latitude and altitude on the intensity of selection for feeding sites. In particular, in the Alps roe deer living at high elevation, and thus exposed to adverse conditions, selected for feeding sites more than their conspecifics living at intermediate and low elevations. In Scandinavia (high latitudes and altitudes comparatively lower than the Alpine range) feeding sites are distributed only at low and intermediate altitudes, where individuals migrate during winter (see e.g. Mysterud 1999).

However, winter severity at these latitudes still pushes roe deer to search for feeding sites, even in their winter range at low elevation (e.g. Gundersen et al. 2004).

Selection for feeding sites looks therefore to be mostly driven by the harsh conditions that roe deer face in winter. Roe deer physical conditions, as well as those of other ungulates, decline during the winter (Parker et al. 2009), to reach the negative peak around the end of the season, when they have been exposed to a prolonged scarcity of resources. Moreover, late winter is also a crucial period for roe deer in terms of energetic demands. Pregnant females enter the last part of gestation (Hoffmann et al. 1978), a period characterized by a strong increase of energetic requirements (Parker et al. 2009), and males become territorial and face strong intra-specific competition (Liberg et al. 1998). As such, roe deer selection of feeding site should peak in the second half of the winter, as empirically observed in a Scandinavian population (Cederholm 2012). Our results partially supported this prediction. The selection of feeding sites peaked around the first half of February in most populations studied, although with large inter-individual differences. Certainly, reproductive status (pregnant, previous summer's lactation status) may have contributed to the large individual variation, but we could not test these effects since we did not have individual-level reproductive history. However, we found some controversy in this general pattern (Figure 2). In the Brandenburg study area, we found a very weak temporal variation of selection of feeding sites. In Baden–Wuerttemberg study area (site 8) the observed temporal variation of selection of feeding sites was rather fluctuating and bimodal. However, the later peak, occurring in late February – early March- well fits our predictions. Finally, in the Italian Alps, this result might be due to the small sample size on which we could rely for this study area early on in the season (Ossi F., pers. obs.).

Winter use of feeding stations: influence of management

The use of feeding stations by roe deer depended on how the feeding stations were managed. In particular, our results demonstrate that roe deer use proper feeding stations more than box traps, especially when competitors are absent. Although the variance explained by these factors in the overall dataset was low, they may exert a very clear effect at a local-scale. Conversely, the effect of the energy content of food provided looks less relevant on shaping this pattern. In presence of competitors, the gain obtained by roe deer from supplemental feeding is expected to be reduced because of hampered access to food (e.g. Focardi et al. 2006). Roe deer have a small body size which does not allow them to compete successfully with any of the other larger ungulates that forage on limiting resources (fallow deer: Focardi et al. 2006, Ferretti et al. 2008; red deer: Richard et al. (2009)). Although inter-specific competition among herbivores generally occurs by means of depression of food resources (Owen-Smith et al. 2010), aggressive interactions at feeding stations have been reported to occur (e.g. white tailed deer: Grenier et al. (1999); red deer: Veiberg et al. (2004)) and access to feeding stations can be determined by social dominance among individuals (Ceacero et al. 2012). For instance, the competition for feeding with fallow deer drastically reduced the use of feeding stations in a Swedish roe deer population (Cederholm 2012), whereas in absence of competitors roe deer strongly used feeding stations in similar environmental conditions (Guillet et al. 1996; Kjellander et al. 2006). The role of fallow deer as an inhibitor of roe deer use of feeding stations is further supported by the lack of any temporal variation in selection of feeding sites throughout the year we reported in Swedish and Brandenburg study areas, which were the only sites where fallow deer had access to feeding sites.

Assuming that the use of feeding stations would be mostly determined by the energetic intake, it was not surprising to find that box traps were consistently less used than proper feeding stations. In fact box traps only include a small amount of food (Ewald et al. 2014), and should be further avoided because they are generally used to lure and catch the individuals. Although this general pattern was respected across the study areas we considered, we found that box traps were more used than proper feeding stations in case of presence of competitors. Large ungulates as red deer or fallow deer cannot accede the food provided in the box traps, which instead is the case for roe deer. Therefore in those contexts box traps are the only feeding sites exclusively available to roe deer, and thus likely preferred. Although this tactic to acquire food might be disadvantageous due to the stress associated with the capture handling, the phenomenon of trap-happy animals, balancing the stress of captures with food intake, is well known, and observed also among the studied populations (i.e., several recaptures of the same individual in the same season) A high quality of the food provided at the feeding stations should increase the energetic intake for roe deer, which consistently select diets with highly digestible energetic content (Duncan et al. 1998), and consequently the attractiveness of the feeding station. Surprisingly this was not the case in our study, possibly because of the scarce quality of the data provided, which did not allow to catch this pattern. However in the most of the study sites, feeding stations were filled with pellets, corn, hay or a combination of these forages, thus indicating that managers generally provide high quality food which is most likely favoured by roe deer and even other artificially supplied ungulates.

In this general context, it was not surprising to find no sex or age differences in the intensity of use of feeding stations, as also reported previously in Sweden (Cederholm 2012). Roe deer is a weakly size-dimorphic species (Andersen et al. 1998), meaning that the energetic needs of the roe deer are similar between sexes, so that access to feeding stations can be relatively beneficial to all classes, and thus they may all access feeding sites. This is not the case in highly dimorphic species (Parker et al. 2009), where indeed segregation and differential use of feeding stations between sexes were observed both in fallow deer (Cederholm 2012) and white tailed deer (Grenier et al. 1999).

Influence of feeding stations on winter home range size

Feeding stations have been reported to influence the spatial behaviour of other ungulates, which all tend to shift their movement patterns towards the stations (e.g. Guillet et al. 1996 on roe deer; Van Beest et al. 2010 on moose), especially when winter conditions are particularly severe and activity highly reduced (e.g. VanOort et al. 2007). Our results support these findings. Morellet et al. (2013) in their multi-population study on roe deer, also based on EURODEER datasets, noted that in conditions of low resources, such as in winter at northern latitudes, an expansion in home range size was to be expected according to the general patterns observed across Europe. However, this expansion was not observed instead, so they hypothesise a role of supplemental feeding in justifying this. We demonstrated that feeding sites can act as central foraging places, thus substantially perturbing the spatial behaviour typical of herbivores.

CONCLUSIONS AND APPLICATIONS

According to the movement ecology paradigm (Nathan et al. 2008), an observed movement path is the outcome of a combination of four main components, i.e. the internal state of an individual, its navigation capacity, its motion capacity, and external factors. In this work, we examined the determinants of the movement path (i.e. the trajectory) of roe deer in relation to the presence of a certain perturbation of the external context, i.e. the availability of a point-resource (the feeding stations) in their environment. As such, we demonstrated that selection and use of feeding stations are the result of a combination of environmental factors (i.e. winter severity in terms of lowest temperatures, activation of the feeding station, absence of competitors, design of the feeding station) and potentially roe deer biological cycle. We argue that the scarce motion capacity to move in the snow (not measured here) combined with good navigation and orienteering skills, can essentially contribute to determine roe deer movement paths in an area where supplemental feeding in winter is practiced.

Our study allows to draw some management indications for the practice of supplemental feeding, in case the target and roe deer and specifically: 1) it is useless to forage when winter conditions are not extreme (where the 'threshold' is linked to minimum winter temperatures more than snow); 2) access of competitors has to be actively prevented. However, the environmental factors that determine selection and use of feeding sites by roe deer are rapidly evolving. Temperatures are increasing (e.g. Iones et al. 2013), snow cover patterns at intermediate latitudes and low–medium altitudes are changing (Steger et al. 2013), and the distribution of natural resources is dramatically modifying (Post and Stenseth 1999). How the predictable and unpredictable changes will eventually shape roe deer selection and use for feeding stations? A first essential step to answer this question is to assess whether roe deer need or not to be supplementary fed. Our results do not provide any indication on the *need* to feed roe deer with emergency feeding programs (*sensu* Mysterud 2010) to enhance their survive over winter. Potential negative consequences as the alteration of natural selection mechanisms (Schmidt and Hoi 2002; Mysterud 2010) or space use, as clearly showed by our results (see also Morellet et al. 2013), act on medium to large temporal scales. Therefore this issue might be well addressed only by comparing long-term performances of contrasting populations, some of which supplementary fed and the others relying only on natural resources – keeping the other environmental conditions as more similar as possible.

Whatever the case, the most apparent drawback of supplementary feeding practice is the potential to enhance disease transmission among individuals (see Sorensen et al. (2014)

for a review). Our results indicate that roe deer tend to restrict their ranges around feeding sites. The tendency of individuals to gather in feeding sites proximity (Sahlsten et al. 2010) might enhance disease transmission risk among individuals, a particularly relevant issue for roe deer, which are the most abundant ungulates in most European countries and reservoirs for several zoonosis diseases, including those with direct transmission among individuals (e.g. Carpi et al. 2009). We invoke further investigation in these direction, e.g. by studying inter-individual behaviour at feeding sites. This can addressed either through a comparative analysis of trajectories (e.g., through spatio-temporal queries, Chapter 3.2 of this thesis, http://move-cost.info/highlights.php), or empirically, through the application of contact loggers to study intra- and inter-specific relationships (Creech et al. 2012, Campbell et al. 2013).

TABLES AND FIGURES

Table 1 Anova based on deviance to determine the framework of the temporal component of the model for selection of feeding sites by roe deer throughout the year. (See Appendix S6.1 for further details).

Model	Res. Deviance	Pr(> χ^2)
Model 1: Logit(P) ~ study area	14054	
Model 2: Logit(P) ~ study area + factor(week)	13873	< 0.001***
Model 3: Logit(P) ~ s(weekly temperature, bs="cc", by = study area)	13822	< 0.001***
Model 4: Logit(P) ~ s(week, bs="cc", by = study area)	13670	< 0.001***
Model 5: Logit(P) ~ s(week, bs="cc", by = study area) + weekly temperature	13649	< 0.001***

Legend: s(covariate a, "bs = cc") = formula to fit a cyclic penalized cubic regression spline smooth of the covariate a in GAM models; s(covariate a, "by = covariate b") = formula to fit an interaction between the spline smooth of a covariate a and a covariate b

Table 2 Summary of the multi-step procedure to identify the best model of selection of feeding sites by roe deer throughout the year. Model selection to identify and retain the models with ΔAIC lower than 2 with respect to the best model is reported in Table S6.2. See Appendix S6.2 for further details. (a) ANOVA based on deviance to determine the relative contribution of the two most parsimonious models retained by AIC-based model selection. The decrease in deviance obtained by the most complicated model (Model 3) was not significant, and the simplest model was retained thus (Model 9).(b) ANOVA based on deviance to assess relative importance of the covariates of Model 9 to evaluate further simplification of the model. All covariates significantly decreased deviance, and Model 9 was retained as best model thus (c) Analysis of deviance (ANODEV) to measure the proportion of the observed temporal variation accounted for by changes in temperatures. Legend: C_T = relative contribution of the weekly temperature to the full temporal variation observed.

(a) ANOVA based on deviance to assess differences between Models with $\Delta AIC < 2$		
Model	**Res. Deviance**	**Pr(> χ^2)**
Model 3: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*WT + SC*WT	13637	
Model 9: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*WT	13639	0.347
(b) ANOVA based on deviance to assess significance of covariates of the best model		
Model	**Res. Deviance**	**Pr(> χ^2)**
Full Model: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*WT	13639	
Model 1: Logit(P) ~ s(W*St) + RY + RI + A*L	13671	< 0.001***
Model 2: Logit(P) ~ s(W*St) + RY + RI + AF*WT	13644	0.011 *
Model 3: Logit(P) ~ s(W*St) + RY + A*L + AF*WT	13619	< 0.001***
Model 4: Logit(P) ~ s(W*St) + RI + A*L + AF*WT	13669	< 0.001***
Model 5: Logit(P) ~ RY + RI + A*L + AF*WT	14202	< 0.001***
(c) Analysis of deviance (ANODEV) to determine the temporal component of interaction WT*AF		
Model	**Log(lik)**	
Model 1: Logit(P) ~ study area	-7341.946	
Model 2: Logit(P) ~ study area * factor(week)	-6588.286	$C_T = 0.56$
Model 3: Logit(P) ~ study area * WT*AF	-6919.422	

Legend: logit (P) = logit of the probability of selection for a given feeding station; s(W*St) = cyclic penalized cubic regression spline smooth of the week by the study area; RY = random effect of the year; RI = random effect of the individual; A*L = two-way interaction between altitude and latitude; AF = activation status of the feeding sites; SC = snow cover; WT = weekly minimum temperature; AF*SC = two-way interaction between the activation status of the feeding sites and the snow cover; AF*WT = two-way interaction between the activation status of the feeding sites and the weekly minimum temperature; SC*WT = two-way interaction between the snow cover and the weekly minimum temperature

Table 3 Summary of the multi-step procedure to identify the best model of use of feeding stations by roe deer in the winter. Model selection to identify and retain the models with ΔAIC lower than 2 with respect to the best model is reported in Table S6.3. See Appendix S6.3 for further details. (a) ANOVA based on deviance to determine the contribution of the terms included in the retained models (Full Model, Model 2) when compared with the most parsimonious model retained (Model 7). (b) ANOVA based on deviance to assess the importance of the covariates retained in the best model (Model 7), (c) ANOVA based on deviance to confirm the relevance of all the terms included in the new best model selected.

(a) ANOVA based on deviance to assess differences between Models with ΔAIC < 2		
Model	**Res. Deviance**	**Pr(> χ^2)**
Full model: time ~ RI + Sex + Age + Comp*Feed + Comp*Ener + Feed*Ener	24780	
Model 1: time ~ RI + Sex + Age + Comp*Feed + Feed*Ener	24780	0.52
Model 7: time ~ RI + Sex + Age + Comp*Feed	24784	0.2

(b) ANOVA based on deviance to assess significance of covariates of the best model		
Model	**Res. Deviance**	**Pr(> χ^2)**
Full Model: time ~ RI + Sex + Age + Comp*Feed	24784	
Model 1: time ~ RI + Sex + Comp*Feed	24786	0.30
Model 2: time ~ RI + Age + Comp*Feed	24786	0.15
Model 3: time ~ Sex + Age + Comp*Feed	25044	< 0.001***
Model 4: time ~ RI + Sex + Age	24838	< 0.001***
Model 5: time ~ RI + Comp*Feed	24788	0.12

(c) ANOVA based on deviance to assess significance of covariates of the new best model		
Full Model: time ~ RI + Comp*Feed	24788	
Model 1: time ~ RI	24840	< 0.001***
Model 2: time ~ Comp*Feed	25064	< 0.001***

Legend (b): time = time spent at feeding station; RI = random effect of the individual; Comp = potential competition for feeding; Ener = Energetic value of food; Feed = design of feeding station; Sex = sex of the individual; Age = age class of the individual; Comp*Ener = two-way interaction between potential competition for feeding and energetic value of the food provided; Comp*Feed = two-way interaction between potential competition for feeding and design of feeding station; Ener*Feed = two-way interaction between energetic value of the food provided and design of feeding station.

Table 4 Summary of the occurrence of peak of selection of feeding sites by roe deer (*Capreolus capreolus*) across the 9 study areas in Europe, years 2005-2013. To note the separation between the areas where feeding peak occurs early in the winter (above) and late in the winter (below).

	Study area	Median(Week)	25% percentile (week)	75% percentile (week)
early winter peak	Site 2	1	0	3
	Site 7	2	1	6
	Site 8	1	0	1
	Site 5	1	50	7
late winter peak	Site 1	6	1	7
	Site 3	6	4	8
	Site 4	7	0	7
	Site 6	5	5	8
	Site 9	6	0	7

Figure 1 Distribution of roe deer (*Capreolus capreolus*) supplemental feeding stations across the 9 study areas in the EURODEER network. Site 1: Bavarian Forest National Park and Sumava National Park; Site 2: Italian Alps; Site 3: Norway; Site 4: Sweden; Site 5: Austrian Alps; Site 6: Bialowieza Forest; Site 7: Brandenburg Forest; Site 8: Baden – Wuerttemberg (low area); Site 9: Baden – Wuerttemberg (hilly area)

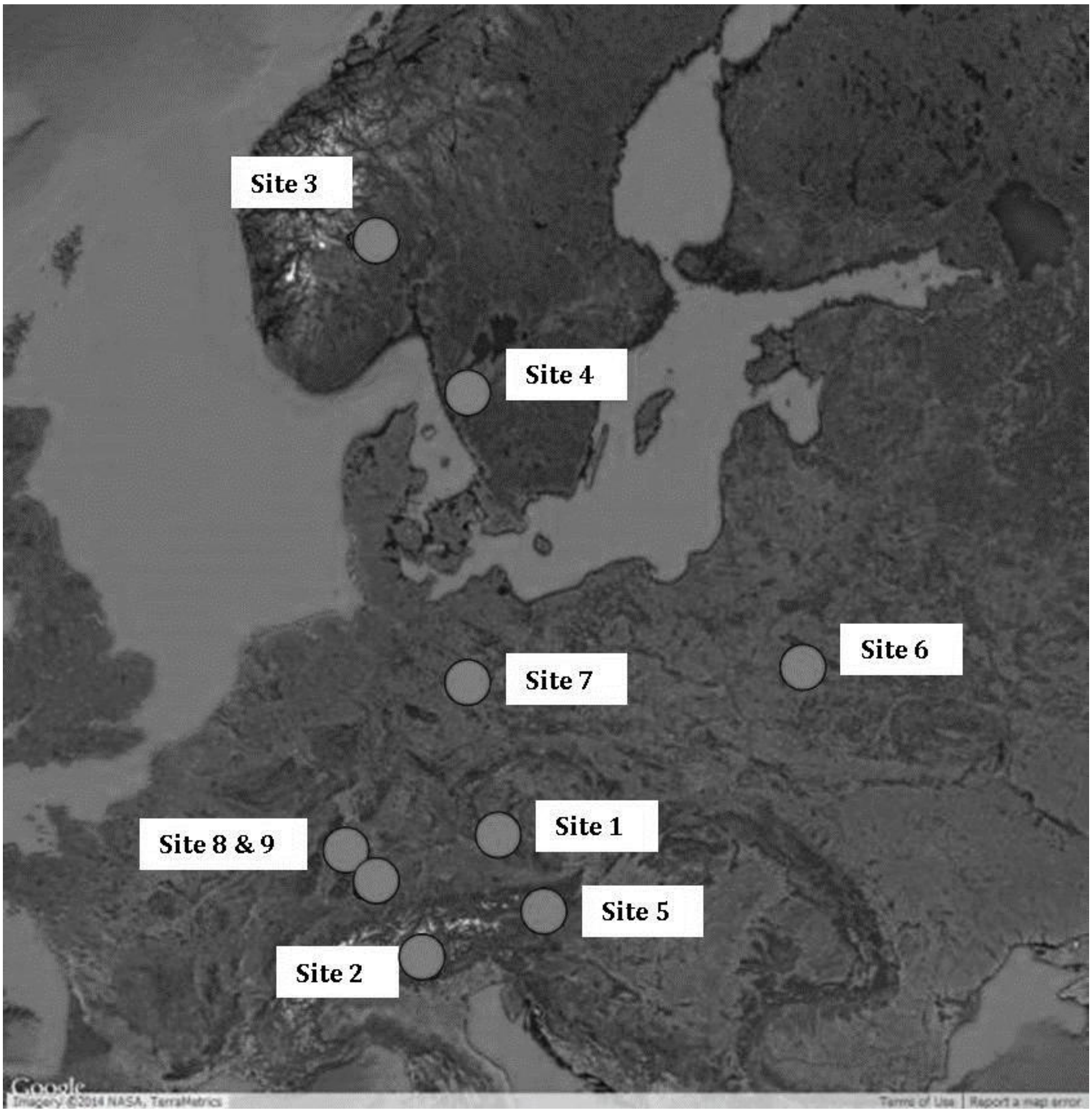


Figure 2 Plot of the predicted probability of selection of feeding sites throughout the year (continuous black line), for each study area separately. Broken lines denote 95% confidence intervals. The bold continuous line indicates the pattern of variation of weekly average minimum temperature by study area. Grey areas represent the period of activation of the feeding stations.

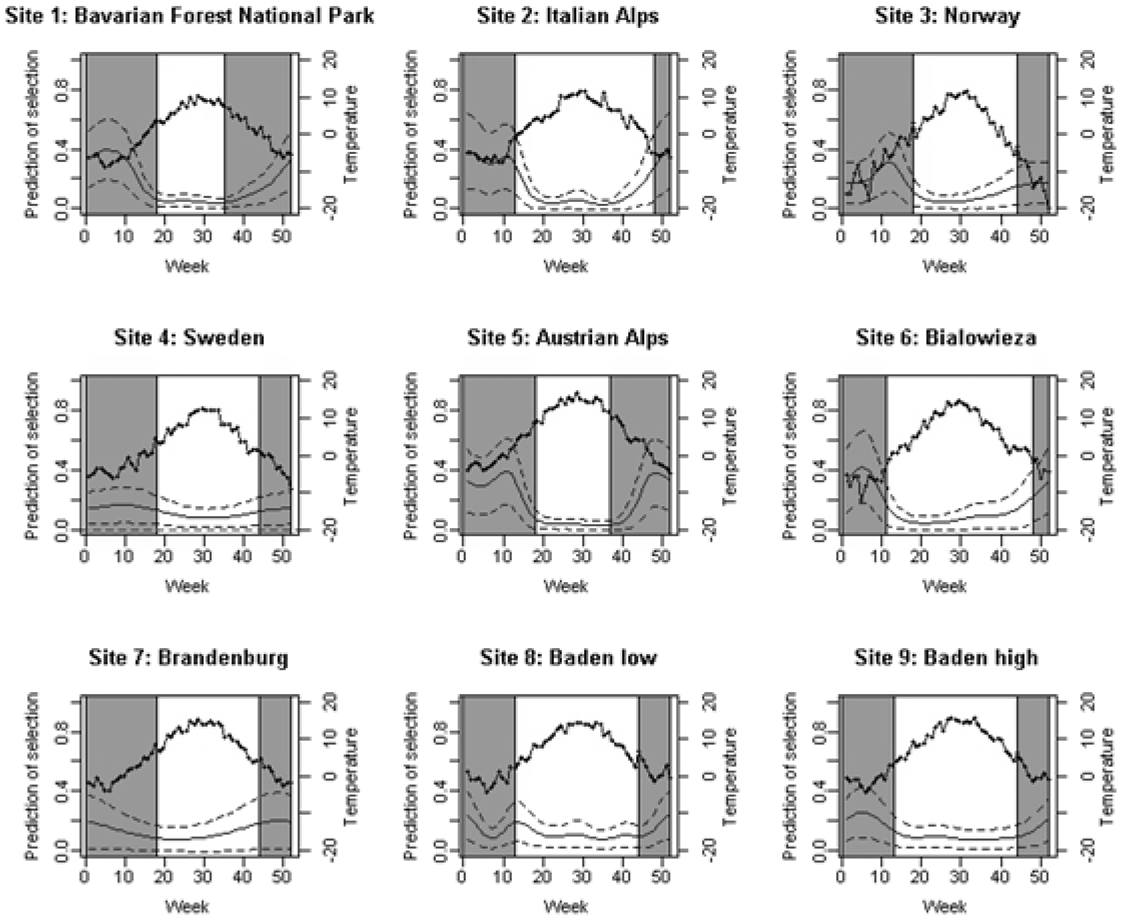


Figure 3 Plot of the predicted probability of selection of feeding sites throughout the year in function to the interaction between the weekly minimum temperature and the activation of the feeding station. Broken lines represent 95% confidence intervals.

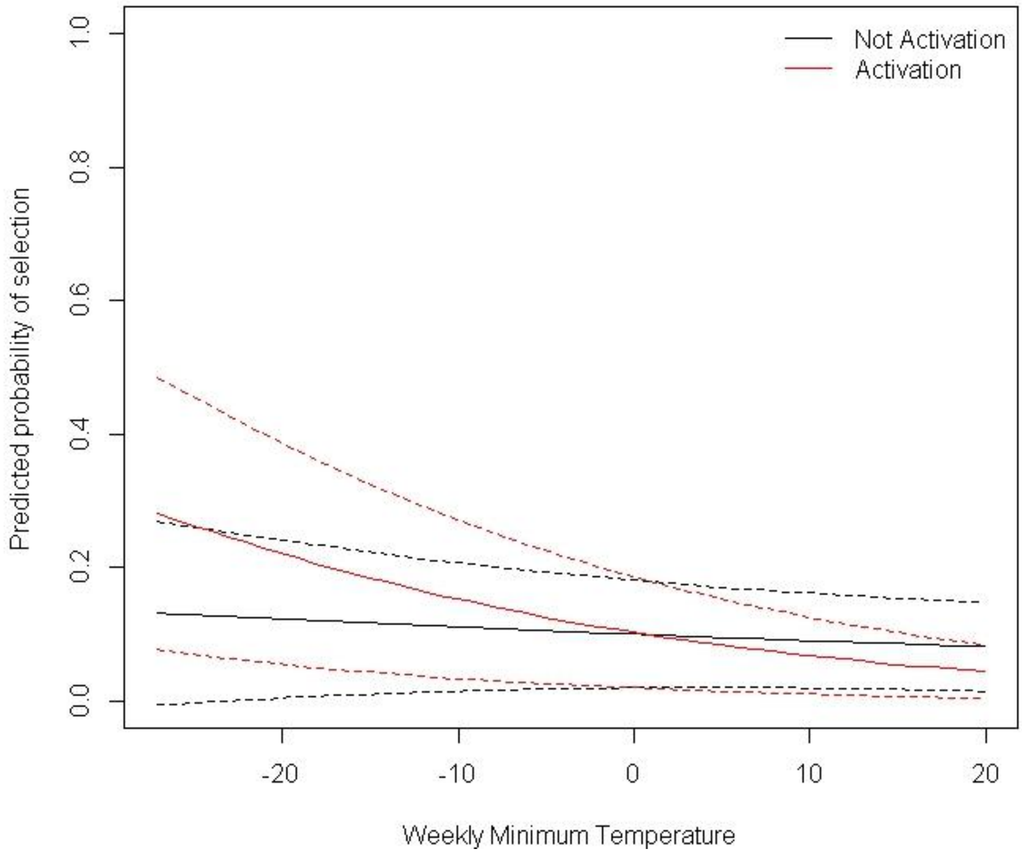


Figure 4 plot of the predicted probability of selection of feeding sites throughout the year in function to latitude (a) and altitude (b). Broken lines represent 95% confidence intervals.

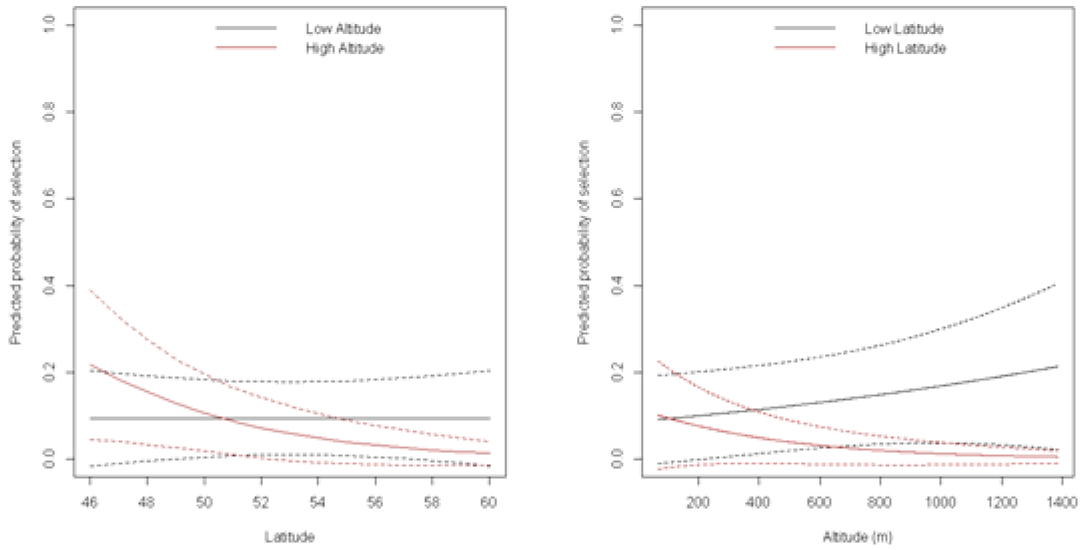
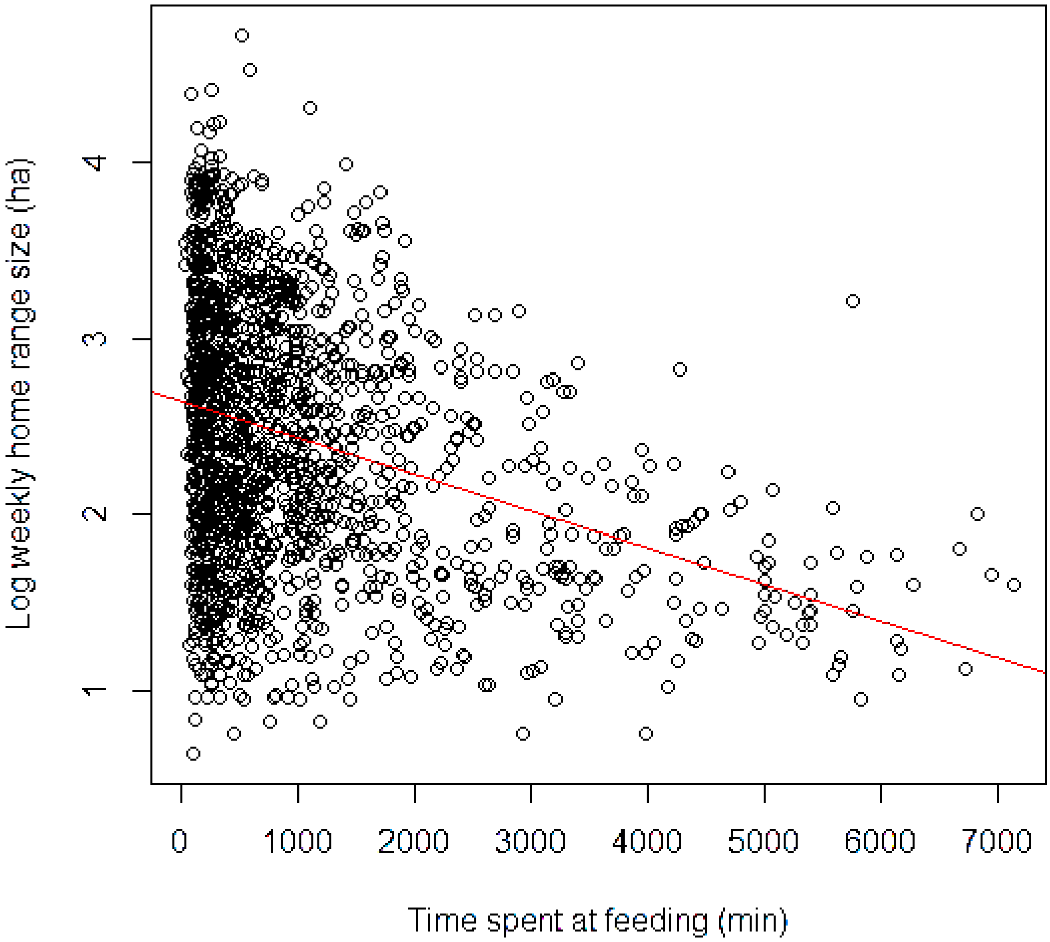


Figure 5 plot of the variation of natural logarithm of the weekly home range size in relation to the time spent (minutes) in the surroundings of the feeding site. The linear model is presented in red.



APPENDIX S1

Summary of the information on the nine study areas included in this analysis.

Site ID	Study area	Data provider	Average coordinates	Elevation range (m a.s.l)	Brief description	Period supplemental feeding
1	Bavarian Forest	Bavarian Forest National Park & Sumava National Park	48.99089N, 13.36584E	600 - 1200	central European sub-mountainous forest	1 September - 30 April
2	Italian Alps	Edmund Mach Foundation	46.08067N, 10.74306E	500 - 1800	Alpine mountain range	1 December - 31 March
3	Norway	Oslo University & Norwegian Institute for Nature Research (NINA)	60.67308N, 8.817776E	200 - 800	hilly area, boreal forest in valleys and tundra at higher elevations	1 November - 30 April
4	Sweden	Swedish University of Agricultural Sciences (SLU)	58.1193N, 12.40749E	50 - 150	mainly flat boreal forest (70%) with some arable land and pastures (~20%)	1 November - 30 April
5	Austrian Alps	Boku University	47.44475N, 15.09543E	700 - 1200	Alpine mountain range	16 September - 30 April
6	Bialowieza Forest	Bialowieza National Park	52.69104N, 23.51883E	140 - 170	lowland primeval forest	1 December - 30 April
7	Brandenburg Forest	Leibniz-Institute for Zoo and Wildlife Research	52.22052N, 12.48458E	30 - 50	mainly forest intersected by pastures	1 November - 30 April
8	Baden-Wuerttemberg lowland	Forest Research Institute of Baden-Wuerttemberg	48.64146N, 7.986901E	100 – 150	wooded patches surrounded by arable land and meadows	1 November - 31 March
9	Baden-Wuerttemberg hilly area	Forest Research Institute of Baden-Wuerttemberg	47.88263 N, 8.725884E	550 - 850	wooded patches surrounded by arable land and meadows	1 November - 31 March

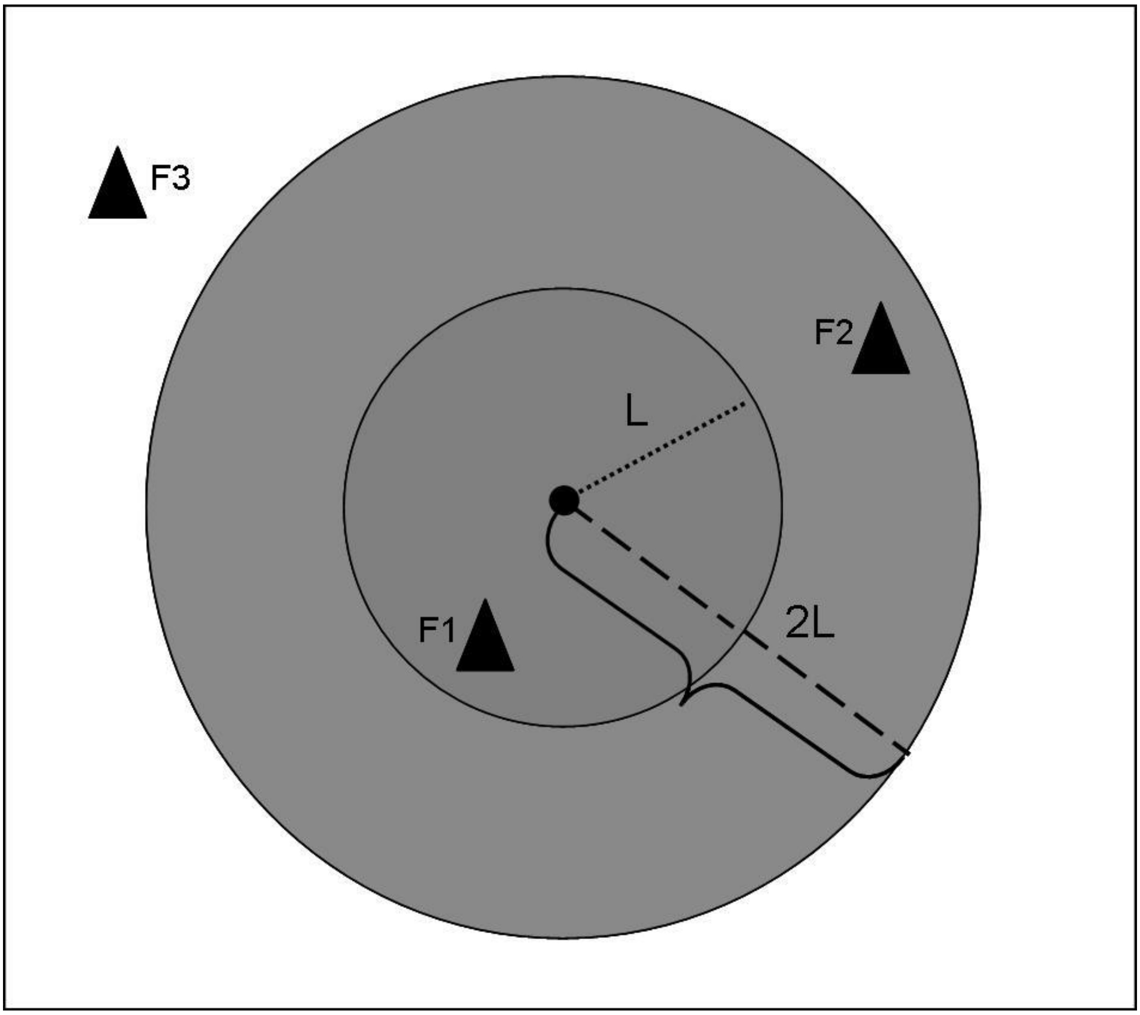
APPENDIX S2

Summary of the information collected at each feeding station, with a brief explanation on the classification criteria.

Management feature	Description
Station Design	**Feeding** or **Box Trap**. 'Feeding' are those sites that are proper feeding stations. Box traps are boxes provided with food to capture ungulates
Energetic value of food	**High** or **low**. Energetic value is high when the feeding stations are filled with pellets, hay or corn (or a combination including at least one of these items). Energetic value is low when these sites are filled with fruit and vegetables
Potential competition	**Present** or **Absent**. Potential competition occurs when there are other ungulates in the area (at least one between fallow deer, red deer, wild boar, moose, bison), without limitation to the access to the feeding stations
Years activation	It indicates the first and last year of management of the feeding station
Seasonal activation	It indicates the first and last day of seasonal management of the feeding station, specifically for each year

APPENDIX S3

Scheme of the criterion for selecting the available feeding stations for each individual. The winter home range size of a given individual is here simplified as a circle of radius L. The buffered home range size of radius 2L encompass two feeding stations, F1 and F2, which are defined as available for the individual, whilst the third feeding station (F3) is not retained in the analysis, for this individual.



APPENDIX S4

We performed a designed pilot study to identify the metric to be used for investigating the selection of feeding sites by any individual in a given week. We considered as potential metrics for the analysis two parameters based on the individual geometric trajectory: the time spent by an individual within a buffer centred on the feeding site, and the number of GPS locations that fell within the buffer itself. Concerning the first metric, we estimated the time spent within a feeding site buffer by multiplying the proportion of the step overlapping the buffer (distance) by the time interval of the movement step (time), for any given step between two subsequent locations (Figure S4.1). We summed the values obtained from each step to get the weekly time spent by an individual in the proximity of a given feeding site. We then weighted this value by the time available for the computation in that week, which was not constant among all the individual due to missing locations, to eventually get the weekly percentage of time spent by an individual in proximity of a given feeding site. Then, for the same weekly trajectories, we computed the number of GPS locations that fell within the buffer centred on the feeding site.

Since both these metrics are based on the individual trajectory, we evaluated their dependence from two factors, i.e. the sampling regime of the GPS locations of the individual and the length of the buffer centred on the feeding site. The former factor is important to assess because the protocol of sampling frequency varies consistently in the source dataset, both between study areas and, occasionally, even between individuals of the same study area. The latter determines the resolution of the analysis on the use of feeding sites. We performed this analysis on a subsample of the full dataset including the locations from the study site 2 (Italian Alps). The GPS sampling regime of the collars used in this project had been set at three hours sampling interval. However malfunctioning of GPS due to weak satellite reception led to the occurrence of a few cases of missed recording locations, with consequent holes in the trajectories under investigation. We investigated the sensitivity to the GPS sampling protocol by regularizing and interpolating the trajectories at fixed intervals of three, six and nine hours, exploiting the functionalities of PostGIS, a spatial database extender for PostgreSQL. Then we computed, for all the individual trajectories (both uncorrected and regularized ones), the weekly number of fixes and the time spent within a buffer of 50, 100, 200 and 400 meters.

We firstly performed an explorative analysis to evaluate, for each of the potential metrics under investigation, if the different sampling regimes of the computed trajectories affected the amount of the data available for the analysis, i.e. the number of fixes in a week and the number of minutes of a weekly trajectory. We did this by analysing the correlation patterns (Spearman coefficients) between the available data, for each pair of different sampling regimes. We found that the degree of correlation was high for all the pairs of available data, both in the case of the weekly number of minutes (Table S4.1) and for the weekly number of fixes (Table S4.2).

We then explored if the pattern of the distribution of the data was similar for the two computed metrics, separately for each sampling regime. We therefore ran a linear model in which we modelled the dependence of the first metric (minutes spent within the buffer) from the second metric (number of fixes within the buffer). We found that the relationship between the two metrics was strong ($p < 0.01$) for each sampling regime, indicating a strong similarity in the pattern of distribution of the data between the two metrics under investigation. We fitted a logistic regression (Hosmer and Lemeshow, 2000) to model the dependence of each of the metrics from the length of the buffer and the sampling regime of the trajectories. For both the metrics we assigned a value 1 (one) to all the cases that were strictly bigger than 0 (zero). Since the number of 0 (zeros) largely exceeded the number of 1 (one) in both the distributions (weekly time spent: 12259 0s and 4621 1s; number of fixes: 12729 0s and 4151 1s), we fitted a zero inflated binomial logistic regression, with a random effect of the number of week nested within the individual, to account for expected variation between individuals and across time. We then investigated the effect of the two covariates, i.e. the sampling regime and the buffer length, on the amount of minutes spent and number of fixes within the buffer. We therefore circumscribed the analyses to the data that were different from 0 (zero). Since the data were continuous and not normally distributed, for both the metrics under exam, we fitted a model in the context of the gamma family, with a random effect of the number of week nested within the individual similarly to what previously done.

We found that the probability to have at least one fix within a buffer decreased significantly at the increasing of sampling regime, with respect to the three hours interval that was used as reference category (six hours: s = -0.16, p =0.016; 9 hours: s = -0.25, p <0.001). Conversely the probability to have a fix in a certain week did not change between the uncorrected trajectories and the three hours ones (p =0.82). This result was expected, since the original sampling protocol was set at three hours. We also found a significant effect of the buffer length on this pattern, with a significant tendency to the increase of probability with the increment of the buffer length (s = 0.004, p < 0.001). The random part of the model accounted for a significant part of the explained variance (animal: 11.5% ± 3.4%; animal*week: 5.6% ± 2.4%).

The model on the pattern of the amount of minutes spent within the buffer gave similar result. All the sampling regimes but not the uncorrected one resulted significantly different from the three hours sampling interval (six hours: r = -0.6, p <0.001; nine hours: r = -0.9, p <0.001). The trend for an increase in the number of fixes with the length of the buffer was confirmed (r = 0.003, p < 0.001). The random part of the model did not explain a lot of the variance (animal: 0.2 % ± 0.5 %; animal*week: 0.7 % ± 0.8 %), although it fitted the data better than the analogous with animal and week as fixed effect (AIC random: 27741.8; AIC fixed: 29675.6). The probability that the individual spent at least one minute within a certain buffer was scarcely influenced by the relocations sampling regime. We found this effect to be significant only in the case of the 9 hours periodicity, with respect to the three hours sampling frequency (s = -0.16; p = 0.01). The sensitivity of this metric to the buffer length resulted similar to what we found modelling the dependence of the number of fixes from this covariate (s = 0.004, p <0.001). Analogously to what previously found, the random part of the model accounted for a significant part of the variance (animal: 11.3 % ± 3.4 %; animal*week: 6 % ± 2.4 %).

The modelling of the amount of time spent within a certain buffer confirmed the scarce sensitivity of this metric to the variation of the sampling frequency. None of the sampling frequencies differed significantly from another. Vice versa the significant effect of the buffer length was confirmed (r = 0.004, p < 0.001). The animal and week fitted as random effect did not explain a lot of the variance (animal: 0.2 % ± 0.5 %; animal*week: 1.03 % ± 1.07 %) although the model resulted better than the same with animal and week as fixed effects (AIC random: 81712; AIC fixed: 83677.8).

The results that we found suggest that both the proposed metrics similarly represent the selection for feeding sites by roe deer. The distribution of data are quite similar, with an almost identical amount of zeros cases over the total (i.e. the cases representing the 'non use' of a feeding site by an animal). However the sensitivity of the number of fixes to the periodicity of the sampling regime, renders the use of this metric advised against, given the high heterogeneity of sampling intervals within the source dataset. Conversely, we found that the time spent within a buffer does not result affected by the sampling interval. Therefore this metric is particularly suitable to be applied in this work. Moreover, the aimlessness of regularization and interpolation of the trajectories is advantageous, since the interpolation creates 'fake' points based on the features of the trajectory, which might not respect the actual behaviour of the animal. The significant but almost inconsistent effect of the buffer size on both the time spent and the number of fixes within a buffer, renders the choice of the buffer length for the analyses robust to any potential bias due to its size. Beyond its methodological importance this result is biologically relevant: it indicates that roe deer that select for feeding sites indeed stay in their close proximity (almost no differences between 50 meters and 400 meters radius).

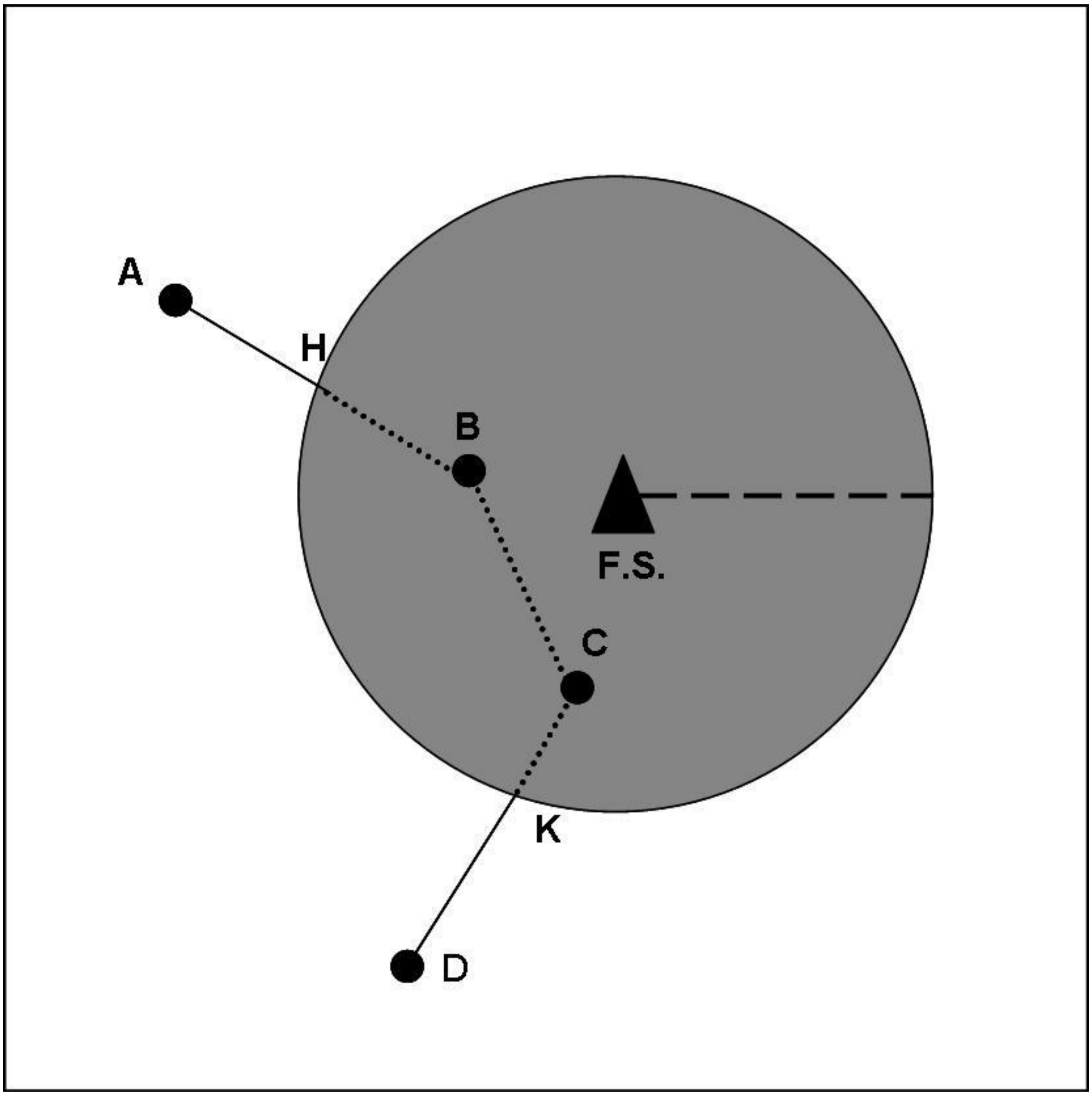
Table S4.1 matrix of Spearman coefficients indicating the degree of correlation of all the pairs of available number of minutes, for every combination between different sampling regimes

	3h	**6h**	**9h**	**uncorrected**
3h	1	0.87	0.56	0.95
6h	0.87	1	0.67	0.83
9h	0.56	0.67	1	0.53
uncorrected	0.95	0.83	0.53	1

Table S4.2 matrix of Spearman coefficients indicating the degree of correlation of all the pairs of available number of fixes, for every combination between different sampling regimes

	3h	**6h**	**9h**	**uncorrected**
3h	1	0.90	0.77	0.74
6h	0.90	1	0.73	0.76
9h	0.77	0.73	1	0.71
uncorrected	0.74	0.76	0.71	1

Figure S4.1 graphical representation of the geometrical computation of the time spent by an individual at feeding sites. The points A, B, C and D represent four GPS locations of an individual, segments AB, BC and CD are three trajectory steps, and the black triangle a feeding site. In order to define the time spent within the buffer, we firstly computed for each step the proportion overlapping the buffer (respectively length BH/length AB, 1 and length CK/length CD, indicated by dotted traits in the Figure). We then multiplied these proportions by the time interval of the movement step, based on locations timestamps, to get the amount of time spent within the buffer of the feeding site. We summed the time intervals of every week to get the time that any individual spent in the proximity of a feeding site in any given week.



APPENDIX S5

In the analysis on selection of feeding sites throughout the year we found strong correlations between the weekly minimum temperature and the presence of snow at ground (r=-0.63), the weekly minimum temperature and the activation of the feeding station (r = -0.66), the presence of snow at ground and the activation of the feeding station (r = 0.52), and, lastly, between the latitude and the altitude of the feeding sites (r = -0.56) (Table S5.1). We took these correlation in account by fitting two-way interactions of the correlated covariates in the full model (see Table S6.1 and Appendix S6.1).

In the analysis on winter use of the selected feeding stations by roe deer, we found a strong correlation between the presence of potential competitors and the energetic value of the food provided (r=-0.62); the correlation between potential competitors and feeding station design as well as that between the energetic value of the food provided and the feeding station design were low (respectively: 0.16 and 0.06) (Table S5.2). However a graphical exploration of the correlation patterns (not reported) indicated the necessity to take in account these correlations in the model, which we did by fitting two-way interactions of the correlated terms in the full model (See Table S6.1 and Appendix 6.3).

Table S5.1 Correlation matrix of the covariates included for the analysis of the pattern of selection of the feeding sites throughout the year.

	Observational week	Snow cover	Activation feeding	Weekly min temperature	Latitude	Altitude
Observational week	1.00	-0.27	-0.24	0.38	0.02	0.00
Snow cover	-0.27	1.00	0.52	-0.63	0.11	0.10
Activation feeding	-0.24	0.52	1.00	-0.66	0.07	0.03
Weekly min temperature	0.38	-0.63	-0.66	1.00	-0.17	-0.04
Latitude	0.02	0.11	0.07	-0.17	1.00	-0.57
Altitude	0.00	0.10	0.03	-0.04	-0.57	1.00

Table S5.2 Correlation matrix of the covariates included for the analysis of the pattern of use of the selected feeding stations in winter.

	Competition	Energetic value food	Feeding Design	Sex	Age class
Competition	1.00	-0.63	0.16	0.23	-0.09
Energetic value food	-0.63	1.00	0.06	-0.22	-0.05
Feeding Design	0.16	0.06	1.00	0.11	0.00
Sex	0.23	-0.22	0.11	1.00	-0.10
Age class	-0.09	-0.05	0.00	-0.10	1.00

APPENDIX S6

S6.1 Identification of full model assessing the influence of abiotic factors on occurrence and timing of selection of feeding sites

The determination of the full model of selection of feeding sites throughout the year included several steps.

1) Firstly, we established an *a priori* list of biological meaningful covariates which could affect the patter of selection, including the activation of the feeding station (dummy covariate: 1 = active feeding station; 0 = non active feeding station), the snow cover (dummy covariate: 1 = presence of snow cover at ground; 0 = absence of snow cover at ground), the weekly minimum temperature, latitude and altitude of the feeding site, the observational week of the year, the year of observation, the individual and the study area.
2) Second, we determined the best modelling framework accounting for the observed temporal variation in the selection of the feeding sites by roe deer. We performed an ANOVA based on deviance (Skalski et al. 1993) to decide how to combine the observational week, the weekly minimum temperature and the study area to model the temporal component of the model. Specifically, we fitted five general additive mixed models (Table 1) of increasing complexity, each of which included as a baseline the two-way interaction between latitude and altitude, activation of feeding station and snow cover as single terms, and the random effect of the year and the individual. In the first model, we fitted only the study area as fixed effect; in the second model we added the week as a factor to Model 1; the third model included the weekly temperature fitted as cyclic penalized cubic regression spline smooth, in interaction with the study area; in the fourth model we fitted the observational week as cyclic penalized cubic regression spline smooth, in interaction with the study area; lastly, in the fifth model

we fitted the cyclic penalized cubic regression spline smooth of the week, in interaction with the study area, and the weekly minimum temperature fitted as fixed effect. Then, we compared each model with the previous one (e.g. Model 2 with Model 1) by means of an ANOVA based on the deviance, to assess what model best fitted the observed data, based on the significance of the difference of the deviance explained. We found that each model had a better goodness-of-fit than the previous one (Table 1). We thus fitted as temporal component of the model of selection of feeding sites throughout the winter the cyclic penalized cubic regression spline smooth of the week, in interaction with the study area. The weekly minimum temperature was fitted in the fixed part of the model framework.

3) Lastly, based on the exploration of the co–linearity patterns (Appendix S5 and Table S5.1), we fitted in the full model (Table S6.1) the two-way interactions between the weekly minimum temperature and the activation of the feeding station, the weekly minimum temperature and the snow cover, the activation of the feeding sites and the snow cover and latitude and altitude of the feeding sites. The random component of the model included two not nested random effects of the individual and the year, to control for expected variability in the pattern of selection between different years and among individuals.

S6.2 Identification of best model assessing the influence of abiotic factors on occurrence and timing of selection of feeding sites

The identification of the best model of selection of feeding sites throughout the year included several steps. As first, we wanted to determine the best way to fit the weekly minimum temperature, activation of feeding stations and snow cover in the model. Since we could not identify a list of models to be considered *a priori* most relevant, with respect to these covariates and their interactions, we prepared a list of models (18), starting from the full model determined above (Table S6.2). Each of these models had the same baseline framework, which included the temporal and random component of the model, plus the two-way interaction between latitude and latitude. We compared these models by means of their AIC scores, retaining those with ΔAIC lower than two. We thus retained for further consideration two models, one including only the two-way interaction between weekly minimum temperature and the activation of the feeding station (Model 9, Table S6.2), the other also comprising the two-way interaction between weekly minimum temperature and snow cover (Model 3, Table S6.2). At this stage, we decided to adopt a reductionist approach, based on the principle of parsimony, to evaluate the contribution of the covariates in improving the goodness-of-fit of the model. We thus performed an ANOVA based on deviance to assess the significance of the two-way interaction between weekly minimum temperature and snow cover, which did not improve significantly the goodness-of-fit of the model (Table 2a). We then ran a second ANOVA based on deviance to assess if all the terms of the retained Model 9 (temporal component, random effects and fixed effects) significantly improved the goodness-of-fit of the model. Since this was the case (Table 2b), we retained Model 9 as the best model: a temporal component accounted for by the cyclic penalized cubic regression spline smooth of the week, in interaction with the study area; a fixed component made up of two two-way interactions, one between weekly minimum temperature and activation of the feeding site, the other between the latitude and altitude; a random component including the year and the individual as not nested random effects.

Lastly, we ran an analysis of deviance (ANODEV) to assess the proportion of the observed temporal variation explained by the interaction between the weekly minimum temperature and the activation of the feeding stations, with respect to the observational week (Table 2c). We fitted three general linear mixed models with the same baseline framework, i.e. the two-way interaction between altitude and latitude, and the random component of the best model. In the first model we fitted a fixed effect of the study area, in the second an interaction between the observational week factorized and the study area, in the third a three-way interaction between the weekly minimum temperature, the activation of the feeding station, and the study area. We computed the natural logarithm of the likelihood (Loglikelihood) of each of these models. We thus determined the relative contribution C_T of the interaction between the weekly minimum temperature and the activation of the feeding station to the full temporal pattern accounted for by the observational week as follows:

$$C_T = [\log(\text{lik}(\text{Model3})) - \log(\text{lik}(\text{Model2}))/\log(\text{lik}(\text{Model1})) - \log(\text{lik}(\text{Model2}))]$$

where lik = likelihood, log = natural logarithm

We found that the interaction between the weekly minimum temperature and the activation of the feeding sites accounted for the 56% of the observed temporal pattern.

S6.3 Identification of best model of winter use of feeding stations

The procedure to determine the best model on the use of the selected feeding stations in winter included several steps. First, we set an *a priori* list of biologically relevant covariates to fit in the model. These included the design of feeding station, the energetic quality of the food provided, the potential competition with other ungulates for feeding, sex and age of the individuals and the individuals themselves. After checking for co-linearity patterns between the covariates (see Appendix S5 and Table S5.2), we evaluated what combination of the covariates 'design of feeding station', 'energetic quality of the food provided' and 'potential competition' better accounted for the pattern of use of feeding stations in winter. Since we had no *a priori* knowledge to select any particular combination of these covariates, we prepared a list of models (18), from the full one including all the three combinations of two-way interactions between the covariates, to a model without any of the covariates (Table S6.3). All the models had the same baseline framework, which included the fixed effects of sex and age as single terms, and the individual as random not nested effect. We selected the models based on their AIC scores, retaining those with ΔAIC lower than two. We thus selected three models (Full Model, Model 1, Model 7 and Table S6.3). We then applied a reductionist approach to evaluate whether it was possible to further simplify the model. We thus performed an ANOVA based on deviance (Table 3a) to assess the significance of the contribution of (i) the interaction between design of the feeding station and the energetic quality of food and (ii) the interaction between potential competition and the energetic quality of food to improve the goodness-of-fit of the model. Since none of these terms, nor their contemporary depletion, significantly reduced the residual deviance of the model, we discarded them from the model. We then ran a second ANOVA based on deviance to assess the significance of each term to improve the goodness-of-fit of the model (Table 3b). Specifically, we compared the new full model (Model 7) with a list of models where we dropped each time one of the terms of the full model. We thus discarded both sex and age from the model, after checking that even their combined removal did not reduce the goodness-of-fit of the model (Table 3b, ANOVA between Full Model and Model 5). We then repeated the same procedure on the new model retained. Both the removal of the two-way interaction between the potential competition and the design of the feeding station on one side, and of the random effect of the individual on the other, significantly improved the goodness-of-fit of the model (Table 3c). Therefore we kept both them in the best model on the use of the selected feeding stations in winter.

Table S6.1 Summary of the full models. The components of the models are divided into a fixed effect component, a random effect component and an interaction between the spline of the observational week and the study area to account for the observed temporal variation (not present for the model of the winter period).

Model	Response variable	Fixed effects	Random Effects	Temporal variation component
Year	Use vs Non Use (0/1)	altitude*latitude + weekly temperature*activation feeding + weekly temperature*snow cover + activation feeding*snow cover	year + individual	week*study area
Winter	Time spent (minutes)	competition* energy food + competition*feeding design + energy food*feeding design + sex + age	individual	

Table S6.2 Model selection to identify and retain the models explaining yearly selection of feeding sites, i.e. those with ΔAIC lower than 2 with respect to the best model. AIC scores of the models retained are indicated by an asterisk (*).

Model	DeltaAIC
Model 9: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*WT	0*
Model 3: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*WT + SC*WT	1.79*
Model 6: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*WT **+** SC	2.01
Model 15: Logit(P) ~ s(W*St) + RY + RI + A*L + WT	2.84
Full model: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*SC + AF*WT + SC*WT	3.8
Model 2: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*SC + AF*WT	3.95
Model 13: Logit(P) ~ s(W*St) + RY + RI + A*L + SC + WT	5.06
Model 11: Logit(P) ~ s(W*St) + RY + RI + A*L + AF + WT	5.38
Model 8: Logit(P) ~ s(W*St) + RY + RI + A*L + SC*WT	6.52
Model 10: Logit(P) ~ s(W*St) + RY + RI + A*L + AF + SC + WT	7.43
Model 4: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*SC + WT	8.71
Model 5: Logit(P) ~ s(W*St) + RY + RI + A*L + SC*WT + AF	8.88
Model 1: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*SC + SC*WT	9.7
Model 17: Logit(P) ~ s(W*St) + RY + RI + A*L	25.51
Model 16: Logit(P) ~ s(W*St) + RY + RI + A*L + SC	27.59
Model 14: Logit(P) ~ s(W*St) + RY + RI + A*L + AF	27.97
Model 12: Logit(P) ~ s(W*St) + RY + RI + A*L + AF + SC	30.02
Model 7: Logit(P) ~ s(W*St) + RY + RI + A*L + AF*SC	31.16

Table S6.3 Model selection to identify and retain the models explaining winter use of feeding stations, i.e. those with ΔAIC lower than 2 with respect to the best model. AIC scores of the models retained are indicated by an asterisk (*).

Model	**DeltaAIC**
Model 1: time ~ RI + Sex + Age + Comp*Feed + Feed*Ener	0
Model 7: time ~ RI + Sex + Age + Comp*Feed	0,2*
Full model: time ~ RI + Sex + Age + Comp*Feed + Comp*Ener + Feed*Ener	1,6*
Model 4: time ~ RI + Sex + Age + Comp*Feed + Ener	2,3
Model 2: time ~ RI + Sex + Age + Comp*Ener + Feed*Ener	4,2
Model 3: time ~ RI + Sex + Age + Comp*Ener + Feed*Ener	4,2
Model 6: time ~ RI + Sex + Age + Feed*Ener + Comp	6,4
Model 8: time ~ RI + Sex + Age + Comp*Ener	30
Model 10: time ~ RI + Sex + Age + Comp + Ener + Feed	30
Model 5: time ~ RI + Sex + Age + Comp*Ener + Feed	30,8
Model 13: time ~ RI + Sex + Age + Comp + Ener	30,8
Model 12: time ~ RI + Sex + Age + Comp + Feed	33,8
Model 15: time ~ RI + Sex + Age + Comp	35,6
Model 9: time ~ RI + Sex + Age + Feed*Ener	38,2
Model 14: time ~ RI + Sex + Age + Feed	41,4
Model 11: time ~ RI + Sex + Age + Ener + Feed	42,8
Model 17: time ~ RI + Sex + Age	48
Model 16: time ~ RI + Sex + Age + Ener	49,6

APPENDIX S7

Contingency table indicating the number of sampling units grouped by year, sex and study area. The '∑ year' column indicates the number of sampling units for year, across all the study areas; The '∑ study area' column indicates the number of sampling units for study area, across all the years and without distinction of sex.

Year	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**		**Site 6**		**Site 7**		**Site 8**		**Site 9**		**Σ year**
	F	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	
2005	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**27**
2006	298	197	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**495**
2007	127	347	0	0	0	0	83	575	46	20	0	0	0	14	0	0	0	0	**1257**
2008	213	178	0	0	156	158	3	180	167	116	68	0	0	20	0	0	0	0	**1259**
2009	840	664	0	0	209	452	169	125	154	140	180	0	0	24	0	0	0	0	**2957**
2010	1256	1541	0	0	80	102	122	51	92	96	606	0	18	28	659	329	0	0	**4980**
2011	1067	1707	0	0	0	0	0	0	0	0	162	0	357	0	905	184	20	24	**4426**
2012	263	295	11	0	0	0	0	0	84	30	33	0	14	0	44	0	660	430	**1864**
2013	26	6	811	10	0	0	0	0	0	0	0	0	0	0	0	0	160	98	**1111**
Σ area	**9070**		**859**		**1157**		**1308**		**945**		**1049**		**475**		**2121**		**1392**		

APPENDIX S8

Summary of the data selected for the analysis on the amount of use of feeding stations. Perc_1 indicates the ratio of the sampling units retained for the analysis (percentage time spent > 0.01) on the total of sampling units, limited to the winter period selected (December 1st – March 31th). The contingencies of the sampling units in relation to the management characteristics of the feeding stations are then presented. Last two columns refer to the mean and standard deviation of the weekly amount of time spent in proximity of feeding stations for every study area.

	Perc_1 (%)	**Feeding_typology**		**Energetic_value_food**		**Competition**		**Amount use (min)**	
		Trapping	**Feeding**	**Low**	**High**	**Absent**	**Present**	**Mean**	**Sd**
Site 1	44	625	15	1	639	0	640	814	797
Site 2	33	3	81	0	84	84	0	3430	2087
Site 4	18	0	71	0	71	0	71	322	294
Site 5	44	0	170	0	170	170	0	1375	1132
Site 6	27	0	60	60	0	13	47	785	631
Site 7	10	0	18	0	18	0	18	592	254
Site 8	50	332	0	332	0	332	0	673	606
Site 9	50	61	169	230	0	230	0	1274	1403

CHAPTER 2.1

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

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ABSTRACT

In alpine environments, snow typically reduces herbivores accessibility 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 minimizing 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 remote-sensed data.

KEY WORDS: Roe deer, winter resource selection, snow sinking depth, supplemental feeding, Resource Selection Function, Snow MODIS.

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 Kersall 1984). 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 large herbivores movement, resource selection and distribution. 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), while 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 Kersall 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 Kersall 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 Kersall 1984) enables individuals to maximise energy intake while 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), provide 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, presence of snow cover and availability of feeding stations coexist in space and time, for the aforementioned management practice. Thus, considering the interplay between 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 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 Kersall 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 (Moderate-resolution Imaging Spectroradiometer) 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 meters) and temporal (eight-day periods) scale of these data may not satisfactorily fit the high local spatiotemporal heterogeneity of 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; Figure 1). Eighteen adult roe deer (four males and fourteen 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 hr intervals. The study area is typically Alpine, characterized by craggy terrain with elevations ranging from 400 m in the main valley bottoms to 3,500 m at the highest peaks. The climate is continental in the valleys while it is strongly Alpine above tree line. Based on data from 1990 to 2013, average yearly rainfall in the area is around 1,100 mm while 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 while it is deeper than 1 meter 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 1,800m) mountain pines (*Pinus mugo)* dominate, while open habitats are covered by alpine herbaceous species. Roe deer is present in the area with a density of 4.5-7.0 ind/ 100 ha, accordingly 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., pers. comm.). 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 two 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 1,000 chamois have been hunted in the same area, while 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 *vs* 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 50m 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 meters radius buffer centred on the 'used site' (Figure 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 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 S1 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 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 randomized 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 3-dimensional 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 eight-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 meters (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 meters, 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 S2). 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 modeled for dependence on predictor variables in the context of the generalised linear mixed models framework (GLMMs) 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 AIC scores (Akaike Information Criterion, 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 meters 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 KWh/m^2 ± 32.39 KWh/m^2) and distance from the closest feeding station (228.89 m ± 203.22 m). Data derived from MODIS indicated that snow cover was present in the 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% of the cases, while 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 cm ± 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:

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

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 = sex of the individual; SC = Index of Snow Cover patchiness; 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 S2 and Table 5 and 6), indicated that roe deer strongly avoided sites without forest canopy ($s = -5.208 \pm 3.612$; $w_i = 1$), characterized by high snow sinking depth ($s = -0.053 \pm 0.023$; $w_i = 1$) and far from the closest feeding station ($s = -0.003 \pm 0.001$; $w_i = 1$). Other averaged coefficients, such as snow derived from MODIS or slope, did not differ from 0 ($s = 0.162 \pm 0.292$; $w_i = 0.097$ and $s = 0.011 \pm 0.016$; $w_i = 0.653$, respectively).

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

Goodness-of-fit of the simplified model using Hosmer-Lemeshow test was satisfactory ($\chi^2 = 9.72$; $p = 0.29$). The integral of Receiving Operating Characteristics (ROC) (Figure 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 food provided in feeding stations are higher than that 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 intermediate elevations, allowed roe deer to prefer spots with absence or shallow snow (see also Guillet et al. 1996), even in 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, 5 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, pers. comm.). 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 *Odocoileus virginianus*: Telfer and Kersall 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 stations 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, while improving thermoregulation and finding hiding shelters.

Indeed, the main driver of roe deer habitat use was presence of canopy cover, not snow presence or feeding stations distribution. Topographic factors, such as terrain steepness and solar radiation, were instead not retained in the 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. While 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 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 meters 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 Moderate Resolution Imaging Spectroradiometer (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 relative low elevation range where roe deer dwelled and snow was sampled (elevation range from 700 m a.s.l 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.

TABLES AND FIGURES

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

Variable	Source & website (optional)	Type, Resolut.	Elaboration & 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/8day)	• NASA-MODIS snow • http://modis-snow-ice-gsfc.nasa.gov/MOD10A2.html	Raster, 500 m	• None • **None**

Table 2 Correlation matrix for the a priori set of covariates, chosen for their biological meaning. Relevant correlations are indicated by a star. Legend: 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

	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

Table 3 Environmental characteristics at sites used by roe deer. For continuous variables we computed the average and standard deviation while 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

Table 4 Comparison between a full model including a random effect of the individual and the same model without the random component. The percentage of variation explained by the random effect of the individual (PVR) is presented. Details are explained in Appendix S2. Legend: 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

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	

Table 5 List of the models retained by AIC model selection (ΔAIC < 2) Details are provided in Appendix S2. Legend: 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

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

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. Details are provided in Appendix S2. Legend: 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>
<tr><th colspan="4">(a) Model averaging</th></tr>
<tr><th>Covariate</th><th>Averaged estimate</th><th>Std. Error</th><th>Pred. weight</th></tr>
<tr><td>ASSD</td><td>-0,0531</td><td>0,0227</td><td>1</td></tr>
<tr><td>DFS</td><td>-0,0027</td><td>0,0008</td><td>1</td></tr>
<tr><td>CP</td><td>-5,2081</td><td>3,6114</td><td>1</td></tr>
<tr><td>SexM</td><td>0,5066</td><td>0,3568</td><td>0.486</td></tr>
<tr><td>Sl</td><td>0,0111</td><td>0,0164</td><td>0.653</td></tr>
<tr><td>CP*Sl</td><td>0,2071</td><td>0,1389</td><td>0.5</td></tr>
<tr><td>SR</td><td>0,0059</td><td>0,0049</td><td>0.368</td></tr>
<tr><td>SM</td><td>0,1615</td><td>0,2919</td><td>0.097</td></tr>
<tr><th colspan="4">(b) Simplified model</th></tr>
<tr><th>Covariate</th><th>Averaged estimate</th><th colspan="2">Std. Error</th></tr>
<tr><td>ASSD</td><td>-0.0549</td><td colspan="2">0.0216</td></tr>
<tr><td>DFS</td><td>-0.0023</td><td colspan="2">0.0007</td></tr>
<tr><td>CP</td><td>-3.0871</td><td colspan="2">0.7465</td></tr>
</table>

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

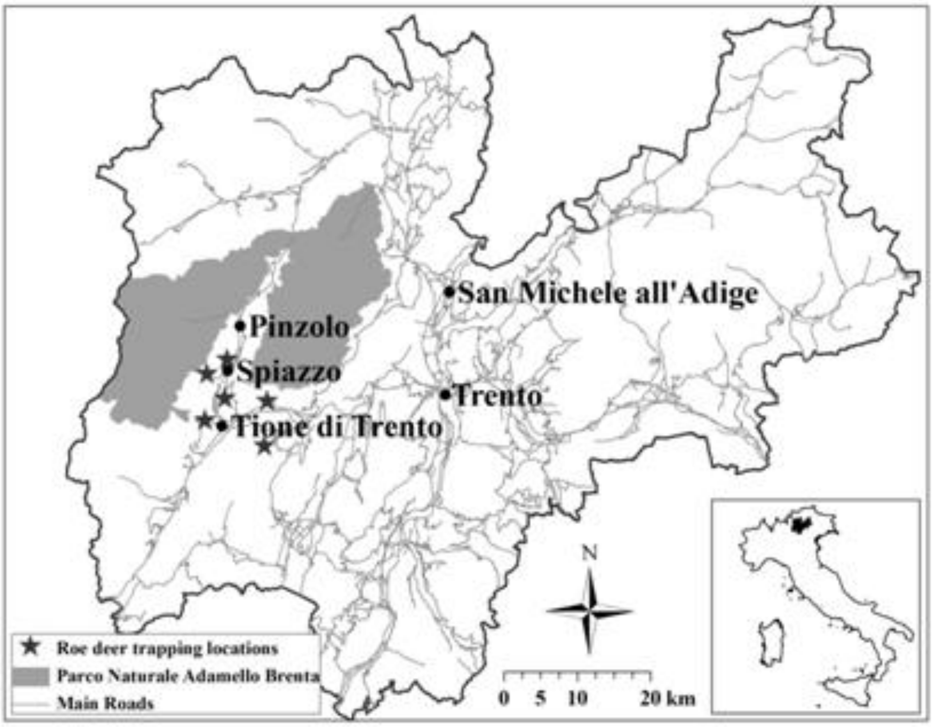


Figure 2 Scheme of the determination of the used and available sites for empirical snow sampling assessment. The size of the buffer is indicated. Filled circles represent GPS locations.

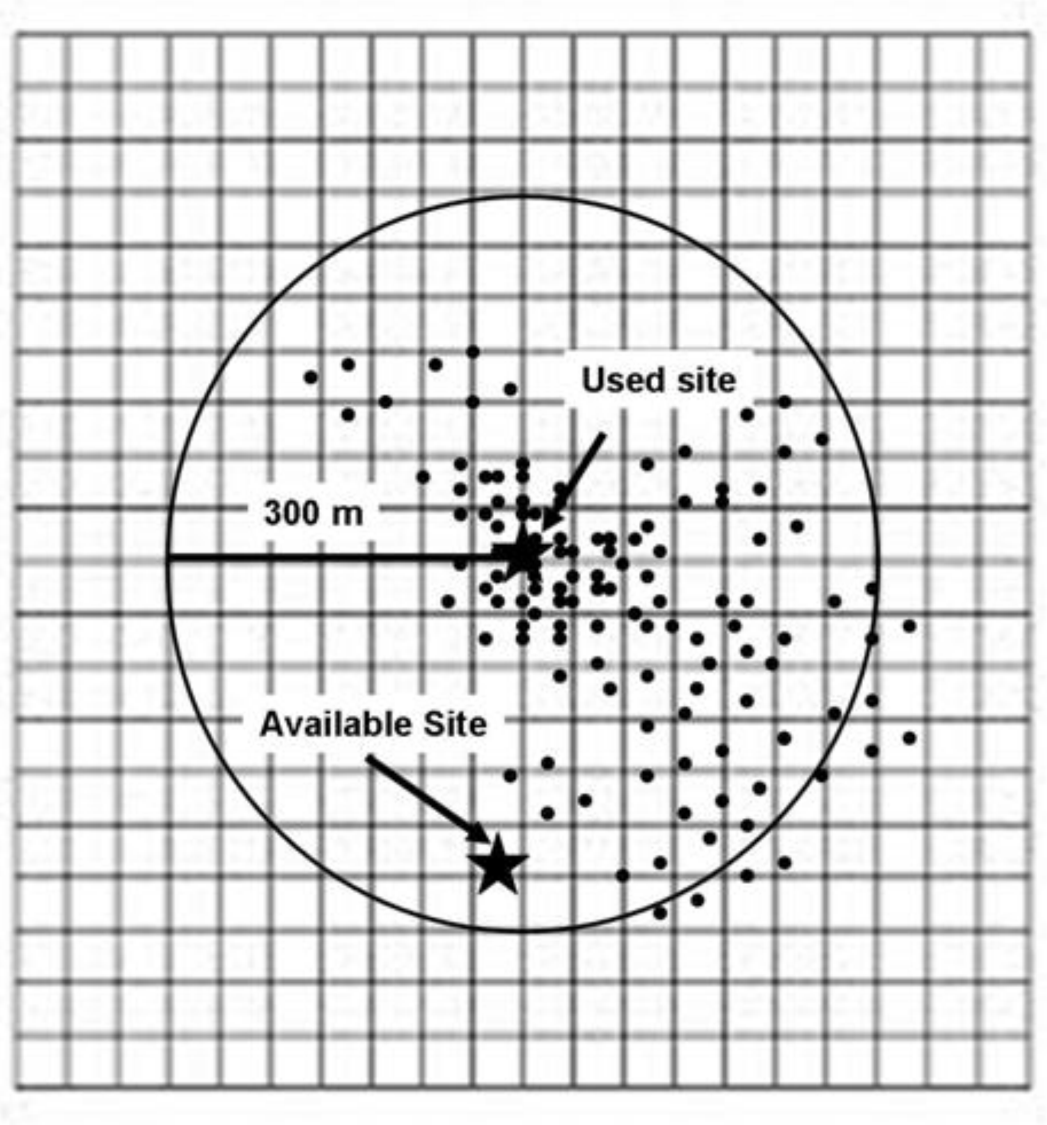


Figure 3 Distribution of used *vs* available plots of roe deer in open and closed habitats

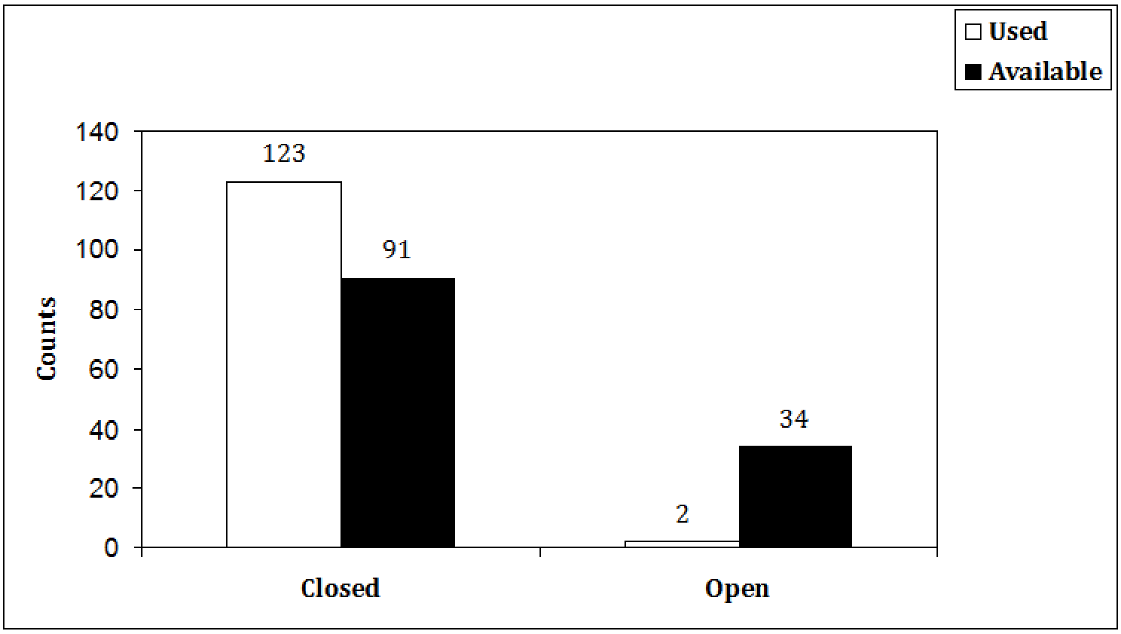


Figure 4 Partial residual plots showing the effects of average snow sinking depth (a) and distance from the closest feeding station (b) on winter resource selection in roe deer, after controlling for the effects of all other covariates in the simplified version of the model (Table 6). A partial residual plot is a plot of $r_i + b_k$ x 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.

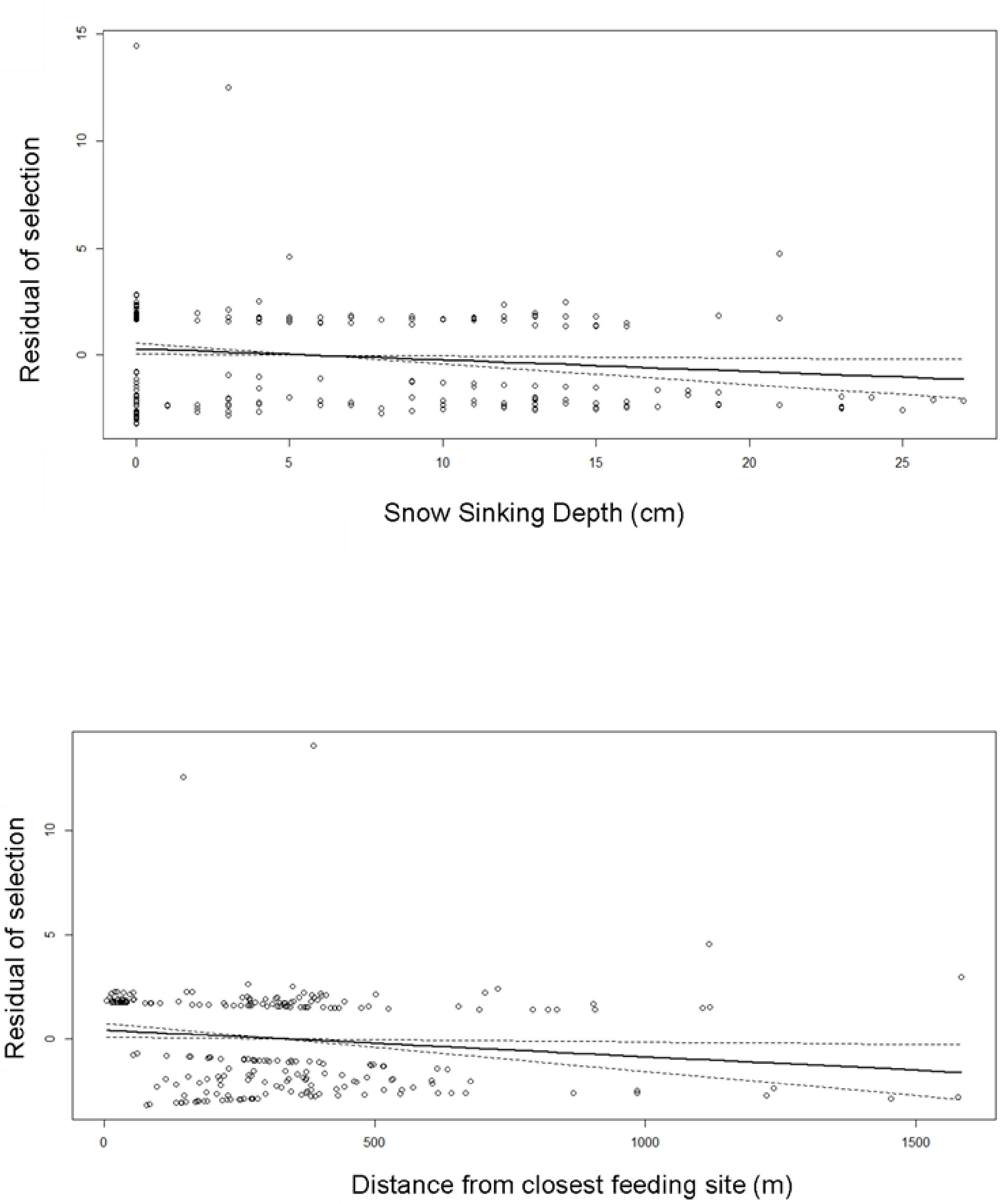
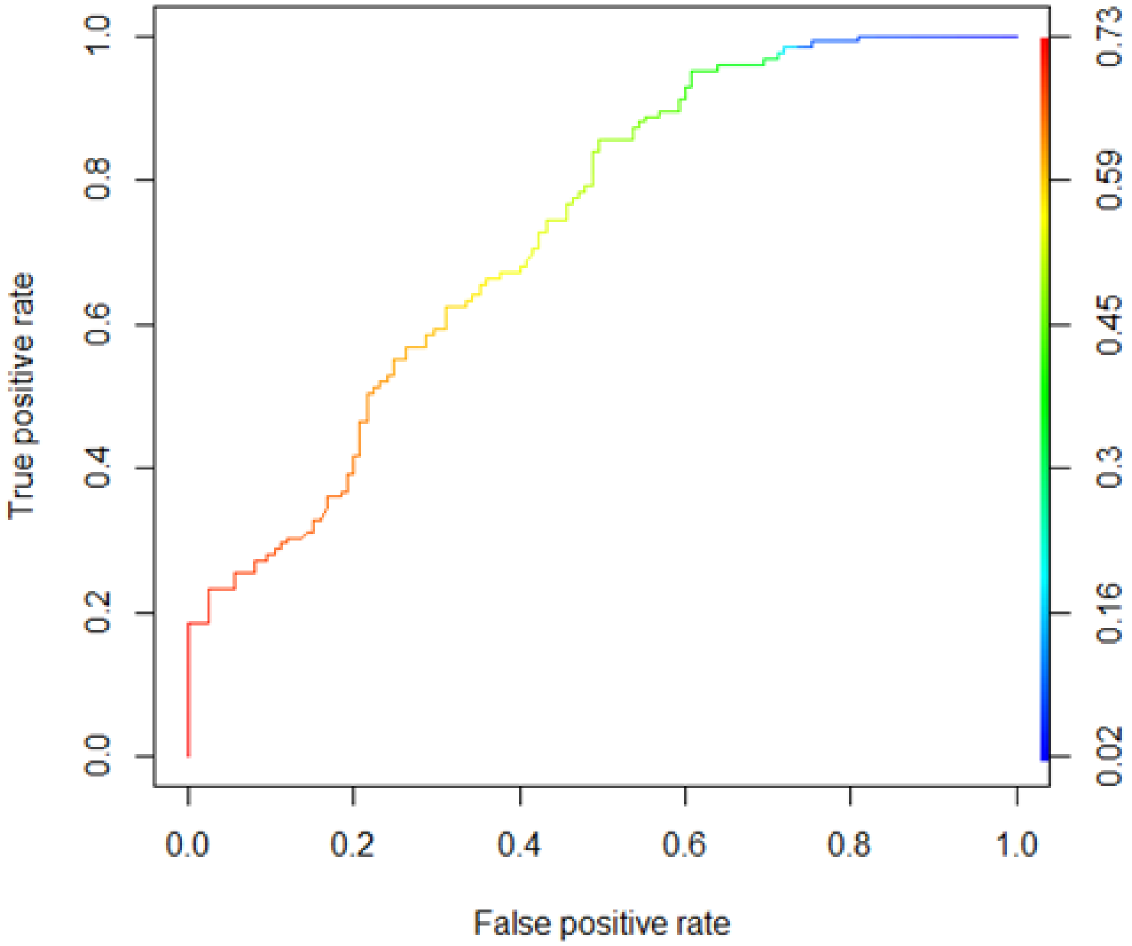


Figure 5 The Receiver Operating Characteristics (ROC) curve from the best model fit. ROC curves compare sensitivity (false negative rate) versus specificity (true positive rate) across a range of values (cut offs) for the ability to predict a dichotomous outcome. The more the specificity increases, the more sensitivity decreases (i. e. false positive rate increases). On the right bar a colour key of cut off values is shown. 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.



APPENDIX S1

Tool for empirical assessment of snow sinking depth

The battage probe (Figure 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 additonal 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); 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

(Figure 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 (Figure 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.

Figure S1.1 The penetrometer and the elements that compound it.

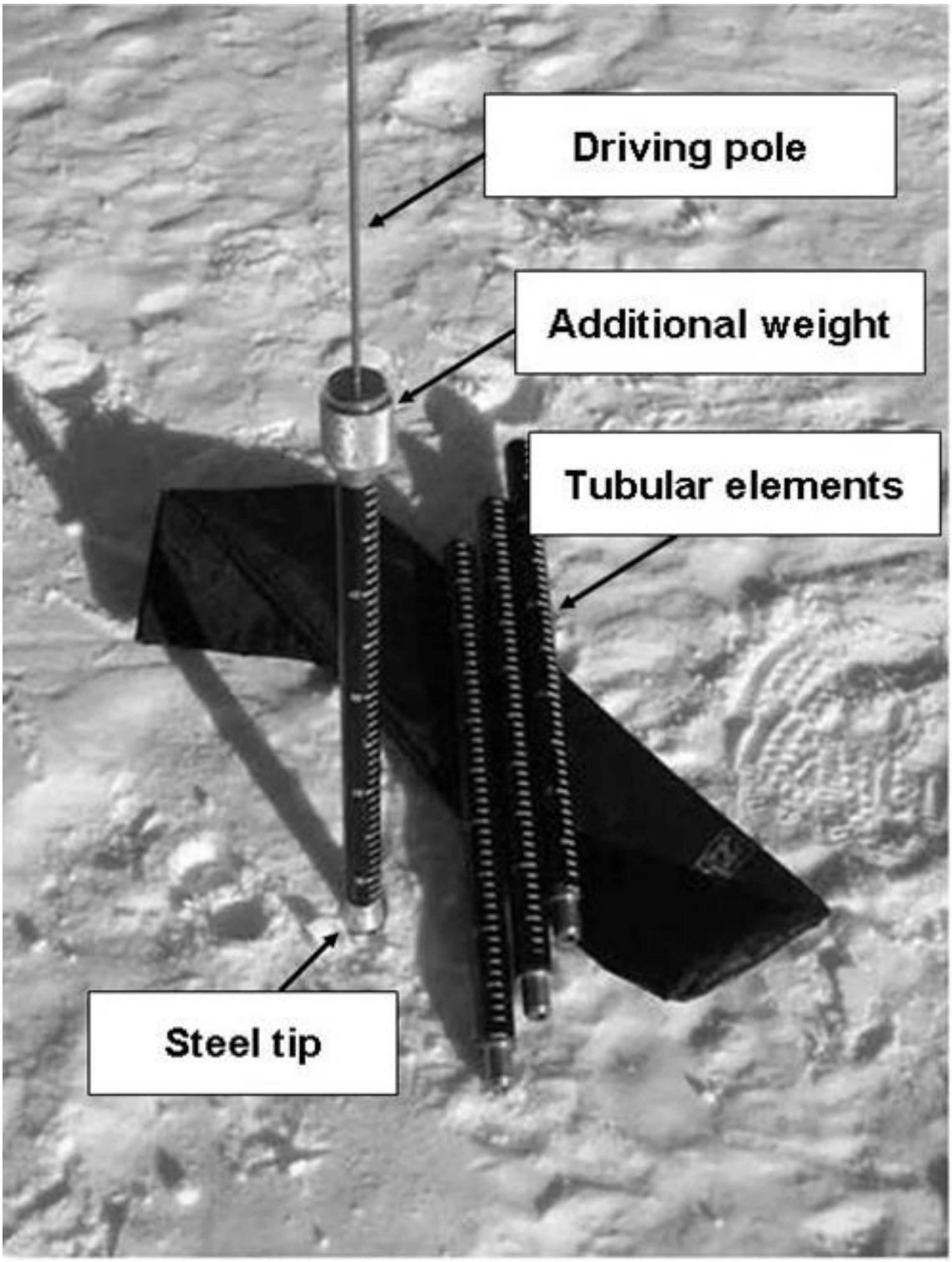
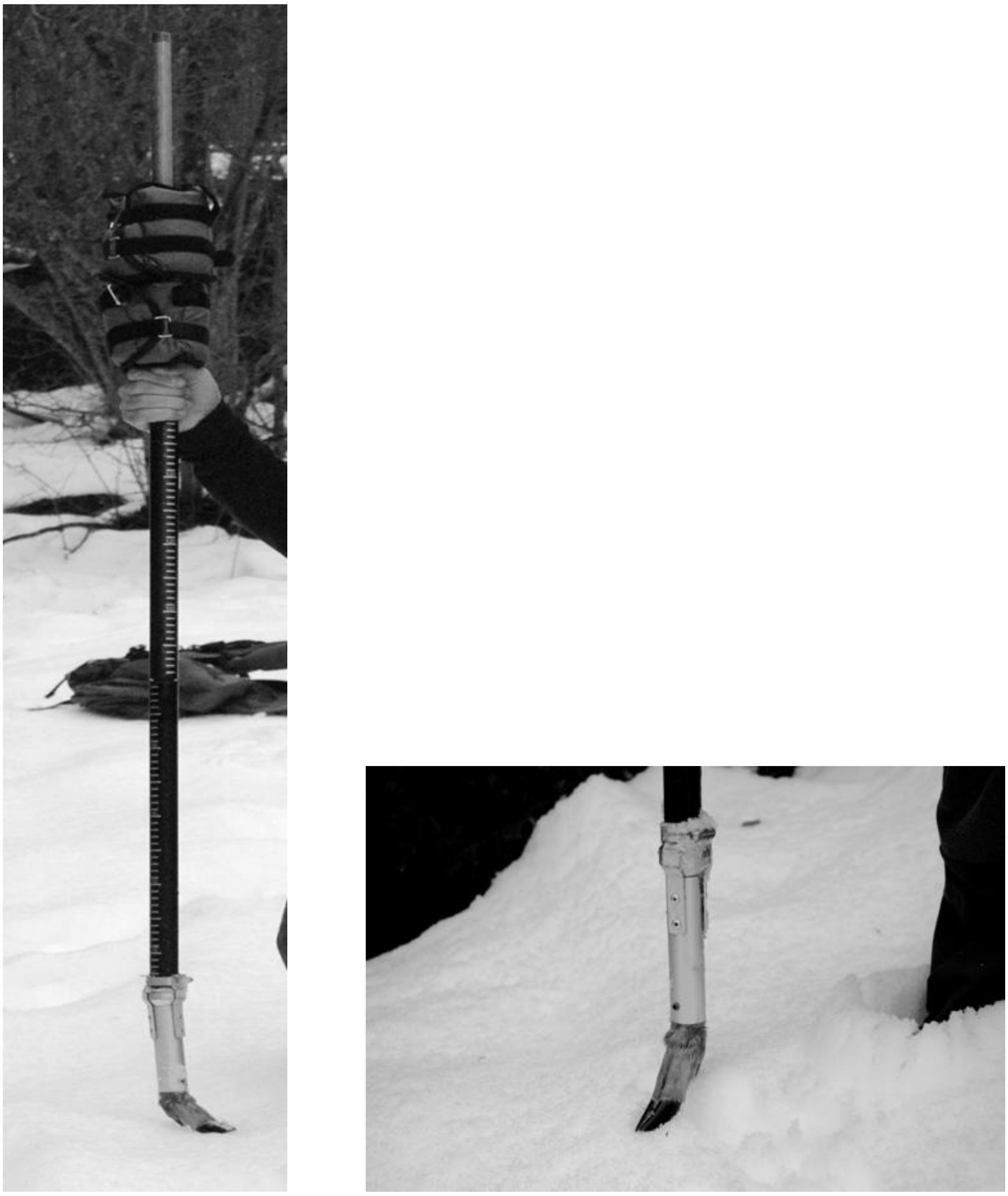


Figure S1.2 The whole penetrometer calibrated for this study (left) and the particular of the tip of the penetrometer (right).



APPENDIX S2

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; identity of the individual.

Based on the co-linearity analysis (Table 2), we retained average snow sinking depth but not average snow thickness n 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; 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 generalised linear mixed model (GLMM) including the terms above mentioned (Model random, AIC = 312.9), as well as a generalised linear model (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 thirteen 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 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).

Chapter 2.2

From roe deer winter resource selection to prediction of roe deer spatial distribution: challenges and proposed solutions to fill this gap

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ABSTRACT

Snow cover, which affects the winter distribution of several species in temperate regions, is one of the environmental factors mostly affected by fast occurring climate change. Understanding the effect of forecasted alteration of snow cover on species distribution patterns is thus a fundamental issue for the preservation of those species that cope with winter severity.

A valuable tool to investigate in this direction are predictive spatial models/maps of species distribution, whose reliability depends upon (i) the assessment of a robust predictive model of spatial distribution of the target species (e.g., a Resource Selection Function, RSF) and (ii) environmental maps of the most important predictors in the model. I investigated the potential to obtain predictive maps for an alpine population of roe deer (*Capreolus capreolus*), the movements of which are highly affected by presence and quality of snow, that in turn is undergoing deep modifications at the intermediate altitudes where roe deer overwinter.

I firstly assessed the robustness of a RSF I previously built for predicting the role of snow sinking depth and other environmental factors on roe deer winter resource selection, testing its performance in out-group by monitoring roe deer in a second winter; then I evaluated whether the replacement of snow sinking depth with snow thickness still provided a valid model to explain roe deer resource selection patterns in winter. This passage would permit to generate roe deer distribution predictive maps starting from the RSF, since snow cover predictive maps usually interpolate snow thickness instead of snow sinking depth.

I found that the model explaining roe deer winter resource selection was robust across years, in spite of relevant differences of snow conditions between the two winters. The replacement of snow sinking depth by snow thickness did not affect the goodness-of-fit of the model explaining roe deer winter resource selection.

I discuss the potential applicability of snow cover distribution models to hindcast and forecast roe deer distribution in an alpine environment, a fundamental issue to address in a period of deep environmental modifications.

INTRODUCTION

The current changes in global climate are causing modifications of species distributions, thus increasing the scientific interest for the response of species to the alteration of climate variables (Parmesan and Yohe 2003; Field et al. 2007). One of the factors that mostly concur to determine species distribution is movement, which in turn is the result of individual response to several environmental components (e.g. Johnson et al. 2002). In temperate environments, snow is one of the most important drivers of individual movement patterns in winter (Telfer and Kersall 1984). At the same time, snow is one of the environmental factors that are undergoing most dramatic modifications due to climate changing (Steger et al. 2013, O'Gorman 2014). In particular, average snow cover is constantly reducing, especially at intermediate and low elevations, whilst extreme snowfall events are less affected by climate alteration (O'Gorman 2014). In this context, using the information on forecasted modifications of snow cover to predict individual response to such alterations is fundamental to correctly preserve and manage wildlife populations.

A valuable tool to understand the effects of environmental change on species and ecosystems is to produce maps of species distribution (Franklin 2010). Species distribution modelling (SDM) include several methods that permit to spatially interpolate species distributions based on models that predict occurrence/use/selection by species wrt environmental covariates. Among those, SDM based on Resource Selection Functions (e.g. Johnson et al. 2004) are produced based on (i) the relative probabilities of selection included in the Resource Selection Function and (ii) the maps of the environmental predictors, which are used to fit the model (Franklin 1995). Therefore, the creation of an accurate predictive map depends on (i) identification of a robust model accounting for the individual distribution and (ii) reliable environmental maps of the most important predictors included in the model.

This is the case also for the evaluation of the effect of snow cover alteration on individual movement patterns. First, it is important to include in model selection for RSF sensible, or meaningful, snow-related variables. This essentially depends on a correct choice of the metric that better describes the effect of the snow cover on individual movement pattern (like e.g. snow depth, snow density, snow hardness) (Dawe et al. 2012). Ideally, the snow measurements should be highly representative of the snow layer conditions and easy to determine. Snow depth is one of the most used candidate metric for estimating snow layer conditions, but its measurements are quite often derived from meteorological stations, which are far from the animal home ranges, and thus scarcely representative of the snow layer conditions (Dawe et al. 2012). On the other side, metrics such as snow density and hardness are difficult to measure (see e.g. Lundmark and Ball 2008).

The second essential requirement for the creation of a predictive map that accounts for the effect of snow cover is the availability of an environmental map of snow cover distribution. Such maps can be generated by predictive models of snow cover. These rather complex models use as input a set of hydrologic and environmental covariates to produce as a typical output the estimate of snow cover depth of the whole snow layer, or *thickness*, at various spatial and temporal scales (see Clark et al. 2011 for a review). Therefore, since predictive models of snow cover distribution provide a measure of snow layer depth, it is necessary to assess whether this metric can indeed be a good predictor of the winter movement patterns under investigation.

In the second chapter of the thesis, I described in detail the factors that mainly drive winter resource selection in roe deer (*Capreolus capreolus*) in an Alpine environment. Among the others, I reported the importance of local measurement of snow sinking depth, which confirmed the rare attitude of roe deer to select snowy spots because of its low adaptation to move in the snow (see Holand et al. 1998). The altitudinal range at which roe deer generally set their winter ranges in the Alps is comprised between 500 and 1300 m a.s.l., i.e. the elevation range where the snow modifications are more evident because it is generally at the limit of freezing level in winter months (O'Gorman 2014). Therefore, for a maladapted species as roe deer, which has been found to depend from supplemental feeding under harsh conditions (see chapter 1 of the thesis), evaluating the effect of snow cover modifications on individual movement patterns might be particularly relevant.

According to the general framework presented above, the generation of predictive maps of roe deer distribution in an Alpine area would require the determination of a robust model accounting for roe deer winter resource selection. This model should include snow layer depth instead of snow sinking depth as the term accounting for the effect of snow cover on the pattern found. In fact this replacement would then permit to apply predictive models of snow cover distribution (see more in the Discussion). I looked for assessing the robustness of the model described in chapter 2.1 and to evaluate whether the replacement of snow sinking depth with the snow layer depth of the snow layer still allow predicting reliably the effect of snow on roe deer resource selection patterns. More specifically, I took advantage of the data collected in a second winter field campaign in the same area, to evaluate first whether the pattern found in winter 2012/2013 was robust across years. In this respect I predicted to find no detectable difference in roe deer resource selection between the two winters. Then, I assessed the effect of replacing measurement of snow sinking depth with the snow layer depth (i.e. the depth of the whole snow layer) in model predictions of winter roe deer resource selection. Since there are clear evidence that snow sinking depth and snow cover depth are often correlated (e.g. Lundmark and Ball 2008), I expected that snow layer depth could efficiently replace snow sinking depth as determinant of roe deer winter resource selection.

Lastly, based on the outcome from previous investigations, I looked for determining a threshold of snow tolerance for roe deer, i.e. a value of snow depth above which roe deer does not go, which might be useful to predict roe deer distribution in space and time in relation to snow cover alteration (see Discussion for more details).

MATERIALS AND METHODS

During the winter 2013/2014 we captured 9 adult roe deer that were equipped with GPS collars. These individuals combined with those captured in winter 2012/2013 led to a total sample of 22 animals (14 females and 9 males). Roe deer resource selection was assessed exactly the same way as in previous winter (see chapter 2 for a detailed description). Globally, 370 used and available matching sites were assessed for local variables during the winter 2013/2014, adopting the procedure described in detail in the chapter 2.

Testing the robustness of the model across years

I firstly explored the distribution of snow sinking depth between the two winter seasons at the sites available but not used, which are likely more representative of the general snow conditions of the area. Then, I modelled the linear dependence of snow sinking depth *vs* winter seasons (2012/2013 or 2013/2014). Lastly, I performed an external validation of the model obtained with the data of winter 2013/2013, using the data of winter 2013/2014 as an out-group.

Replacing snow sinking depth with snow layer depth to spatially predict the effect of snow on roe deer winter resource selection

As a first step, I explored the correlation between snow sinking depth and snow layer depth for both winters, by means of graphical plots and correlation tests. Since the correlation between snow sinking depth and snow layer depth was high (see Results) I decided to retain for further analysis the latter as a predictor of the snow effect.

Thus, I analysed roe deer winter resource selection in winter 2013/2014. I identified the final model by means of a procedure analogous to that described in the chapter 2.1. I firstly chose an *a priori* list of variables based on our biological knowledge, and I checked for possible co-linearity using a scatterplot matrix and correlation tests. I accounted for co-linearity patterns fitting two-way interactions between co-linear terms.

I fitted a logistic regression within a generalized linear model (GLM) framework (Hosmer & Lemeshow, 2000) to assess the winter resource selection of roe deer. 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). I 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). I ran a model selection based on AIC scores (Akaike Information Criterion, Burnham and Anderson 2002) on all possible models derived from a full model including the covariates retained. I then obtained a final model averaging the weighted coefficients of the models with $\Delta AIC<2$. In parallel, I decided to simplify the model in accordance with the principle of parsimony, selecting those covariates that were included in all models with $\Delta AIC<2$ (i.e., predictor's weight=1). I then fitted a General Linear Mixed Model (GLMM) with the same framework of the simplified model and the individual as random effect, to evaluate the importance of the inter-individual variation in the pattern found. Since this effect was not statistically significant (see Results), I operated model validation on the simplified general linear model as in the classic Resource Selection Analysis framework (Boyce et al. 2002). In particular, I assessed the goodness-of-fit of the model by means of classification table, Receiving Operating Characteristics (ROC) and internal k-fold cross-validation. I further assessed the robustness of the model by means of an external validation, using the data collected in the previous winter (2012/2013) as out-group (Boyce et al 2002). Lastly, I assessed whether the pattern accounted for by the simplified model was consistent across years. To do this, I added the winter season as fixed dummy covariate (winter

2012/2013 or winter 2013/2014) in the simplified model, which I then fitted to a unique dataset including the data of both the winter campaigns. I evaluated the significance of the predictive power of the winter in explaining roe deer winter resource selection.

Assessing a threshold of snow layer depth tolerance for roe deer

I firstly computed the predicted values of the model of roe deer winter resource selection obtained with the data of the winter 2013/2014. I then chose the optimal cut-off value that maximized the sensitivity and specificity of the model, i.e. which more correctly classified the predicted 1 and 0 values with respect to the observed ones. Based on several trials, I selected 0.5 as the cut-off value. I used this threshold to reclassify the predicted values of the model in 0 and 1; in other words, the predicted values lower than 0.5 were reclassified as 0 (i.e. available locations), whilst those higher than 0.5 were reclassified as 1 (i.e. used locations). At this stage, I analysed the percentile distribution of snow layer depth only at the reclassified used sites, and discarded the records where snow cover was absent. I chose these conditions because I was interested in assessing the threshold of snow cover at the sites that roe deer actually used; moreover the inclusion of the records of used sites without snow would have biased leftward the distribution of snow cover, leading to erroneous conclusions. I was not looking for the *average* snow layer depth used by roe deer, but the tolerated *threshold* of use. I assumed as threshold value of tolerance the 95th percentile of snow layer depth distribution, to exclude the most extreme cases that might overestimate the threshold of tolerance for the individuals. Lastly, I replaced in the simplified model the snow layer depth variable with the new dummy covariate ‘snow tolerance’, which was obtained by reclassifying the snow layer depth in ‘tolerable’ or ‘excessive’ accordingly to the determined threshold of snow tolerance. I assessed whether this covariate was still a statistically significant predictor of pattern of roe deer winter resource selection.

The whole procedure was then repeated using the data of the winter 2012/13.

RESULTS

Testing the robustness of the model across years

The trend of snow sinking depth distribution at available but not used sites was similar between the two winters, although the absolute values were different (the winter 2013/2014 was more snowy than the winter 2012/2013) (Figure 1). In support of this, I did not find any statistically significant effect of the winter on the pattern of snow sinking depth. The validation of the model describing the pattern of winter resource selection by roe deer demonstrated the robustness of the model found (rho=0.842 p=0.004).

Replacing snow sinking depth with snow layer depth to spatially predict the effect of snow on roe deer winter resource selection

The inspection of co-linearity patterns between snow sinking depth and snow layer depth showed that the correlation was higher in winter 2012/2013 (Spearman' coefficient = 0.953 $p=2.2*10^{-16}$) than in 2013/2014 (Spearman' coefficient=0.58 $p=5.81*10^{-12}$) (Figure 2). However, the correlation was still high, such permitting to replace snow sinking depth with snow layer depth for the following analyses.

The correlation analysis of the *a priori* selected covariates (Table 1) led to the identification of a full model based on the data of winter 2013/2014, which included a two-way interaction between the distance from the closest feeding station and sex, a two-way interaction between canopy presence and terrain slope, and main effects of snow layer depth and solar radiation.

Based on the multi-model inference approach, I retained a model indicating that roe deer avoided sites without canopy presence (s = -1.88 ± 0.41), where snow layer depth is high (s = -0.02 ± 0.01) and far from feeding stations (s = -0.002 ± 0.001), especially in females (interaction between sex (male) and distance from closest feeding station: s = 0.002 ± 0.001) (Table 2). The averaged coefficients of solar radiation and terrain slope did not result statistically differed from zero (solar radiation: s = 0.001 ± 0.004; terrain slope: s = - 0.008 ± 0.01).

The simplified version of the model with covariates with w_i = 1 included snow layer depth (β = - 0.01 ± 0.007), canopy presence (β = - 1.87 ± 0.41) and the two-way interaction between sex and the distance from the closest feeding station (β = 0.002 ± 0.001). The coefficients in this simplified model did not change in sign or magnitude with respect to the averaged coefficients showed above (Table 2). The individual identity fitted as a random effect did not improve the goodness-of-fit of the model (AIC model with random effect: 475.2; AIC model without random effect: 473.2), and was not retained for the rest of the analyses.
The validation of the simplified version of the model supported the model selection performed: classification table (with a cut-off equal to 0.5) indicated that the model rightly classified the 63% of the data, and the integral of Receiving Operating Characteristics (ROC) indicated that the model fitted satisfactorily the data (ROC value = 0.71) (Figure 3). Both the internal k-fold cross-validation (rho = 0.8, p = 0.02) and the external validation with the data of winter 2012/2013 as out-group (rho = 0.79, p = 0.006) showed the robustness of the selected model.

When the simplified model was fitted to the data of both field campaigns I could not detect any statistically significant effect of the winter on the pattern of roe deer winter resource selection.

Assessing a threshold of snow layer depth tolerance for roe deer

Both for models of winters 2012/2013 and 2013/2014 I reclassified the predicted values based on a cut-off threshold of 0.5. The distribution of snow layer depth at used and available sites, for both the winters, is shown in Table 3. Winter 2012/2013 was less snowy than winter 2013/2014: the 95th percentile of snow thickness at used sites was equal to 16 centimetres in the first winter and 27 centimetres in the second one. Even at available sites, the differences between the two winters were relevant, with the 95th percentile of snow thickness equal to 50 centimetres in winter 2012/2013 and 85 centimetres in winter 2013/2014. The dummy covariate 'snow tolerance' resulted to be highly statistically significant both for the model fitted to the data of winter 2012/2013 ($\beta = 1.45 \pm 0.48$) and for that fitted to the data of 2013/2014 ($\beta = 0.73 \pm 0.43$).

DISCUSSION AND PERSPECTIVES

This work clearly evidenced that the ‘environmental package’ including snow cover, presence of a canopy and, at a lesser extent, the proximity to feeding stations (although in interaction with the sex of the individuals), drives roe deer winter resource selection in an alpine environment exposed to artificial feeding. This evidence is further supported by the robustness of the model across two winters, in spite of consistent differences in terms of snowfalls.

A relevant difference with respect to the model accounting for roe deer winter resource selection described in the chapter 2.1 is the importance of the interaction between the distance from the closest feeding station and the sex of individuals. I argue that the lack of statistical significance of this interaction in winter 2012/2013 was due to the highly unbalanced sex ratio of radio-tracked individuals (4 males and 14 females) captured in the first winter. I can hypothesize that the tendency of females to select sites closer to feeding sites might be related to the energetic needs of accompanying fawns. This matches the outcome of the capture campaign (‘Material and Methods, Section 2’), where females and fawns were by far the most captured and re-captured individuals.

This work also showed that snow layer depth can be clearly used to assess roe deer winter resource selection. In the chapter 2 I discussed in detail the issues in relation to the difficulty of measuring the effective snow sinking depth of roe deer. In winter 2013/2014, snow cover was more abundant, and consequently the differences between the snow sinking depth and the global snow thickness should be more pronounced. Our finding of a lower correlation between the two snow condition measurements confirms this idea, but probably the overall snow cover in the study area was not deep enough to clearly separate the two measurements. Although I have no evidence in this direction, I might hypothesize that in extremely snowy environments the measurement of snow sinking depth more realistically depicts animal movement patterns. However, roe deer in winter generally move towards areas where snow cover is not too deep. In this regard, the assessment of the effect of snow on roe deer winter movement patterns can be effectively carried out by measuring the snow layer depth instead of its sinking depth. Based on these considerations, I might argue that the determined threshold of snow tolerance of 27 centimetres found in the more severe winter is probably close to the acceptable limit for this ungulate. Roe deer chest height is around 40 – 50 centimetres (Holand et al. 1998), close to the maximum snow depth that I found at used sites. However, it is reasonable to expect that roe deer can deal with such a deep snow layer only in the most limiting situations (e.g. immediately after a snowfall), whilst it generally prefers to select spots where snow cover is less abundant and permits to reduce costs of locomotion.

Our finding that snow layer depth well explains the roe deer winter resource selection opens the exciting scenario of applying snow cover predictive models to extrapolate predictive maps of roe deer spatial distribution. In particular, I aim at using a recently developed snow predictive model, GEOTOP (Zanotti et al. 2004), after assessing the quality of its predicted snow estimates by means of an accurate calibration based on our empirical assessment. The identification of the snow thickness threshold might permit to simplify snow cover maps in categorical maps defining the suitability of a given location for roe deer. Concerning the other two main drivers of roe deer winter resource selection, i.e. presence of a canopy and distribution of feeding stations, land use maps (CORINE) are available to spatially assess the presence of a canopy, and maps on the distance of each point from the closest feeding station in a given area can be extrapolated from a map on the distribution of feeding stations within a given area (see chapter 2 for technical details). The interpolation of these three maps would allow to extrapolate the 'optimal overwintering areas' for roe deer at any desired spatial scale for which these data are available.

A second and even more exciting perspective is to predict roe deer distribution in relation to the spatiotemporal modification of its winter environment, which is especially due to the alteration of snow cover in relation to climate change (Steger et al. 2013). There are two main ways to explore this issue: first, one could hindcast roe deer spatial distribution according to the past environmental conditions. Assuming that canopy presence and feeding station management were stable over years, maps of snow cover of last winters would be required to investigate in this direction. GEOTOP provides such maps, taking advantage of available long-term environmental and meteorological data series. A second and not mutually exclusive approach is to forecast roe deer spatial distribution, keeping the same assumptions on canopy and distribution of feeding stations, and applying forecasted snow cover maps estimated by the GEOTOP model. The use of one or a combination of these approaches might permit to understand the ecological response of this species to the ongoing climatic changes, and might be relevant to manage properly Alpine populations of roe deer in the future.

TABLES AND FIGURES

Table 1 Correlation tests performed on an *a priori* list of variables based on our biological knowledge. The correlation coefficients for the covariates which were fitted as two-way interactions in the model are reported in bold. Legend: DIST: distance from the closest feeding station, ST: average snow thickness (snow layer depth), CAN: canopy presence, SL: terrain slope, SR: solar radiation, SEX: animal sex.

	DIST	**ST**	**CAN**	**SLOPE**	**SR**	**SEX**
DIST	1	-0.06	0.08	-0.12	-0.04	0.39
ST	-0.06	1	0.17	-0.22	-0.12	0.02
CAN	0.08	0.17	1	-0.29	0.01	-0.04
SL	-0.12	-0.22	**-0.29**	1	-0.03	0.03
SR	-0.04	-0.12	0.01	-0.03	1	0.01
SEX	**0.39**	0.02	-0.04	0.03	0.01	1

Table 2 (a) Weighted averaged coefficients and standard errors of parameters estimated in the 11 models retained by AIC. The predictor's weight of each term is provided. (b) Coefficients and standard errors of the covariates retained in the simplified version of the model (w_i = 1). Legend: DIST: distance from the closest feeding station, ST: average snow thickness (snow layer depth), CAN: canopy presence, SL: terrain slope, SR: solar radiation, SEX: animal sex, DIST*SEX: two-way interaction between distance from the closest feeding station and sex.

(a) Model averaging

Covariate	Averaged estimate	Std. Error	Pred. weight
DIST	-0.002	0.001	0.42
ST	**-0.02**	**0.01**	**1**
CAN (open)	**-1.88**	**0.41**	**1**
SL	-0.008	0.01	0.28
SR	0.001	0.004	0.18
SEX (male)	-0.58	0.41	0.36
DIST*SEX	**0.002**	**0.001**	**1**

(b) Simplified model

Covariate	Averaged estimate	Std. Error
DIST	-0.002	0.001
SEX (male)	-0.59	0.41
ST	-0.02	0.01
CAN (open)	-1.87	0.41
DIST*SEX	0.002	0.001

Table 3 Percentiles of snow layer depth at used and available sites in winter 2012/2013 and 2013/2014.

	Used 2012/2013	Used 2013/2014	Avail. 2012/2013	Avail. 2013/2014
0	2	1	1	1
5	3	2	3	5
10	3	3	5	7
15	3	4	6	11
20	3	5	7	12
25	4	6	9	14
30	4	6	10	17
35	5	7	11	19
40	6	8	13	21
45	6	9	13	24
50	7	10	14	26
55	8	10	14	30
60	8	11	15	33
65	8	13	18	36
70	10	13	19	42
75	11	15	21	44
80	12	16	23	50
85	13	21	26	53
90	16	22	36	65
95	16	27	49	85
100	20	44	69	100

Figure 1 Frequency distribution of the snow sinking depth during winter 2012/2013 (left) and 2013/2014 (right).

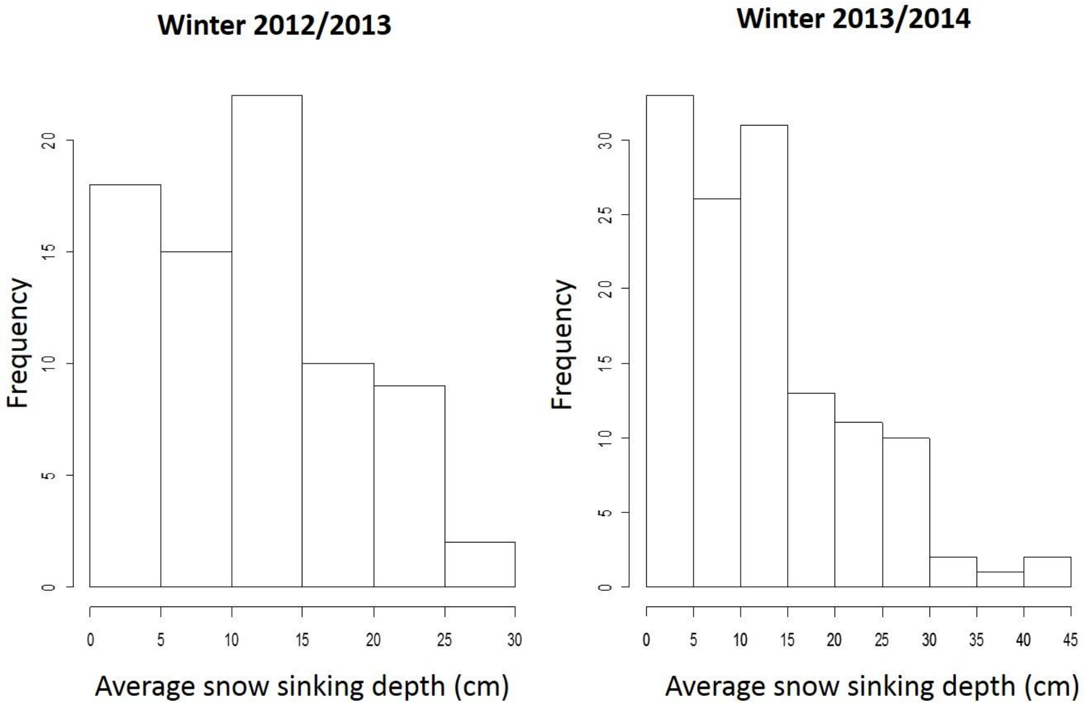


Figure 2 Correlation plot between snow sinking depth and snow thickness (snow layer depth) in winter 2012/2013 (left) and 2013/2014 (right).

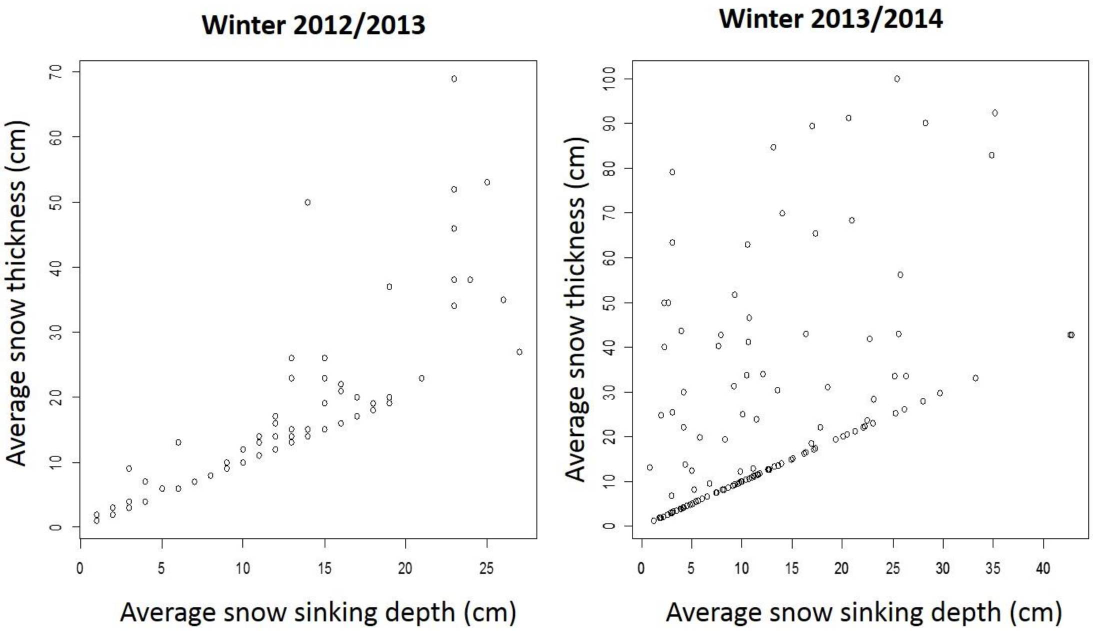
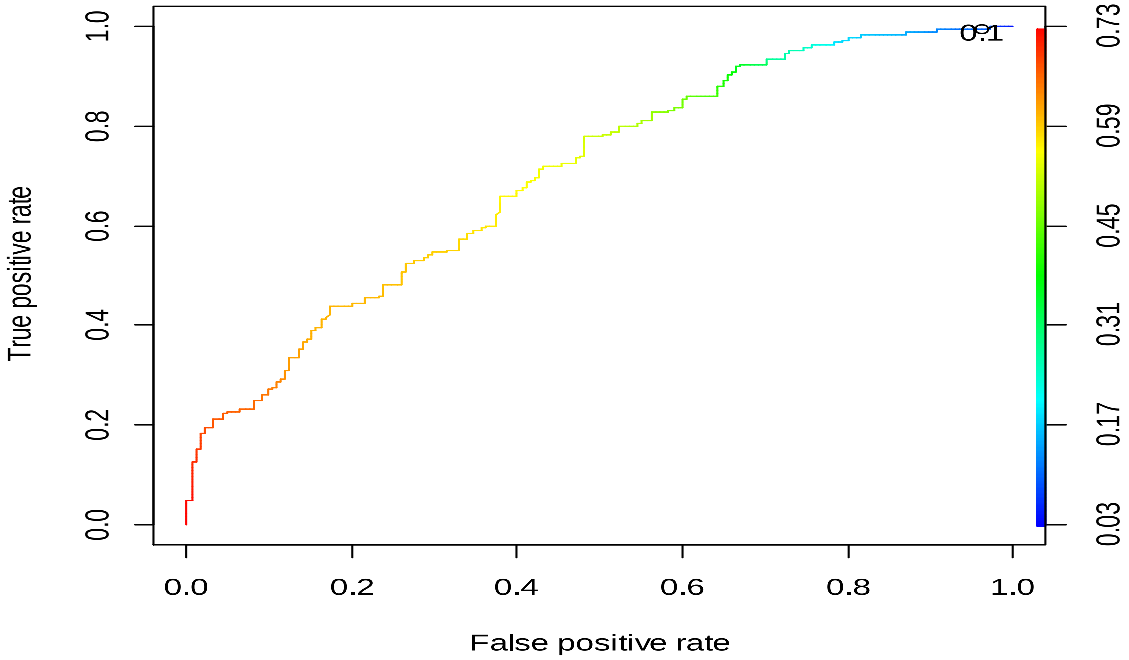


Figure 3 ROC curve



CHAPTER 3.1

Connect to contacts: accounting for proximity detection error by proximity loggers in studies of animal ecology

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ABSTRACT

1. Proximity loggers have been recently introduced in animal ecology for the assessment of spatio-temporal contacts between individuals, a variable providing valuable information for a diversity of research fields, such as disease transmission or social interactions. However a detailed investigation of the errors associated with contact detection and of the factors which influence the reliability of these systems does not go hand in hand with their increasing application, risking to hinder the associated ecological inference.

2. We aimed to measure the bias of contact detection through radio transmission and in particular to quantitatively evaluate the effect of the radio transmission power on detection distance, while accounting for potentially disturbing factors.

3. We performed a comprehensive analysis of contact detection on a new proximity logger based on Wireless Sensor Network technology (Wildscope), compared to commercial loggers (Sirtrack Ltd.). We evaluated contact detection patterns in scenarios of increasing complexity, from controlled settings to experiments on animals in semi-wild conditions (horses and deer). We also tested the integration of contact detection with GPS technology, a novel feature available in Wildscope, with the potential to reconcile movement ecology and social network studies.

4. Under controlled conditions, a reduction of the radio transmission power and the height of sensors from ground limited the range of contact detection both in Wildscope and Sirtrack loggers, although the range of contact detection resulted significantly higher for the former logger type. Both the experiments on horses and deer confirmed the expected inverse relationship between radio transmission power and the contact distance. However, in semi-wild conditions the probability of contact detection at a certain distance never reached 1, whereas the probability of unexpected contacts beyond a certain distance increased with the power of transmission. We were able to measure the precision of proximity loggers set at a

certain radio transmission power at a desired distance of reference, in the semi-wild settings used for the experiment.

5. Proximity loggers represent a valid tool for the investigation of contact patterns in animal ecology. However, the relation between radio transmission power and distance by no means can be considered deterministic, since it is influenced by a complexity of physical factors, especially in wild settings. We recommend that the users of proximity loggers would validate the instrument on the target species and typical study settings, to account for the bias when investigating the biological patterns of interest. The integration of GPS and proximity systems, that proved highly reliable, opens up interesting avenues of research.

Key words: proximity pattern, calibration, biologging, bio-telemetry, animal ecology, GPS, false positive and false negatives.

INTRODUCTION

In ecology, the concept of contact is defined as spatial and temporal proximity of two agents. In general terms, two agents are defined 'in contact' when they are located at or below a threshold distance, within a defined interval of time, without necessarily coming in physical touch (Cross et al. 2012). For example, for diseases transmitted through contaminated faeces, a contact might be defined as the interaction of susceptible individuals with dejections, before infective pathogens decay (Creech 2011). In this case, a physical synchronic contact between infected and susceptible individuals is not required, but a very high spatial overlap is necessary. Alternatively, an ecological interaction such as prey stalking by predators implies a elevated temporal synchronisation, but a high physical spatial separation with the prey can be kept as a predatory tactic. Instead, a direct social interaction may involve both spatial proximity and temporal synchronisation, such as mating or parental care (but interaction based on scent marking does not). Typically, our definition of contact does not imply awareness of agents in establishing a spatial or temporal correlation.

One decade ago proximity loggers have been introduced in animal ecology research (Ji et al. 2005). The application of proximity loggers to animals is part of the 'biologging revolution' (Ropert-Coudert and Wilson 2005), a discipline taking advantage of technological advancements and miniaturisation to measure individual state and environmental variables by means of animal-borne devices (Cooke et al. 2004; Ropert-Coudert et al. 2009; Cagnacci et al. 2010). Proximity loggers directly detect contacts and acquire related parameters, such as the duration of the interaction. This technological innovation has the potential to prompt a big leap in the formalisation of social and ecological interactions, since proximity loggers allow to measure contacts as a quantifiable variable without relying on an external observer (Krause et al. 2013). In particular, an appropriate use of such devices requires 1) the reliable identification of the connecting individuals; 2) a clear definition of the threshold distance to define a contact event and 3) the setting of the minimum permanence within such threshold to detect a contact. Thus, a contact can be exhaustively described by three variables: the identification of connecting individuals, the distance at which the contact occurs and the duration of the contact itself.

The main technology which has been used so far to integrate proximity detection into animal devices is based on Wireless Sensor Networks, WSN (Yick et al. 2008). WSN are spatially distributed systems composed by loggers (*nodes*) able to communicate one to each other in a network by means of radio transmission which work on Ultra High Frequency (UHF, range 300 MHz - 3 GHz). WSN are typically associated to sensors, that have been used to monitor a variety of physical and environmental variables (e.g., air quality, forest fires). In WSN, the node computational module is a programmable unit that provides computation, storage, and bidirectional communication with other nodes in the system (Polastreet al. 2004). Therefore, WSN offers a major advantage as contact data logging systems, i.e. the communication between nodes is controlled by instructions embedded in the programmable unit. Altogether these characteristics render WSN proximity loggers particularly suitable for investigating proximity detection for wildlife. So far, proximity loggers (mainly from Sirtrack Ltd., Havelock North, New Zealand) have been used to address a variety of themes in animal ecology, such as intraspecific social systems (e.g. Prange et al. 2011; Marsh et al. 2011; Vander Wal et al. 2012; Rutz et al. 2012), disease transmission patterns (e.g. Ji et al. 2005; Böhm et al. 2009; Hamede et al. 2009), predation events (e.g. Tabling & Benton 2009) or mother – offspring interaction (e.g. Swain and Bishop-Hurley 2007). Other applications of WSNs include their use to facilitate retrieving of location data (e.g. ZEBRANET, Zhang et al. 2005).

Another interesting specific feature of WSN loggers is that they can include both ‘static’ and ‘mobile’ nodes, since the communication mode among both types is functionally identical. Therefore, ‘mobile nodes’ (i.e., loggers deployed on mobile agents, such as animals) can communicate with a fixed network deployed in the environment, opening even further exciting perspectives of ecological research. Traditionally, habitat preference by animals has been related to the proportion of time spent in habitat types with respect to their availability (Johnson 1980; Boyce and McDonald 1999). However, visits of animals to specific focal habitats may be important *per se*, and not necessarily correlated to the proportion of time spent at them. Examples include drinking bouts at water holes, denning, or feeding at winter supplementary stations. This type of habitat use has been largely overlooked, probably as a consequence of technical constraints to observe it (but see Rovero et al. 2014 for the use of camera traps to model habitat preferences). Early works on proximity loggers indeed foresaw the potential of these systems to measure the use of focal habitats by marked animals in a controlled and reproducible manner (Prange et al. 2006).

Last but not least, very recent engineering attempts have juxtaposed GPS technology with proximity loggers (Rutishauser et al. 2009; Anthony et al. 2012), although currently these two technologies are not properly 'integrated', i.e. they work autonomously in parallel. The development of a system that couples contact data and spatial locations would bridge this gap, providing ecologists valuable information on 'motivations' to move or, vice versa, on the 'movement patterns' underpinning ecological interactions (Lavelle et al. 2014). In other words, the integration of GPS-based telemetry and proximity loggers may enhance the understanding of movement ecology of target species (Nathan et al. 2008).

However, the researcher aiming to exploit the advantages of proximity loggers shall also consider potential drawbacks. For example, the application of proximity loggers is limited to assess synchronic contacts. Most importantly, proximity loggers are based on specific technologies, which are subject to stochastic effects and thus errors and bias in the derived measures (e.g. Boyland et al. 2013; Drewe et al. 2012; Lavelle et al. 2014). Indeed, a fundamental step for transferring a technology to scientific or applied purposes, is the measure of error and recognition of factors influencing reproducibility and reliability of measures (e.g. Cross et al. 2012). In animal ecology, this was the case in the recent past for GPS technology: the initial enthusiasm for its application, as early as in the 90's (Rodgers et al. 1996), was moderated by subsequent work assessing potential bias in its use, especially for habitat selection studies (Frair et al. 2010). Even if all these technologies provide to biologists devices to address specific ecological relevant issues, the information on the quality of the data provided does not keep pace with their increasing application. A correct evaluation of the reliability of the contact detected is of uttermost importance to derive proper conclusions on the biological system under examination. As noticed above, the measurement of contacts by proximity loggers technically corresponds to transmission and receiving of radio waves. As such, occurrence, distance and duration of contacts shall depend mainly on the intrinsic settings of the radio used, and especially the power of transmission. Remarkably, the few studies assessing proximity loggers performance, did not focus on this issue (Prange et al. 2006; Drewe et al. 2012; Boyland et al. 2013). In addition, it is a known fact that radio transmission depends on the mean where radio waves propagate, including effects of obstacles. Therefore, the environmental context can add noise to contact detection which can become substantially different than in ideal and perfectly controlled settings (Marfievici et al. 2013).

Here, we aimed at modelling contact detection distance in relation to radio transmission power. To account for the environmental noise, we conducted tests in scenarios of increasing complexity referable to terrestrial mammals of mean-large size (i.e.: controlled open-air situation; simulated situation of animal movement; observation of domestic animals in semi-controlled settings; deployment on wildlife species in semi-controlled settings). Transmission noise introduces variability in the modelled system. As such, one could observe 'false positive' events, i.e. contacts happening at larger distance than expected, or 'false negative' events, i.e. missing contacts when expected at a certain distance. Therefore, we further modelled the probability of detection at a certain distance in dependence of radio transmission power. Then, we modelled the precision of our system in all the consider settings.

To do so, we used a prototype of WSN proximity loggers (Wildscope), comparing the output, where possible, with commercial proximity loggers (Sirtrack Ltd). Finally, we reported a first description of the functionality of GPS and proximity loggers integrated.

MATERIAL AND METHODS

In this work we tested Wildscope contact loggers performance in a sequence of tests of increasing complexity, from baseline assessment of connectivity in a controlled situation, to deployment on model species in a semi-wild setting. We compared the baseline performance (i.e. in controlled settings) with commercial proximity loggers working on lower UHF frequencies (Sirtrack Ltd, Havelock North, New Zealand), to be able to generalise our conclusions and for comparison with existing literature. First, we briefly describe the technical features of loggers and their functioning; then, we present test design and relative statistical analyses.

Proximity loggers

WILSCOPE PROXIMITY LOGGERS

Wildscope contact loggers are prototypes developed by a collaborative work between Department of Information Engineering and Computer Science (DISI), University of Trento, Italy; Fondazione Bruno Kessler, Trento, Italy; Fondazione Edmund Mach, San Michele all'Adige, Italy. The hardware architecture (*Tremateb*: Tretec s.r.l., Trento, Italy) of the logger includes a radio for contact detection, a Global Positioning System component for individual localization, a quadriband GSM/GPRS modem for remote data download and a microcontroller unit to coordinate the other components and elaborate the data collected.

Radio transceivers work with a UHF radio frequency operating in the 2.4 GHz ISM band. Technical details on contact detection recording and processing are provided in Appendix S1 and in Picco et al. (2015). Each logger transmits and 'listen to' radio beacons. The frequency of transmission of beacons corresponds to a logical time unit, or 'epoch', that defines the recording timeline of Wildscope. Thus the duration d corresponds to the time resolution of contact detection that typically depends on biological or ecological definitions. In fact, d is a user-defined parameter. A logger a opens a contact with a logger b when receives a beacon from *b* within an epoch. The contact lasts until the logger *a* keeps receiving from *b*. When the two nodes separate, the logger *a* counts the number of epochs in which it does not detect any contact with the other logger *b*. When this number, defined as '*time missed epochs*', overcomes a given value decided by the user, the contact is closed. This corresponds to the 'separation time' parameter of Sirtrack loggers. Contact data recorded by the logger include the identity of the two loggers in contact, and the time in which this contact occurred. Moreover, the loggers have been programmed to record a GPS triggered by any new open contact, on top of 'classic' periodic acquisition. Indeed, number of triggered locations, time out and periodicity of GPS scheduling are all parameters definable by the users.

The retrieving of the data (both contacts and GPS locations) can be done in three ways: remotely via Wireless Sensor Network to another logger, either deployed as a fixed logger or connected to a personal computer (operator node); remotely by means of the quadriband GSM/GPRS modem; by means of physical connection to a personal computer.

Finally, the radio transmission power is again user-defined, ranging between predetermined values from 3 to 27 (corresponding to power between -25 dBm to -1 dBm)

SIRTRACK PROXIMITY LOGGERS

The functioning and technical details of Sirtrack Tracking Solutions loggers (Havelock North, New Zealand) have been described in detail in Prange et al. (2006). Current models of Sirtrack loggers mainly work on 916.5 MHz (Prange et al. 2006). Contact detection works similarly to what described for Wildscope loggers, allowing the user to set the radio transmission power value and the separation time. However Sirtrack loggers (at least the model here tested) are not provided with a GPS sensor, nor with a quadriband GSM/GPRS modem. The radio transmission power values adopted in Sirtrack loggers are ranked inversely to their strength (e.g. power 0 is the strongest one and 31 is the weakest). For displaying convenience (i.e. to avoid confusion), we express them as ranked categories: minimum (original 31), medium (original 15) and maximum (original 0).

Logger tests

Since our overall objective was to quantify the relationship between radio transmission power and contact distance, in all tests we aimed at relating distance between loggers and contact occurrence, at different power settings. In each test, we then accounted for other potential confounding factors, since they interfere with radio transmission. The general framework of the experiments is reported in Figure 1. We firstly explored the baseline performances of loggers by modelling the dependence of the measured contact distance on different typology of loggers, radio transmission power and height of the loggers from ground (test 1). In this case, we measured the distance at which a given contact occurred. So, the 'ground-truth' are contacts. Then, in all other tests (closer-to-real settings), we measured the contact occurrence at given distances. So, the 'ground-truth' are recorded distances. In test 2 we performed simulated scenarios of multiple encounters between loggers. In test 3, we measured contact occurrence between horses in natural semi – controlled conditions. Finally, in test 4 we detected contacts between a mobile logger fitted on an animal and a fixed logger to simulate the use of a specific focal resource (roe deer in a fenced arena). The results of tests 1 and 3 have been used for a technical oriented performance evaluation of Wildscope also in Picco et al. (2015).

Since Wildscope integrated GPS acquisition and contact detection, contextually to test 2 we also assessed the reliability of GPS acquisition triggered by contact detection.

We ran tests 1 and 2 also on Sirtrack loggers to compare the performance of Wildscope prototypes with an established product already used for contact detection. We then deployed Wildscope loggers only on animals, in view of their use on free-ranging animals.

TEST 1 – BASELINE ASSESMENT OF CONNECTIVITY

Data collection

The rationale of these tests was the evaluation of the effect of radio transmission power, height from the ground and logger type on contact distance.

We ran the tests on three types of loggers, i.e. coated and naked Wildscope loggers, to evaluate the importance of the coating system on the connectivity between loggers, and Sirtrack coated loggers, to be used as comparison term for Wildscope loggers performances. We performed the tests on a range of available radio transmission powers, which are 3, 7, 15 and 27 for Wildscope and minimum, medium, maximum for Sirtracks. For each combination of type/power, we also tested the effect of height of the loggers from the ground (adapted from Drewe et al. 2012). Specifically, we ran the experiment at three different combinations of height (equal high: 100 cm – 100 cm; mixed height: 100 cm – 20 cm; equal low: 20 cm – 20 cm) which should mimic several potential situation of encounter between individuals (e.g., territory defence in the first case, mother – fawn interaction in the second, two individual feeding or resting in the third).

We performed the tests in San Michele all'Adige, Italy, from September 3rd to October 25th 2013, for a total of 22 effective working days which were characterized by dry and windless conditions, since both rain and wind can affect signal propagation. We ran the tests in a treeless field characterized by a grassy, regular and flat terrain, thus minimizing connectivity limitations due to the presence of obstacles and to irregular morphology of the terrain (Ceriotti et al. 2010). We also checked for the absence of other wireless networks in the area, which could potentially interfere with our tests. We fitted the loggers to two-litres bottles filled with a saline solution to mimic the body size of an animal (Drewe et al. 2012). We fixed the bottles to rigid woody supports, with the antenna oriented upwards. We configured parameters of contact detection, i.e. the epoch duration and the time missed epoch, at one minute for Wildscope loggers, and separation time to one minute for Sirtrack to standardize our experimental protocol.

In each single trial, we used two loggers, which we put on a line of sight (i.e. without obstacles in the middle) at a distance at which they were out of contact range (Figure S1). We kept one logger steady, while we moved the other one towards the former at 0.5 meters steps each minute, i.e. the epoch duration. At each step we checked if the logger recorded the contact by watching the led on the logger (for Sirtrack type and naked Wildscope type) or by connecting the logger to a personal computer (Wildscope coated type, where an external led was not installed). For each trial, we recorded the following distances:

- Maximal distance of contact opening (MaxOpen): distance at which the mobile logger opened the contact with the steady one.
- Maximal distance of contact closing (MaxClose): distance at which the mobile logger closed the contact with the steady one. To get this distance, we went backward at 0.5 meters/minute after the contact had opened until the contact was lost.

For mixed-heights trails only we also measured the minimal distance of contact opening (MinClose). This was done to take into account potential differences in radio wave propagation on vertical and horizontal axis, which is due to the anisotropic design of the antenna (Zhou et al. 2006). When two loggers are close each other at different heights, the transmission of the signal can be severally reduced, eventually leading to the breakdown of contacts, especially at low radio transmission power. To verify this issue we continued moving the logger *towards* the steady one at steps of 0.5 meters/minute after the contact was opened, recording if/at what distance the contact closed, *while approaching*. We then went backward as already described, until when the threshold of contact closure (MaxClose) was reached.

For each experimental combination (i.e. logger type/power/height from ground) we ran 20 trials (replicates), using interchangeably five loggers, to avoid any systematic bias due to an eventual malfunctioning of a given logger (Boyland et al. 2013). For Wildscope naked loggers, we performed less replicates (from 12 to 14) due to malfunctioning of two loggers. We reported all the tested combinations in Appendix S2.

Data analysis

Total contact failures. We firstly checked the occurrence of failures (i.e. no contact recorded in a given trial, even at zero distance), and their dependence from the logger type, by means of a non-parametric Kruskall-Wallis ANOVA.

MinClose. We then evaluated the occurrence of unexpected closure of contacts during the approaching phase (MinClose) in the mixed-heights case.

MaxOpen vs power, logger type, height. We modelled the dependence of MaxOpen on radio transmission power, the logger type, the height from ground as an ordinal variable (in the order equal low, mixed heights, equal high), by performing model selection based on AIC scores (Burnham and Anderson 2002). The full saturated model consisted in a three-way interaction between factors (Table S3). However, we could not use this model to estimate the effect of radio transmission power, since the power levels of Sirtrack and Wildscope are not comparable, and indeed we ignore how they scale one to each other. For this reason, we used a simplified model, with MaxOpen depending on radio transmission power nested within logger type.

Given the complexity of all interactions, we evaluated *post-hoc* the significance (Fisher's test) of the two-way variation between contact distance and combination of covariates (logger type*height from ground and radio transmission power|logger type, respectively; *= 'interaction with', |= 'nested within'). We also tested the significance (Student's t test, also with Bonferroni correction) of one-way variation for those covariate pairs that we considered relevant to the scope. We did not repeat the same analysis for the maximal distance of contact closing (MaxClose) because we found that the values of the two distances (MaxOpen and MaxClose) were similar within each combination tested (Table 1).

TEST 2 - CONTACT LOGGERS AT WORK: ESTIMATION OF SUCCESS OF CONTACT DETECTION

Data collection

In this test we simulated situations of encounters between individuals and individuals with focal habitats, in scenarios of increasing complexity. We developed a series of predictions on occurrence of contact detection for each scenario, using the observed means in Table 1. Then, we matched the predictions with the occurred outputs of contact detection. We explored the causes of potential mismatches (i.e. false positive and false negative occurrence), for each logger type and radio transmission power. We ran the tests on Wildscope coated (the ones appropriate to fit to animals), and Sirtrack loggers.

Since the experimental arena was very small (ca 2000m^2), we ran the trials only on the two lowest powers of Wildscope logger (3 and 7), and on the minimum and maximum powers of Sirtrack loggers. Such way we could compare the performances of (i) the weakest powers of the two logger types (3 of Wildscope and minimum of Sirtrack) and (ii) of Wildscope power 7 with the maximum power of Sirtrack. We set configuration parameters of contact detection, i.e. the epoch length and the time missed epoch, at one minute for Wildscope loggers, and the separation time to one minute for Sirtrack.

We performed the test in San Michele all'Adige, Italy, from May 14th 2014 to May 20th 2014, in dry and windless conditions, for a total of 7 effective working days. The arena used for this test was characterized by a regular and flat terrain, with some trees and bushes. We designed three different experimental scenarios (see Appendix S3 for details). In the first scenario, we used two fixed loggers and a single moving agent carrying a mobile logger, whilst in the second and in the third scenarios we used two and three agents, respectively. Scenarios were toy representation of the biological processes of interest, such as resource use and inter-individual encounters. We fitted the mobile loggers on the same setup as for test 1, while the two fixed loggers were put on trees (Figure S2). The agents then moved the mobile loggers on a prefixed path for a maximum duration of 17 minutes, with intermediate stops over the path at pre-established times from the start of the single trial. This experimental setup allowed us to know the exact distance of each logger from the other ones at any time of the trial. We ran three replicas for each scenario, power and logger type, using the same loggers across the replicates.

Data analysis

We predicted the occurrence or not of a contact at each minute and for each mobile logger involved in the scenario, based on the combination of the known positions of each logger with respect to the others on one side, and the outcome of the Test 1 (i.e., the measured variable MaxOpen) on the other (Appendix S3). Then, for each logger we compared the list of expected events with the contacts actually recorded by the logger. The outcome of this process was a list of (i) true positive events, when the expected contact occurred; (ii) false negative events, when expected contacts were not recorded by the loggers; (iii) false positive events, when unexpected contacts were registered by the logger.

We computed the success rate (i.e. the rate of true positive events) on the total of expected events, and the proportion of failures which were false negatives (i.e., false negatives events/[false negative events + false positive events]). We modelled the dependence of (i) the success rate and (ii) the false negative rate on the radio transmission power by fitting a generalised linear mixed model with normal random effects, assuming a binomial distribution with logit link. As for Test 1, we took into account the non-independence of the power settings from the logger type by fitting a nested effect (radio transmission power|logger type).

Moreover, we fitted the number of agents as random effect to test the expected robustness of the network to the number of loggers. We evaluated *post-hoc* the significance (Fisher's test) of the two-way variation between the response variables and combination of covariates. We also tested the significance (Student's t test, also with Bonferroni correction) of one-way variation for those covariate pairs that we considered relevant to the scope.

TEST 3 – WILDSCOPE GOES "REAL" I: EVALUATION OF CONTACT LOGGERS PERFORMANCE DEPLOYED ON HORSES IN A SEMI-CONTROLLED ENVIRONMENT

The scope of this test was to expand the evaluation of the performance of coated Wildscope loggers to a setting 'close-to-target', i.e. less controlled conditions than Test 1 and Test 2. The deployment of contact loggers on real animals, in a semi-controlled environment, permitted to control for some of the expected relevant factors affecting radio connectivity, such as distance between loggers and radio power transmission, but not all. For example, body size or body orientation are also relevant factors, which did not interfere (or, were fully controlled and standardised), in Test 1 and Test 2. Thus, we expected that the deployment on animals would have added 'noise' to the system. Therefore, we modelled the probability of contact detection as a function of distance between individuals (i.e., mobile loggers) and radio transmission power. This way, we could quantify the noise of the system, by explicitly modelling the probability of false negative (i.e. expected contact that were not recorded) and false positive cases (unexpected contact registered by the loggers) as function of distance, and radio transmission power.

Data collection

We ran the test in a fenced hilly area (about 3 ha) in Central Italy (Scorgiano, from February 16th 2014 to April 17th 2014, 28 effective days of tests), fitting Wildscope loggers to 4 horses (Figure S3). These semi - domestic conditions facilitated the operations of fitting and removal of Wildscope loggers, which were fixed on easily removable collars. Animals were free to roam, feed or rest within the fence.

We tested four radio transmission powers (3, 7, 11, 15) and we set the epoch duration *d* and the time missed epoch to one minute. The number/type of radio transmission powers were selected to explore as many power settings as possible, while accounting for the size of the fenced area (and thus excluding the maximum power, 27).

For each radio transmission power tested, we performed several trials in which we considered couple of individuals wearing loggers (dyads). For each minute of observation, i.e. *d* (temporal unit of analysis), we measured the distance between animals using a telemeter, and we recorded the timestamp of the observation. In our trials, we attempted to get a sample balanced for distances and logger combinations. We recorded a range of distances from 0 meters (horses side by side) to 70 meters, that we considered the threshold for a 'biologically meaningful' contact detection (i.e., 'an encounter'). At the end of the tests we downloaded the data from the loggers.

Data analysis

We extracted the information on contact occurrence at a given distance matching the timestamp of contact recorded by the loggers with the timestamp of the operator's observations. We assigned 1 (one) or 0 (zero) to each minute of observation depending on the occurrence or not of the contact in that given minute. We thus obtained a list of cases of successes (i.e. contact occurred) and failures (no contact recorded) for any given distance of observation.

We used a general linear mixed model (GLMM) with a binomial distribution and logit link to model the probability of contact detection in dependence of distance between loggers in interaction with radio transmission power. We accounted for repetitions of logger dyads fitting them as random effect. Then, we used the model to predict the probability P(x) to detect a contact at a given distance x, for each radio transmission power.

From the P(x) distribution, it is immediate to read the probability of first type errors, or false negatives (FN(x)), defined as the probability to miss the other logger at a given distance x, and that corresponds to:

$$\mathbf{FN}(x) = \mathbf{1} - \mathbf{P}(x)$$

Moreover, one may search for the probability of second type errors, or false positives (FP(x)), defined as the probability to detect a contact with a logger at a *larger* distance than x. Formally, this probability corresponds to the area under the curve between x and infinite. To provide a synthetic approach, we expressed the true positives rate P(x) as a function of the false positives rate FP(x), i.e. we used the ROC (Receiving Operating Characteristic) curve. As an established tool to evaluate model robustness, the ROC allowed us to assess (i) the quality of discrimination of the system and (ii) the reliability of the four predictive models of contact detection (by measuring the AUC, area under the ROC curve).

TEST 4 – WILDSCOPE GOES “REAL” II: EVALUATION OF CONTACT LOGGERS PERFORMANCE ON ROE DEER IN A SEMI-CONTROLLED ENVIRONMENT

The scope of this test was to evaluate the performance of coated Wildscope loggers on an animal with body size substantially different from horses (Test 3). We chose roe deer (*Capreolus capreolus*), since this species is a potential target of application in wild settings. To trade-off measurability and ‘close-to-target’ conditions, we fitted contact loggers to roe deer individuals in a fenced semi-natural alpine area.

Data collection

We ran the tests in two fenced areas (about 1.5 ha in total) in the Italian Alps (Pejo, from June 14th 2014 to June 18th 2014, 5 effective days of tests). We fitted mobile loggers on two roe deer (one for each portion of the fenced area). Since each roe deer was ‘solitary’, we fitted fixed loggers to a woody supports and measured the distances from roe deer to fixed nodes (Figure S4). The loggers were set to power 7, given the size of the area (and maximum measurable distances thus) and our focus on medium range contacts (Test 1).

Data analysis

The assessment of the contact distance between fixed loggers and roe deer, as well as the statistical analyses and modelling, were performed as described for Test 3.

MULTI-SENSOR PLATFORM AT WORK: ESTIMATION OF SUCCESS OF GPS ACQUISITION IN CASE OF CONTACT

During Test 2, we also evaluated the functioning of the triggered system of GPS acquisition in case of occurrence of a contact (see Methods, Proximity loggers).

This test was done only on the mobile coated Wildscope loggers for the combinations of power 3 and 7/number of agents (1, 2 and 3, see Methods, Test 2).

We expected a triggered GPS location for each new contact occurred. More specifically, the GPS schedule was designed to get a location either in the same minute of the contact detection, or one minute later (see Appendix S1 for further details). Based on the combination of this scheduling and the known occurred contact detected (see Test 2), we prepared a list of expected GPS locations for each minute of observation. We then compared these predicted events with the GPS locations actually recorded by the loggers, based on the timestamp. We thus obtained a list of true events, i.e. expected and occurred GPS acquisitions, and false negative events, i.e. expected but not recorded GPS acquisitions. We did not consider for this analysis false positive events, i.e. unexpected but occurred GPS locations, because these data, which indeed we recorded, solely represent superfluous information that does not hamper the analyses. In all cases, the 4 replicates of Test 2 were used to estimate the variance.

We modelled the observed pattern of success probability with a binomial distribution of residuals, using a logit link function. We performed the model selection procedure starting from a full saturated model, that included a two-way interaction between the number of agents and radio transmission power, and retained the most parsimonious model based on AIC scores (Burnham and Anderson 2002) (Appendix S4).

All the statistical analyses were programmed in SAS 9.3 (SAS Institute, Inc.). Analysis of variance was computed using PROC MIXED. GLMM were computed using PROC GLIMMIX. Log-Likelihood is approximated using the method of Laplace. To display data we used least squares or population marginal means with respect to the effects of interest, to account for unbalance designs.

RESULTS

TEST 1 – BASELINE ASSESMENT OF CONNECTIVITY

A summary of the range of contact detection for different combination of logger type and radio transmission power is provided in Table 1. Within each type of loggers tested, the average MaxOpen increases with radio transmission power. Within each combination of logger type radio transmission power, the variability among trials is not negligible. Indeed, the coefficient of variation is always large, with maximum values for the lowest and highest power setting of Sirtrack loggers, power 3 of coated Wildscope loggers, and power 27 of naked Wildscope loggers.

Contact failure and MinClose. We found that the probability to completely miss a contact (even at zero distance) was significantly different among the logger types tested (Kruskall-Wallis ANOVA, $\chi^2 = 44.5$, $p < 0.0001$). The majority of failures were relative to tests at mixed height, and especially for Sirtrack loggers with minimum power (80% of undetected contacts) and with medium power (65% of undetected contacts). In the remaining cases (20% and 35% for minimum and medium power respectively), Sirtrack loggers closed the contacts during the approaching phase (minimum power: MinClose = 1.1 ± 0.66 m; medium power: MinOpen = 1.4 ± 0.26 m).

MaxOpen Model selection (Appendix S4) supported the full model including three-way interaction between logger type, height from ground and transmission power. We found that the range of contact detection differed significantly in relation to the height from ground across all logger types ($F_{4,440} = 4.56$, $p = 0.0013$; Figure 2). The paired comparisons (letters in Figure 2) showed that the range of contact distance increased with the height from ground for all logger types, with the exception of the Wildscope coated loggers that did not differ significantly when kept at mixed height or equal high position ($t_{440} = 0.09$, $p = 0.92$, $P_{\text{Bonferroni}} = 1$). We also found that the range of contact distance was significantly different among

Wildscope and Sirtrack logger types, at each combination of height from ground. Conversely, Wildscope coated and naked loggers performed similarly at all the three heights from ground tested (equal low: $t_{440} = 2.1$, $p = 0.04$, $P_{Bonferroni} = 1$; mixed height: $t_{440} = 2.77$, $p = 0.006$, $P_{Bonferroni} = 0.21$; equal high: $t_{440} = 2.51$, $p = 0.01$, $P_{Bonferroni} = 0.45$).

The model accounting for difference in contact detection distance in relation to the effect of radio transmission power nested within the logger type was highly significant (power within logger type $F_{8,552} = 101.2$, $p < 0.0001$) (Figure 3). The paired comparisons (letters in Figure 3) showed that the two Wildscope logger types performed similarly for all powers tested, except the 27 ($t_{552} = -6.83$, $p < 0.001$, $P_{Bonferroni} < 0.0001$). Moreover, for Sirtrack loggers we could not detect any significant difference between the lowest power tested and the intermediate one ($t_{552} = 0.6$, $p = 0.54$, $P_{Bonferroni} = 1.0$), whilst contact detection distance resulted significantly higher for the strongest power ($t_{552} = 3.6$, $p = 0.0003$, $P_{Bonferroni} = 0.02$). Contact detection range did not differ significantly for the lowest radio transmission power between Sirtrack and both Wildscope naked loggers ($t_{552} = 0.9$, $p = 0.19$, $P_{Bonferroni} = 1.0$) and coated ones ($t_{552} = 1.3$, $p = 0.19$, $P_{Bonferroni} = 1.0$).

TEST 2 - CONTACT LOGGERS AT WORK: ESTIMATION OF SUCCESS OF CONTACT DETECTION

The success rate of contact detection in the simulated scenarios of encounters was high across all the logger types and radio transmission powers (0.77 to 0.91; Figure 4), although with significant differences across combinations ($F_{2,30} = 23.3$, $p < 0.001$). Wildscope loggers exhibited consistent patterns at both the radio transmission power tested ($t_{30} = -0.69$, $p = 0.49$, $P_{Bonferroni} = 1.0$). Conversely, the success rate was lower for both the Sirtrack powers tested, when compared with the power 7 of Wildscope loggers (Sirtrack power min: t_{30} = -

9.81, $p < 0.0001$, $P_{Bonferroni} < 0.0001$; Sirtrack power max: $t_{30} = -3.31$, $p = 0.002$, $P_{Bonferroni} = 0.015$).

The analysis of failures indicated that these significantly differed for radio transmission power nested within the logger type ($F_{3,30} = 44.43$, $p < 0.0001$) (Figure 5). Specifically, the rate of false negatives did not differ significantly for Wildscope loggers at the two radio transmission powers tested ($t_{30} = 0.85$, $p = 0.4$, $P_{Bonferroni} = 1.0$). Instead, the power 7 of Widlscope loggers had a significantly lower rate of false negative events than the lowest power of Sirtrack loggers (Sirtrack power min: $t_{30} = 6.15$, $p < 0.0001$, $P_{Bonferroni} < 0.0001$), but higher than the highest power of Sirtack loggers (Sirtrack power max: $t_{30} = -7.1$, $p < 0.0001$, $P_{Bonferroni} < 0.0001$).

TEST 3 – EVALUATION OF CONTACT LOGGERS PERFORMANCE BETWEEN HORSES

As expected, we found that the probability to detect a contact decreased with the distance between loggers, for all the radio transmission powers tested (Table 2). The predicted models of contact detection indicated that even at zero distance between the loggers (i.e. the intercept with Y axis) there was no certainty of contact occurrence, for all the powers tested (power 3: 0.7; power 7: 0.69; power 11: 0.66; power 15: 0.72) (Table 2 and Figure 6). The decrease was sharp for the lowest power (power 3: $r = -0.44$, $p < 0.0001$), never exceeding a range of 15 meters. For intermediate powers (7 and 11) the probability of contact detection decreased less abruptly (power 7: $r = -0.11$, $p < 0.0001$; power 11: $r = -0.07$, $p < 0.0001$), with a contact detection range that ended around 50 – 70 meters. For the highest power (15), the probability of contact detection decreased smoothly (power 15: $r = -0.02$, $p < 0.0001$), thus exceeding the range of contact distance considered in this work (70 meters). The complementary to 1 of the curves in Figure 6 represents the probability of occurrence of a first type error at x distance.

The AUC values computed from ROC curves indicated that the predictive models of contact detection were highly reliable for all the powers tested. All the ROC curves were significantly different from the random model (Table 2 and Figure 6), although power 15 performed poorly with respect to the others radio transmission powers tested.

For low and intermediate radio transmission powers (3, 7 and 11) the ROC curve showed that the probability to have a false positive event at high rate of true positive events (more than 0.5 - 0.6) is slightly bigger for the intermediate powers (7 and 11) than for the lowest one (3) (Figure 6). However, the lowest power is not the most reliable at each distance, since it crosses the ROC curve of the other two powers at true positive rates of 0.6 (power 7) and 0.5 (power 11), that correspond to a distance of about 4 - 5 meters (Figure 6). Beyond this distance, the trade-off between sensitivity (i.e. the rate of true positive events) and specificity (i.e. the rate of true negative events or (1- false positive rate)) is therefore slightly more favourable to powers 7 and 11.

TEST 4 – EVALUATION OF CONTACT LOGGERS PERFORMANCE IN ROE DEER

The general performance of the loggers fitted to roe deer was quite similar to what we observed for horses (Table 2). The predictive model indicated that the probability to detect a contact decreased to zero at around 25 meters (Figure 7), while the probability to have a first type error at zero distance was equal to 0.19. The model was highly reliable (Table 2, Figure 7), whilst the rate of occurrence of false positive events was very low even at high rates of true positive events.

MULTI-SENSORS AT WORK: ESTIMATION OF SUCCESS OF GPS ACQUISITION IN CASE OF CONTACT

The ratio of successes of GPS detection was overall very high (0.9 ± 0.03). Model selection (Appendix S4) supported a best model including an additive effect of number of agents ($F_{2,14}$ = 4.7, p = 0.03) and radio transmission power ($F_{1,14}$ = 4.5, p = 0.05). Least square estimates are reported in Figure 8. Trials with power 3 are characterised by a larger variance with respect to power 7. The trials with 2 agents performed worse that the ones with 1 and 3 agents.

DISCUSSION

In this study, we investigated the performance and reliability of proximity loggers to detect synchronic spatial encounters. Our experimental setting, progressing from highly standardised setup to semi-natural contexts, allowed us to observe and quantify the variability of proximity logger response as a function of their distance. This represents a substantial extension of current knowledge on the potentialities and limits in the use of proximity loggers in animal ecology. A common approach to previous studies, was the measurement of average contact distance and its variation (e.g., Prange et al. 2006; Drewe et al. 2012), but without explicitly accounting for the *probability* of contact detection. Instead, we showed that the relation between occurrence of contacts and distance is not fully deterministic, rather radio propagation is influenced by transmission settings (i.e. power), and stochastic fluctuations due to intrinsic (e.g., logger technology) and context-dependent factors. For example, the effect of body mass and encumbrance of animals wearing the loggers, as well as their movement can substantially alter the basic patterns of radio-transmission.

In this respect, one of our main indications is that the commonly described approach of 'setting loggers to a certain distance by selecting a radio transmission power' (e.g., Böhm et al. 2009; Walrath et al. 2011; Drewe et al. 2012; Boyland et al. 2013) is based on wrong assumptions. In fact, we showed that there is not a deterministic relationship between distance and power, since contact detection based on radio transmission is substantially affected by type I (false negatives-missed contacts at certain distances) and type II (false positives-contacts at greater distances than expected) errors. Even in the most controlled experimental settings of our study (Test 1) that mimicked previous attempts to measure logger bias (Prange et al. 2006; Drewe et al. 2012; Boyland et al. 2013), proximity loggers failed to get some contacts, or interrupted contact detection unexpectedly. Further, when contacts were recorded, we observed a high coefficient of variation among single trials (Table 1), revealing that the average contact distance cannot be taken as a reliable reference value for detection of encounters. The results obtained in Test 2 support this view. Our predictions on contact occurrence were based on the average contact distance measured in Test 1, as elsewhere suggested. If the relationship between distance and contact detection had been deterministic, we should have found almost no errors. This was not the case (Figures 4 and 5), especially for Sirtrack set at minimum radio transmission power which interestingly was also that with the highest coefficient of variation in Test 1 (Table 1). In summary, these findings demonstrate the importance of modelling the relationship between contact and distance as a probabilistic function, with errors of first and second type inextricably linked to contact detection. This is particularly important for a technology for which 'expected occurrence' in real deployments is not known *a priori*, which instead is typically the case of GPS based tracking with pre-determined schedules (Friar et al. 2010).

Indeed, the existence of false negatives was recognised by several studies (e.g., Drewe et al. 2012; Boyland et al. 2013; Lavelle et al. 2014), but not modelled upfront. For example, Boyland et al. (2013) measured the bias of single loggers as mean percentage difference in contact logging, and used this information to correct the association matrix for social network analysis. We moved beyond, providing the first attempt, to our knowledge, to model contact detection (and its associated errors) as a function of distance, radio transmission power and noise (Test 3 and Test 4). We found that the intercept was lower than 1 for all power tested, i.e. false negatives were common also at 0 distance between loggers. Typically, this pattern emerges as the stochasticity of the context increases (see for example Wildscope power 7: no false negative events in Test 1 (Table 1) *vs* 23% of false negative events in Test 3 (Figure 6 and Table 2). Moreover, our results showed that the inverse relationship between contact detection and distance is well modelled by an exponential function (Figures 6 and 7, left panels). Operationally, the detection signal does not 'fall' abruptly. This implies that (i) the probability of false negatives increases with the distance, as expected, but also that (ii) the *likely* contact distances (i.e., with high contact probability) are substantially lower than the *maximum threshold* beyond which the contact probability becomes null, or very low. In other words, the false positive rate is not negligible. For example, Walrath et al. 2011, interpreted the lower number of visually observed contacts with respect to logger detected contacts as a bias due to the operator. Since the operator recorded proximity at 1 m only, we instead suggest that loggers sampled also at larger distances, and thus recorded more contacts than the operator. Indeed, in communication technology, the function linking connectivity and distance is described by a declining step function, defining a range of 'full connectivity', or *white zone*, between 0 and a distance d_1, and a zone of null connectivity, or *black zone*, beyond a distance d_2. Usually the transition between d_1 and d_2 is not abrupt, and a *grey zone* can be identified, where contact detection is not guaranteed (Mullen and Huang 2005; Ceriotti et al. 2010). Therefore, contact detection within the *grey zone* is a probabilistic and not a deterministic event. Our predictive models of contact detection for Test 3 and Test 4 confirmed the scenario just described, with the noteworthy exception that a white zone where contact is guaranteed did not exist. For all radio transmission powers, but not for power 15, we could instead detect a black zone, since the exponential function asymptotically tends to 0 within the ranges of distances that we measured.

These findings should *direct* choices of ecologists, rather than discourage them. In particular, we suggest that the setting of radio transmission power is a trade-off between two contrasting needs. On the one side, one would choose the power that minimises the false negatives at the 'desired distance', or the distance at which the biological phenomenon of interest is expected to occur. On the other side, though, one should also take into consideration the 'acceptable' type II error for the case of interest, which can be expressed as the ‘threshold distance’ beyond which contact detection probability is very low, at that power. As already mentioned above, these two distances can be substantially different, especially when increasing radio transmission power. We indicate ROC curves as useful tools to operate the choice of power settings. Best ROC curves are those lying in the left-upper side of the graph, since this 1) indicates a substantial difference from random classification and 2) minimises false positive rate for most values of true positive rate. In our Tests 3 and 4 (Figures 6 and 7, right panels), we found that Wildscope loggers set at power 3, 7 and 11 performed well both when deployed on horses and roe deer (power 7 only), i.e. proximity loggers detected contacts with respect to distance with a function substantially different from random (AUC> 0.8). For example, Wildscope with radio transmission power= 7, detects contacts at 5 m in 70% of cases, and thus has a false negative rate of 30% (Figure 6, left panel). In such case, the correspondent ROC curve (Figure 6, right panel), shows a false positive rate of 20%. Instead, if one aims at minimising the false positive rate, e.g. at 1%, this would correspond to a distance of 35m. Biologically, this means that if the encounter of interest happens at a distance of 5m, setting Wildscope at power 7 allows to detect it in 70% of cases. However, the detected encounter may also have happened beyond that value in the 20% of cases, until an approximate maximum distance of 35 m.

The actual choice of the radio transmission power settings should therefore be driven by biological questions, while taking into account the reasoning above. For example, if the ecological investigation regards close proximity patterns (within the range of 2 – 3 meters, e.g. disease transmission), the use of the lowest power is recommended. In fact, for this setting the probability to record a false positive event is very limited, with a high true positive rate. For a desired range between 4 - 5 to 10- 12 meters (e.g., competition at feeding sites), the selection of the suitable radio transmission power depends upon a trade-off between acceptance of a high false positive events rate at low probability of false negatives, or vice versa. Indeed, the curves show that for radio transmission 3, the rate of false positive events is low at those desired distances, but at the same time the probability to miss an occurred contact is high. Conversely, for both the power 7 and 11, the probability to miss an occurred contact is low, but the likelihood that a recorded contact would happen beyond the desired range is much higher. For detection of encounters beyond 12 meters (e.g. defence of territories), the user can only select intermediate powers (7 and 11), knowing that the ratio between false negative events and false positive events increases with the distance.

It is worthy to underline that the guidelines provided above have to be 'tuned' according to the context of loggers deployment. In particular, some characteristic of target species are particularly relevant for animal ecology applications. Indeed, body encumbrance *per se* may represent an obstacle for radio wave propagation (Hauer et al. 2009, Ceriotti et al. 2010). Accordingly, we expect a more efficient contact detection for loggers deployed on smaller and slender species than on bulky ones. This effect can probably explain the different average contact distance of standalone Sirtrack loggers (Prange et al. 2006) compared to the same loggers fixed on bottles, that simulate body effect (Power min: 1.4 m ± 0.04 and 0.5 ± 0.08, respectively). The reduction of radio wave propagation can be further enhanced by animal movement. For instance, two individuals within contact detection distance, may unexpectedly interrupt radio transmission if they move in a back-to-back position, thus interposing both their bodies between loggers. This may be one of the reasons why in our deployments on animals (Test 3 and Test 4) contact detection probability never attained to 1. Anecdotally, we indeed observed some obvious missed contacts in Test 3 when horses turned the backs even at very close distances. In this view, we should have expected to detect contacts at longer distances for roe deer than for horses. Interestingly, we found the opposite. We argue that this result can be explained by other environmental and context-related factors, such as for example the greater steepness of Test 4 w.r.t. Test 3 sites. Indeed terrain unevenness is recognized as a factor limiting radio connectivity (Anastasi et al. 2004). Related to this, another aspect to consider is the direct effect of height from ground on contact detection performance (Ceriotti et al. 2010), as it happens between different-size species or between individuals engaged in different activities (e.g. feeding, resting, etc..). Accordingly, the results of Test 1 demonstrated that for each logger type and radio transmission power the closeness to ground reduces contact detection distance (Figure 2). In summary, not only animals size and their reciprocal position, but also focal activity can influence contact detection patterns.

An undesired consequence of radio transmission stochasticity are 'unpaired contacts', i.e. asymmetric detection between a couple of loggers, or dyad (e.g. Boyland et al. 2013). This event might be the consequence of missing detection, as well as false positive contacts by either logger in the dyad. Whether we 'trust' the unpaired contact detection or not, this fact might be of particular relevance when contact data are used to perform a Social Network Analysis, e.g. to assess learning behaviour (Rutz et al. 2012), or disease transmission patterns (Perkins et al. 2009). In the latter case especially, unpaired contacts might cause an underestimation of the connectivity rate between individuals, which is one of the key parameters to model disease transmission dynamics. In this paper we did not focus on corrective solutions to deal with this problematic, like instead recently proposed by Boyland et al. (2013). Rather, we focused on the *causes* of the problem, illustrating scenarios where stochasticity increases and consequently biological patterns from loggers data should be inferred with caution. As a perspectives, the rate of unpaired contacts could be used to as an estimate of the noise affecting the performance of the system.

In spite of the above mentioned intrinsic limitations of proximity technology, we recognize its enormous potentiality to ameliorate the study of animal encounters, and related ecological phenomenon. Thanks to this technology, contact studies can be extended to several habitat and species, whereas they were previously limited to conditions particularly favourable to direct observation, such as open habitats, confident species, or controlled set up (Henzi et al. 2009; Focardi and Pecchioli 2005). This way, the potential interference or bias of the observer's point of view is also eliminated, as well as sampling biases arising from lack of observations in habitats available to animals, but with low observability (Krause et al. 2013). In our empirical comparison, we contrasted a commercial logger with a prototype developed by us. Interestingly, their performance was optimal at different distance ranges, suggesting a flexible consideration of both according to the ecological questions under investigation. At low powers, Sirtrack proved less variability than Wildscope, but also a greater rate of false negatives. Conversely, Wildscope permits to substantially widen the contact detection distance range that can be studied, thus extending the use of proximity loggers to new research topics of animal ecology, like e.g. competition, predation, group living, group hunting, group defence.

An overlooked potentiality of WSN system use in animal ecology is the combination of mobile and fixed networks to address ecological questions. Since the first wildlife application of WSN (ZEBRANET, Zhang et al. 2005), fixed networks have been aimed to data retrieval from mobile loggers (Anthony et al. 2012, Rutz et al. 2012). In this work, we considered an alternative scenario both in controlled and semi-natural experiments (Test 2, Test 4), by explicitly recording contact detection between mobile and fixed loggers, thus proving applicability of this technology to investigate the use of focal habitats by animals. This provides exciting perspectives, such as the monitoring and control of problematic individuals habituated to anthropic features or the evaluation of wildlife corridors efficacy. Typically, these are examples of use of habitats highly meaningful for animal performance or survivorship, which is not captured by a classic used *vs* available design (Manly et al. 2002). In other words, animal fitness does not depend solely on habitats where time is spent most, but we did not have a valid technology to investigate this component of habitat selection. Although other tools for this kind of investigations have been introduced (e.g. camera traps: Rovero et al. 2014; RFIDs: Cagnacci and Massei 2008), WSNs overcome some limitations of current techniques, e.g. by permitting a 360° and adjustable range detection (Picco et al., 2015).

In this work, we assess for the first time a new biologging feature: the coupling of GPS based telemetry and proximity detection. Technically, we proved the reliability of GPS location acquisition triggered by contact detection. Formally, this represents a proper integration, and not only juxtaposition, of the two technologies, combining the advantages of both. The enrichment of encounters data with spatial information is by far an important step towards a process-based interpretation of these observations. Indeed, the technology advancement here presented helps to contextualise occurrence of contacts in the environment, thus increasing the robustness of inference on animal encounters. This may promote a completely new set of questions, e.g., is territorial defence modulated in close versus open habitats? Do aggregation patterns in winter depend from resource distribution? Although virtually continuous GPS tracking (i.e. sequences of GPS locations at high frequency) may allow to address similar questions, this approach has very little applicability in wildlife studies, especially for species with low recapture rate and/or when battery consumption is an issue.

Encounters between individuals, of the same or different species, may correspond to a variety of interactions, e.g. aggressive interactions for food access, see e.g. Vander Wal et al. (2012), or shared use of space to compete on resources or females, e.g. Stradiotto et al. (2009). According to the movement ecology paradigm (Nathan et al. 2008), other individuals can be seen as components of the 'external environment' *sensu latu*, and thus contribute to determine the individual movement path. Therefore, a correct identification of encounters between individuals by means of contact detection, and its integration with a triggered system of GPS location acquisition, might importantly enhance our ability to link individual movement to the motivation to move.

For this and the many reasons examined above, the assessment of the reliability of these biologging tools is a major challenge to appropriately exploit the opportunities they offer. As already recognized by Prange et al. (2006), and we fully agree, one cannot blindly trust previous performance assessments, unless they were undertaken in analogous conditions to those of interest. Our results indicate how proximity detection can be affected by variation in connectivity and what the prevalent causes might be. This way, our work can be taken as a reference to set guidelines on the operational way to ascertain proximity detection performance, rather than providing absolute values of reliability of the system. In particular, we encourage researchers working with proximity loggers to investigate the *probabilistic* relationship between inter-individual distance and contact occurrence by deploying loggers on test animals in semi-controlled conditions, as close as possible to the final target species/context of application. This probabilistic assessment would permit to associate the measurement error to observations, thus leading to reliable biological conclusions from the observed patterns.

TABLES AND FIGURES

Table 1 Contingency table of contact detection distance in Test 1. For each combination of radio transmission power per logger type, contact occurrences and averaged distances of contact opening (MaxOpen) and closing (MaxClose) are reported. To note the lower sample size (N) for Wildscope naked loggers, which was due to malfunctioning of two loggers. We report also the range of MaxOpen and the correspondent coefficient of variation (%)across all combinations of logger type*radio transmission power. All values are in m.

Logger Type	Radio transm. power	Contact occurrence		MaxOpen ± SE	MaxOpen range	% CV	MaxClose ± SE	N
		NO	**YES**					
Sirtrack	min	16	44	0.5 ± 0.08	(0.0-3.0)	108.7	0.6 ± 0.08	60
Sirtrack	med	13	47	1.4 ± 0.09	(0.4-3.9)	45.2	1.5 ± 0.1	60
Sirtrack	max	0	60	5.4 ± 0.5	(0.3-15.7)	72.0	5.9 ± 0.5	60
Wildscope naked	3	6	66	1.7 ± 0.12	(0.4-4.9)	60.1	1.9 ± 0.13	36
Wildscope naked	7	2	36	5.7 ± 0.41	(1.4-11.5)	42.6	6.5 ± 0.45	38
Wildscope naked	15	2	34	14.6 ± 1.15	(2.5-28.0)	46.1	16.9 ± 1.4	36
Wildscope naked	27	0	36	20.6 ± 2.16	(3.0-45.0)	63.1	23 ± 2.18	36
Wildscope coated	3	0	60	2.3 ± 0.2	(0.5-7.8)	68.1	2.5 ± 0.21	60
Wildscope coated	7	0	60	7.2 ± 0.4	(1.3-15.0)	42.9	7.7 ± 0.4	60
Wildscope coated	15	0	60	13.6 ± 0.75	(5.0-30.0)	42.8	14.5 ± 0.77	60
Wildscope coated	27	0	60	30.4 ± 2.01	(10.0-61.0)	51.3	31.4 ± 2	60

Table 2 Summary of the models of contact detection in function of the distance between loggers, for different radio transmission powers in Test 3 on horses, and for power 7 in Test 4 on roe deer. We report the estimate (and standard error) and the intercept (and standard error) of the predicted curves. The ROC association statistics indicate the goodness-of-fit of the predicted curves (Area Under Curve, AUC; for random curve: AUC=0.5). To note that the complement of the intercept to 1 gives the predicted estimate of type I error. Legend: SE = Standard Error; DF = degrees of freedom; p = p value; AUC = Area Under the Curve: DR = Difference with Random Curve

Detection curves							**ROC Association Statistics**		
Power	**Intercept**	**SE**	**Estimate**	**SE**	**DF**	**p**	**AUC**	**SE**	**DR**
Test 3 (Horses)									
3	0.78	0.08	-0.44	0.029	205	< 0.0001	0.88	0.0077	2418.5 ***
7	0.77	0.09	-0.11	0.007	106	< 0.0001	0.86	0.0114	987.6 ***
11	0.76	0.11	-0.07	0.006	58	< 0.0001	0.823	0.0177	332.6 ***
15	0.72	0.16	-0.02	0.005	52	< 0.0001	0.618	0.0271	18.9 ***
Test 4 (Roe deer)									
7	0.81	0.16	-0.26	0.025	67	< 0.0001	0.92	0.0176	581.8 ***

Figure 1 Conceptual scheme of the tests we performed. In the ovals on the left, a brief summary of the experimental set up is reported; each test is linked to its motivation (squared box on the right).

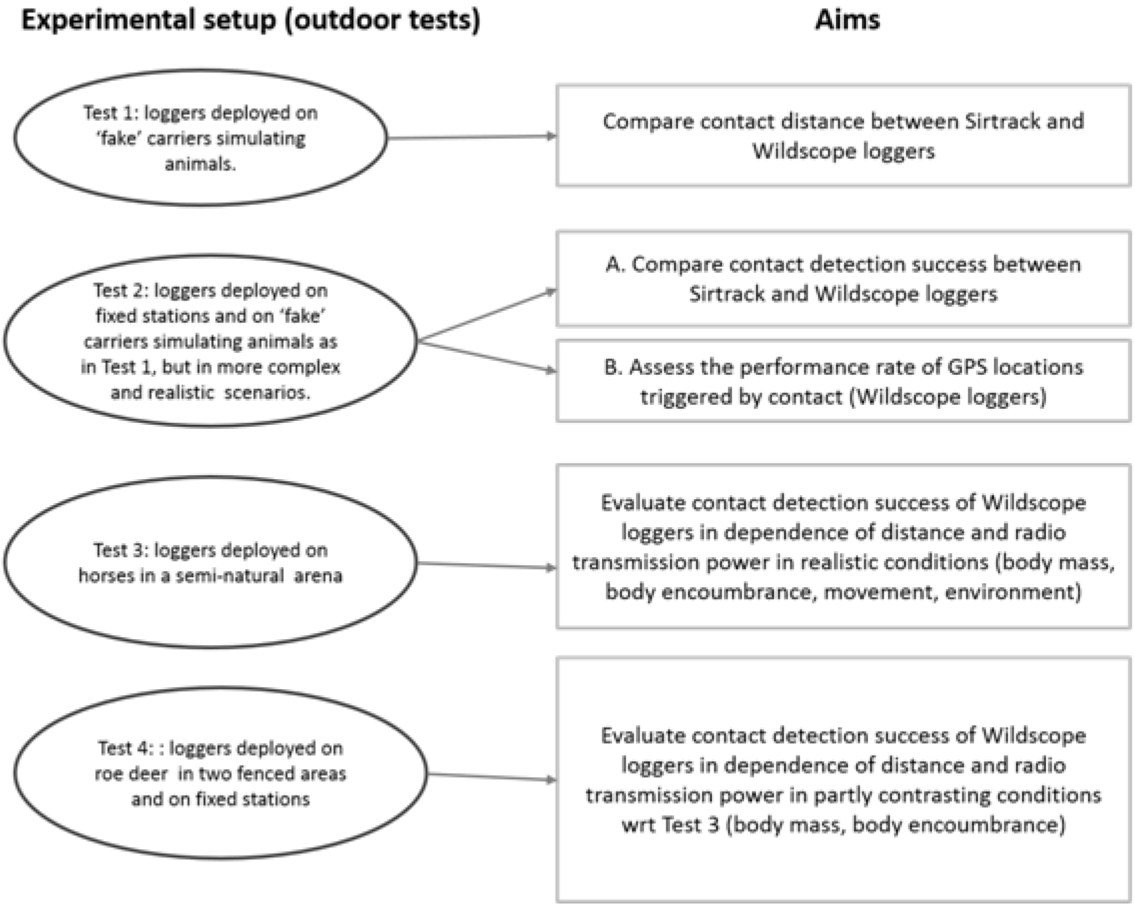


Figure 2 - Test 1 Plot of the least square estimates of the maximal distance of contact opening (Max Open) in relation to the height from ground (equal low: both loggers at 20 cm; mixed: one logger at 20 cm and the second at 100 cm; equal high: both the loggers at 100 cm) obtained from the model in Table S3.1. Letters and numbers indicate the significance of one-way variation for covariate pairs, and specifically different capital letters refer to significant differences of MaxOpen between logger types at the same height from ground; different numbers refer to significant differences of MaxOpen for the same logger type at various height from ground. Lines are drawn to facilitate the visualization but do not describe any interpolation. Bars denote 95% confidence Intervals. Small shifts around the tick marks of the abscissae were necessary to improve plot readability. Legend: continuous line = Sirtrack loggers; long broken line = Wildscope coated loggers; long broken line = Wildscope naked loggers.

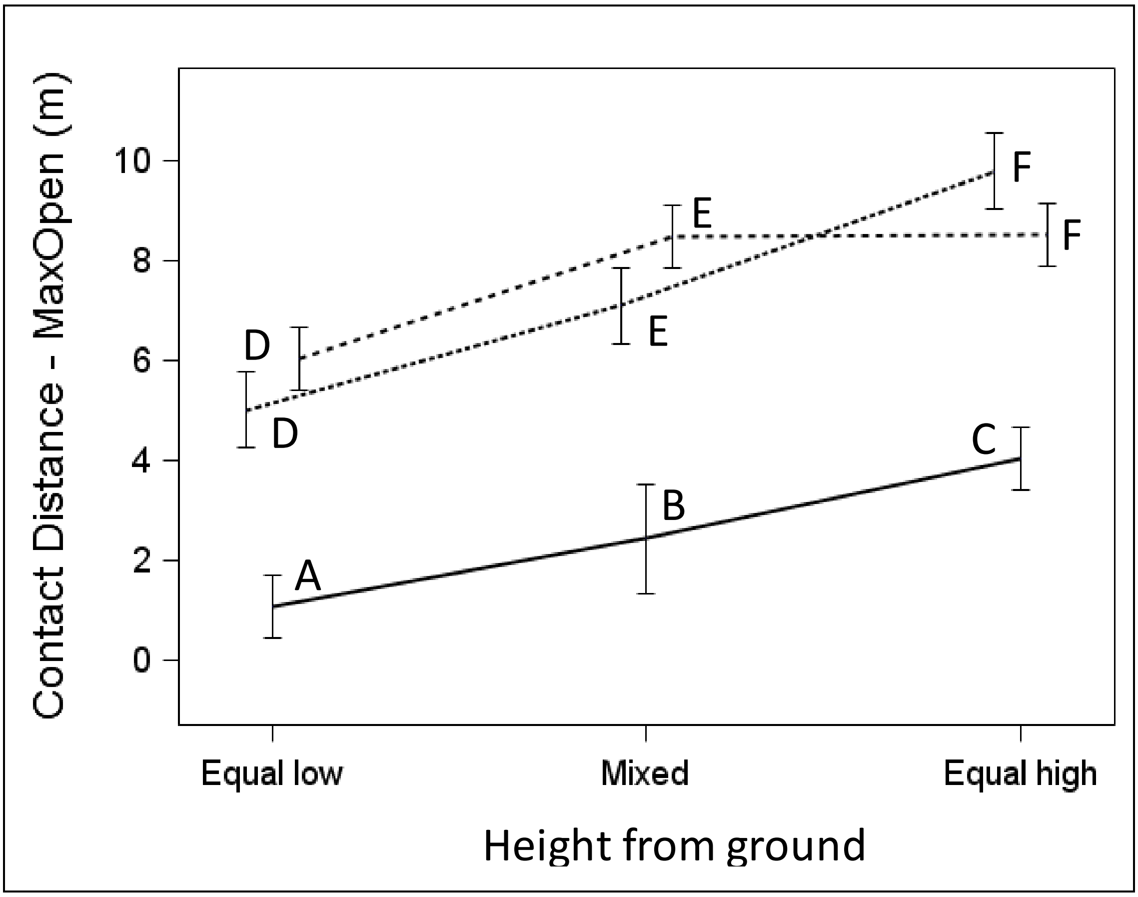


Figure 3 - **Test 1** Plot of the least square estimates of maximal distance of contact opening (MaxOpen) in relation to the radio transmission power, for Sirtrack logger (left panel) and Wildscope loggers (right panel). Letters indicate the significance of one-way variation for covariate pairs, and specifically differences of MaxOpen derived from combinations of logger type and radio transmission power (i.e., also across panels). To note that the lines are drawn only to facilitate the visualization but do not describe any interpolation pattern. Bars denote 95 % Confidence Intervals. Small shifts around the tick marks of the abscissae were necessary to improve plot readability. Legend: long broken line = Wildscope coated loggers; short broken line = Wildscope naked loggers.

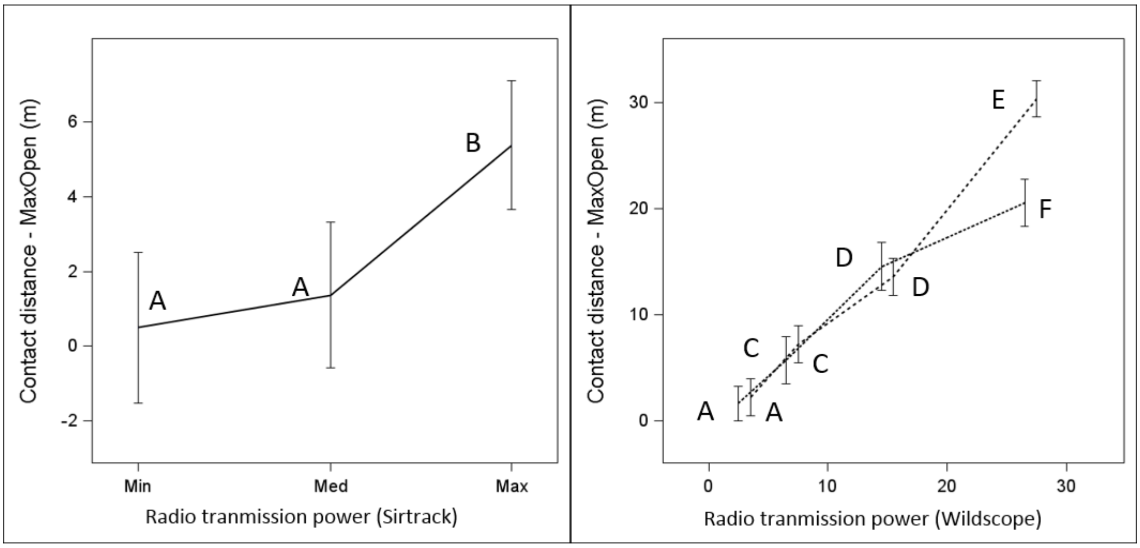


Figure 4 - Test 2 Box-and-whiskers plot of the least squares means of the success ratio of contact detection on the total of expected events, in function of the logger type and the radio transmission power.

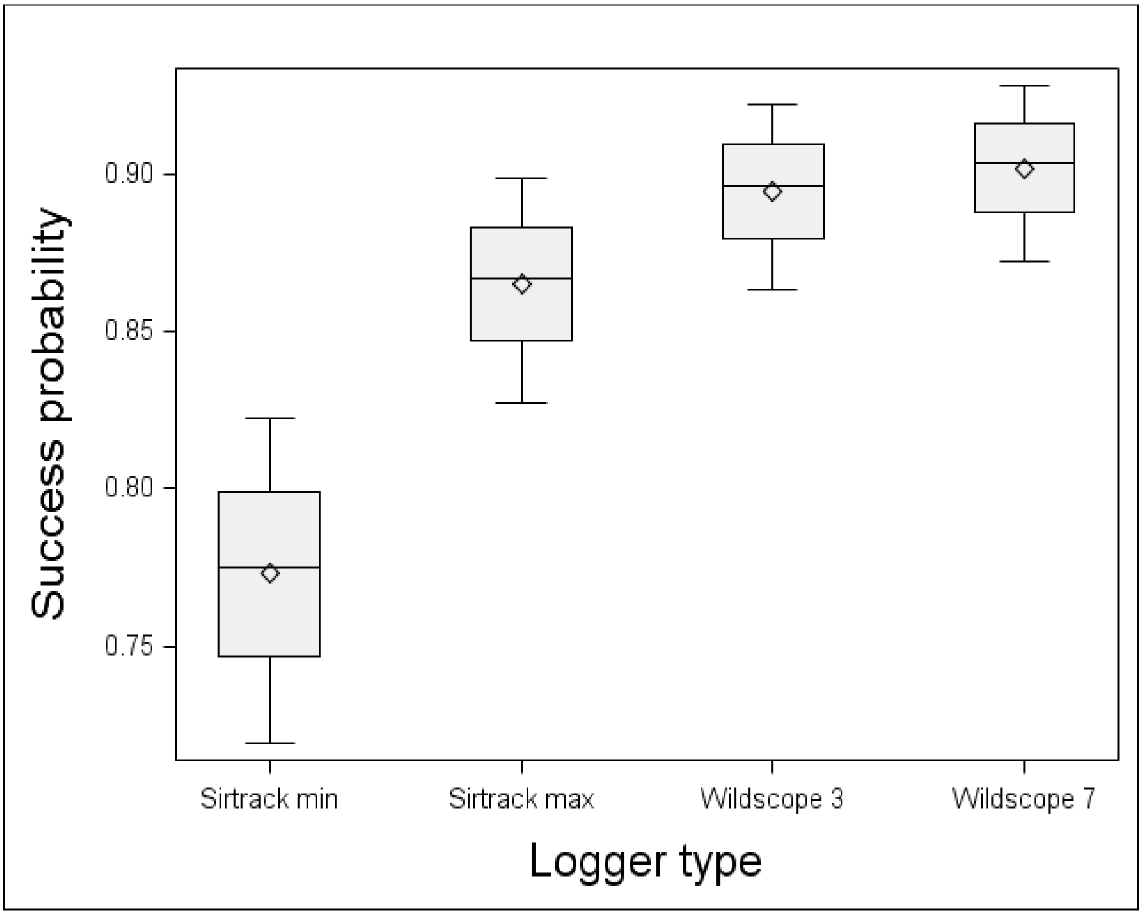


Figure 5 - Test 2 Box-and-whiskers plot of the least-square means of the ratio of false negative events on the total of failures, in function of the logger type and the radio transmission power.

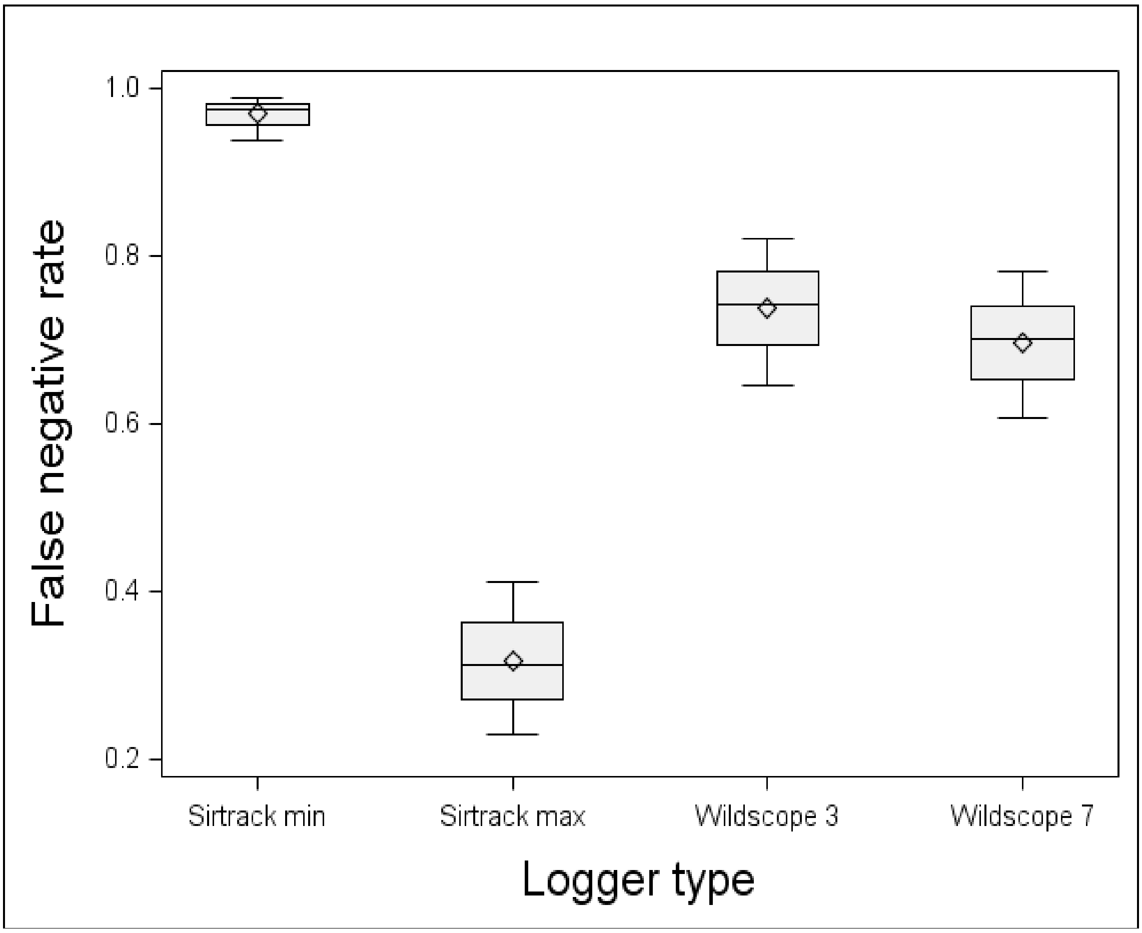


Figure 6 - Test 3 Left panel: plot of the predicted models of contact detection between horses, summarised in Table 2, for each power separately. Grey area represents the 95% confidence interval. To note that the intercept of the curves to the y-axis is not in 1, indicating the occurrence of first type errors (undetected contacts) even at distance between loggers equal to zero (see Table 2 for the values of the intercept and standard error). Legend: continuous line = power 3; short-broken line = power 7; medium-broken line = power 11; long-broken line = power 15. Right panel: the Receiver Operating Characteristic curve (ROC) associated to the four predicted models of contact detection (left panel). False positive rate or (1-the specificity) is plotted against the rate of true positive events, or sensitivity. The perfect classifier is represented by the point of coordinates (0, 1), while the bisector represents the random classifier (continuous thin line). Legend: continuous line = power 3; short-broken line = power 7; medium-broken line = power 11; long-broken line = power 15.

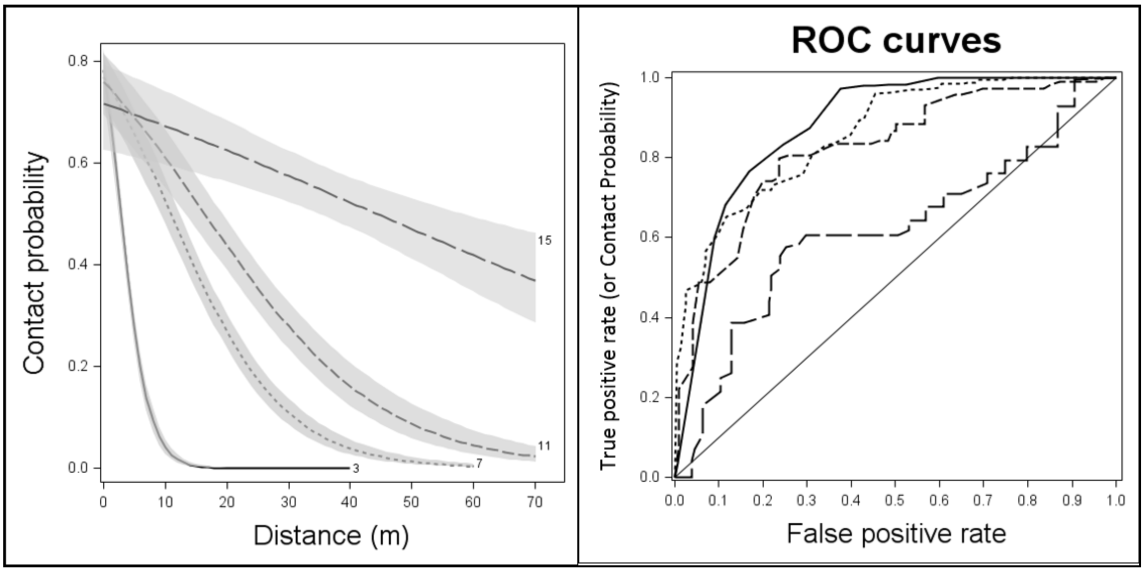


Figure 7 - Test 4 Left panel: plot of the predicted curve of contact detection between roe deer and fixes station, for power 7 (the only one tested), and relative 95% confidence intervals (grey band). Right panel: ROC curve for the model of contact detection (thick black line). Interpretation as in Figure 6.

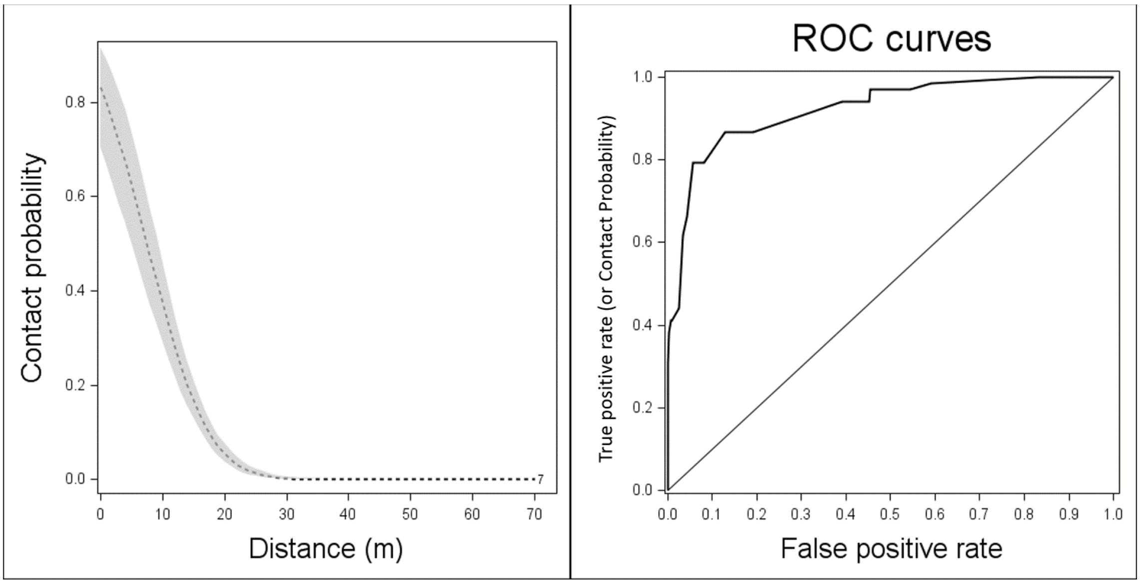
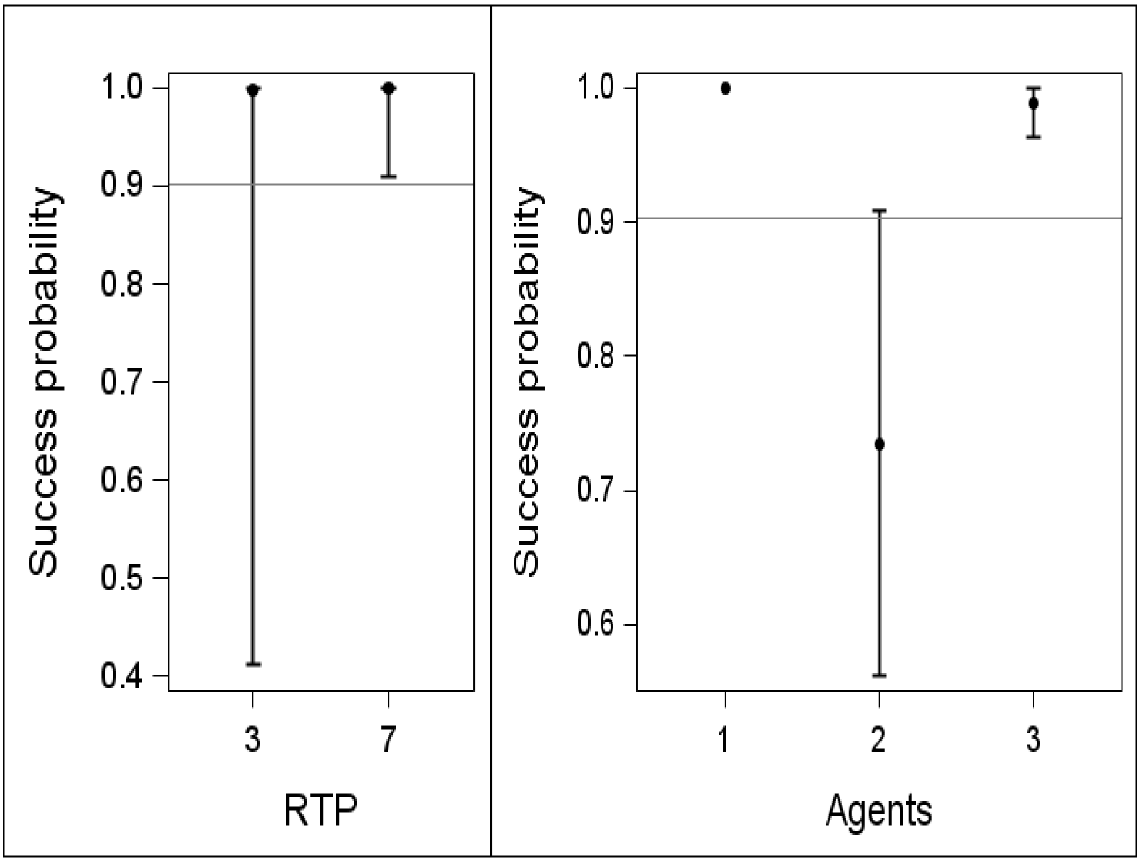


Figure 8 - Test GPS Plot of the least-square means of the ratio of successes on the total of expected GPS locations, in function of the radio transmission power (RTP, left panel) and the number of mobile loggers involved in a given test (agents, right panel). Vertical bars denote 95% confidence limits, truncated at 0 and 1. The horizontal line indicates the average success rate across classes.



APPENDIX S1 – Technical details of Wildscope proximity loggers

Contact detection

Wildscope radio transceivers work with a RF operating in the 2.4 GHz ISM band with 5 MHz bandwidth channels. Interferences with devices working on the same frequencies are attenuated by mean of Direct Spread –Spread Spectrum (DS-SS) technique.

All the loggers compounding the network are tuned on the same radio channel so that they can communicate each other and record the occurring contacts. Contact detection works as follows. The timeline of each node is expressed into epochs, or *logical time*, of duration *d* (e.g. one minute), that represents the time resolution of the system. Within an epoch, the logger broadcasts the radio signal and can detect a new contact. The reception of a beacon from another node causes the creation of a contact tuple in the persistent memory (FRAM) of the node, compounded by the receiver ID, the sending node ID, the starting epoch of the contact and the final epoch of the contact (logical time). The tuple is continuously updated at the start of each new epoch, thanks to the temporary memory of the node that is used to follow the evolution of the contact. If two loggers remain in the range of contact for a given number of epochs, they keep exchanging messages at each epoch. When the two loggers separate, the temporary memory counts the number of missed beacons, i.e. the number of epochs in which the two loggers are not in contact. When the number of epochs of missed contact overcomes a given value decided by the user (i.e., the time-missed-epoch), the contact in the persistent memory is closed and data about that contact are erased from temporary memory. The setting of this value is important, as a too low choice might separate two contacts due to temporarily interruption of radio communication, whilst a too big value can lead to the unification of two distinct biological contacts. Therefore, the definition of both epoch and time-missed-epoch parameters are a trade-off between technical knowledge of the system, and the biological/ecological assessment of the deployment conditions on wildlife.

GPS acquisition

Wildscope proximity loggers support the acquisition of periodic and contact-triggered GPS locations (*acquisition mode*). The periodic locations are recorded at predetermined intervals of time independently from animal movement and encounters, to guarantee the monitoring of the individual, thus allowing the biologist to model individual space use patterns. The acquisition of GPS triggered by contacts is independent from periodic scheduling and permits to geo-reference contact detection, enriching the information on contact detection patterns. Specifically, the acquisition of a GPS location from the node is identical for both the acquisition modes. The GPS tuple stored in the FRAM contains the global time (UTC), latitude, longitude, altitude, HDOP (horizontal dilution of precision), number of satellites used, the acquisition mode (triggered or periodic), the epoch of acquisition (logical time) and indexes on the quality of the data. We set a time out of three minutes for the GPS *to acquire* the location, after which it is switched off and the localization is marked as failed, and a time out for the GPS *to switch on* again after a precedent location (e.g., 15 minutes) to save battery lifetime. Both timeouts are settable parameters. Finally, also the periodicity of triggered contacts (e.g. one at contact detection only, or one every 15 minutes for the whole duration of the contact) is a user-defined parameter.

Data download

The data stored by the loggers can be downloaded remotely in three different ways. First, data can be retrieved by GSM-GPRS modem that establishes a TCP/IP connection with a server to send it the data and the node status. However this system is energetically demanding and requires GSM coverage. Therefore Wildscope platform was established to download data remotely via Wireless Sensor Network, either to a Base Station or to an operator node (up to 250 kbps data transmission rate).

The Base station has the same hardware structure than mobile loggers, with a more spacious persistent memory. It can potentially forward the stored data to biologists by means of a modem connection.

The operator node is a *TMote Sky* node connected to a PC that collects the data and sends them to the PC for storing. It requires the presence of the field biologist in the proximity of the animals loggers carrying the data loggers.

In the case none of these systems works, data can be downloaded by dumping the memory; however this operation requires a physical connection to a PC, and therefore retrieval of loggers.

Data processing

The data collected are stored in a Database Management System (PostrgreSQL). The contact data contain records of the first and last epoch of contact, and need to be realigned with global time. The conversion from logical to global time is obtained by means of the GPS tuples, where both times are collected (see section above). The global time of the GPS is used as the baseline to synchronize all the recorded contacts on a global time scale. Consequently it is possible to compute contact duration and build contact temporal sequences at the time resolution d.

APPENDIX S2 – Detailed description of Test 2

In Test 2 we simulated various scenarios of encounters between one or multiple individuals (i.e., mobile loggers), in presence of a static network (i.e., fixed loggers). In the Figure S2.1 we graphically describe the 'scripts' according to which we performed the test scenarios. Each scenario was performed three times. The path followed by each logger is described by a line (continuous, long dashes, short dashes). The dashed circles around the fixed loggers represent the expected range of contact detection for various power setting (from the smallest cycle to the biggest one: power minimum Sirtrack, Power 3 Wildscope, power maximum Sirtrack, power 7 Wildscope). The radii of these circles, which are not reported here on the proper scale, were derived from the outcome of the Test 1. The filled circles represent trees and bushes of various size that could likely affect the connectivity of the network. Each mobile logger was moved from an agent along a predetermined path, accomplishing several actions (maximum 8 actions/agent), with an established schedule (i.e. each action is controlled in space, and time). Contemporary actions of different agents are indicated with the same letters in the sketches. Such way, we knew the position in time and space of every logger and we could compute the distance from the other loggers at any time. In each scenario, we included a set of stereotyped encounter patterns between two or three individuals, as reported in Figure S2.2. In the upper left panel, we sketched a typical case of encounter and avoidance (e.g. territory defence), with animals approaching from different directions towards a point and changing their direction after the encounter. The upper-right panel simulates two individuals moving in parallel directions, as it might happen for a mother with calves. In the lower left panel, the situation is similar to the one of the upper left panel, but with one more individual involved. Lastly, the bottom right panel represents the typical case of random movement of three individuals in the same surroundings (e.g for feeding purposes).

Based on the outcome of Test 1, we developed predictions on contact detection patterns. As an example, we report in Table S2.1 the expected outcome of contact detection for the mobile logger in the first scenario (one agent and two fixed loggers) for the trials with power 3. In the first four minutes the logger was kept stopped out of the range of the fixed loggers. Therefore we expected no contact to occur. Then in the fifth and the sixth minute the agent moved the logger, entering in the predicted range of contact detection of the first logger. Thus we expected the opening of a contact between the mobile logger and the fixed logger one, as well as a GPS triggered by this contact. In the seventh minute the logger was moved in proximity of the fixed logger, still remaining in its range of contact detection, whilst at minute 8 we moved the mobile logger out of the range, therefore expecting the termination of the contact. In the ninth minute we moved the logger again within the range of the first fixed logger, thus expecting a new opening of the contact and a new GPS, but then in the following two minutes we moved away the logger from the first fixed logger towards the second one. In this case we expected the closing of the contact with the first fixed logger, the opening of a new contact with second logger and a new GPS triggered from this last event. In the following minutes we repeated a similar procedure with a moving away and approaching phase to the second fixed logger.

Similar tables were prepared for all the loggers (fixed and mobile) involved in any scenario tested. After the test we compared our expectations with the outcome of contact detection recorded by the loggers, as reported in the main test.

Figure S2.1 graphical description of the ‘scripts’ according to which we performed the test scenarios. See the text of the appendix S2 for more details.

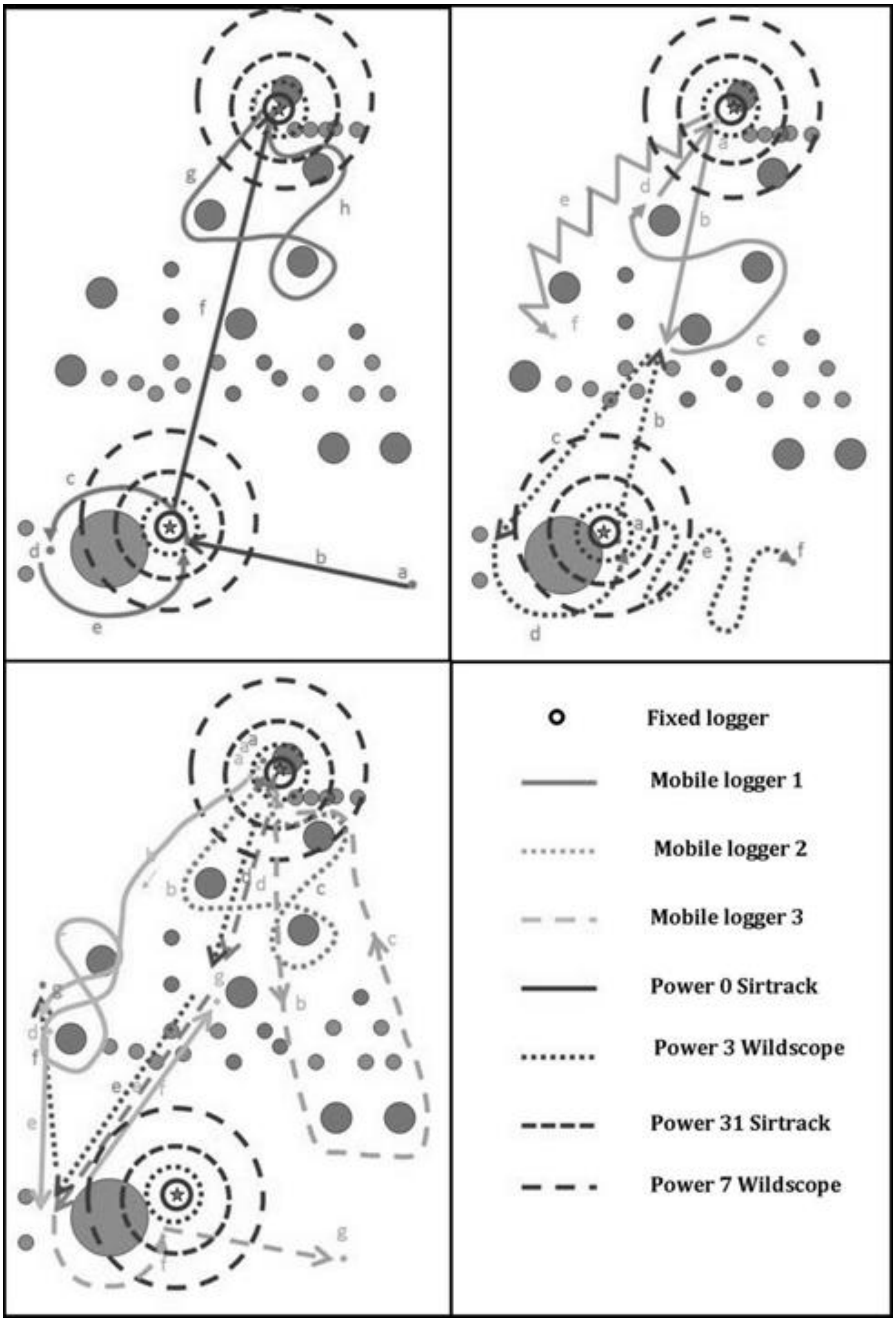


Figure S2.2 graphical representation of stereotyped encounter patterns between two or three individuals. Circles indicate bushes and trees.

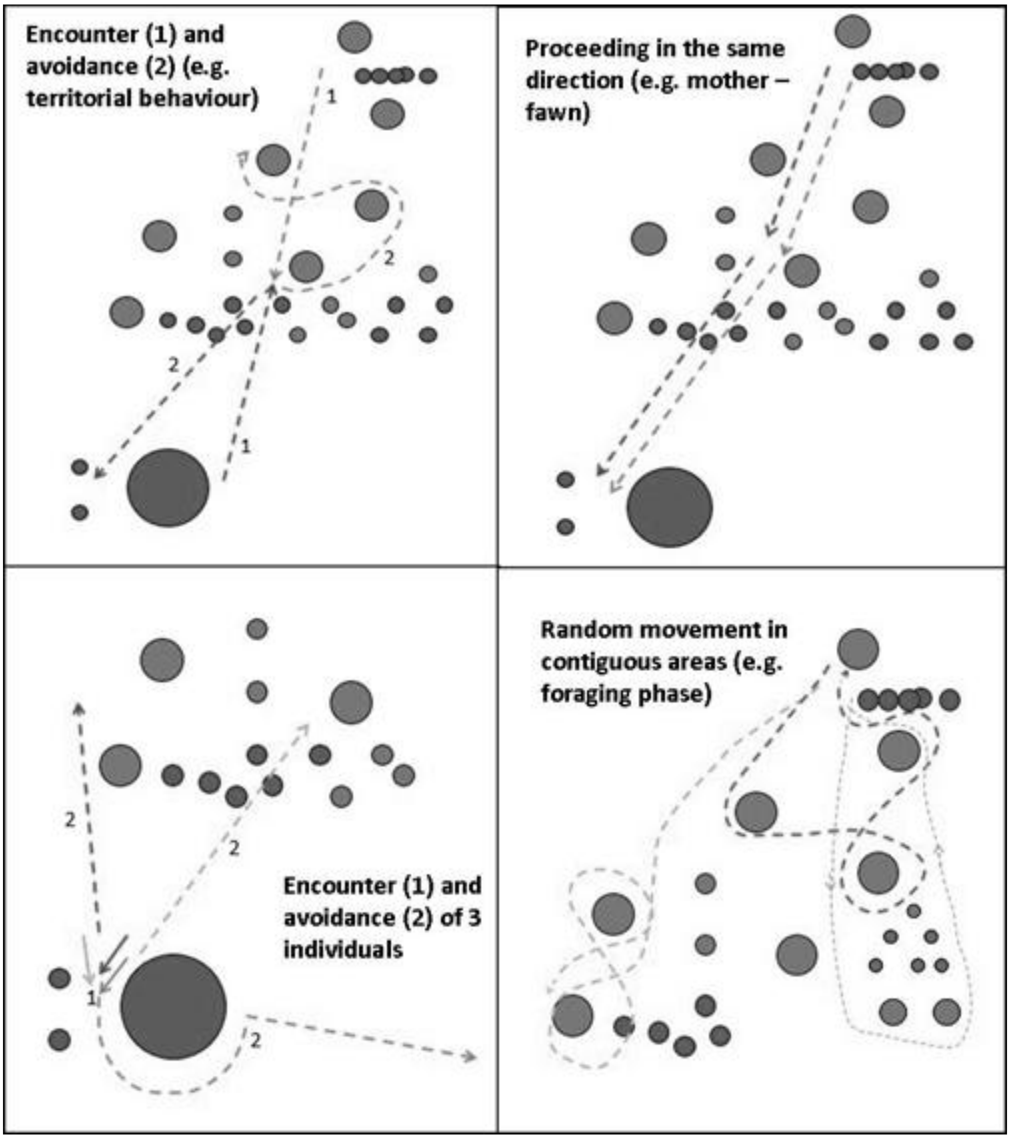


Table S2.1 example of predictions on contact detection patterns. See the text of Appendix S2 for more details

Minute	Action	Agent action	Expected event	Reason of expectation
1 2 3 4	a.	Stop	No contact	Distance > 2,3 m
5 6	b.	Movement	Start contact with fixed node 1; GPS Triggered	Distance < 2,3 m
7	c.	Movement	In contact with fixed node 1	Distance < 2,3 m
8	d.	Stop	End of contact with fixed node 1	Distance > 2,3 m
9	e.	Movement	Start contact with fixed node 1; GPS Triggered	Distance < 2,3 m
10 11	f.	Movement	End of contact with fixed node 1; start contact with fixed node 2; GPS Triggered	Distance > 2,3 m with fixed node 1; Distance < 2,3 m with fixed node 2
12 13	g.	Movement	End of contact with fixed node 2	Distance > 2,3 m
14 15	h.	Movement	Start contact with fixed node 2; GPS Triggered	Distance < 2,3 m
16 17	i.	Stop	In contact with fixed node 2	Distance < 2,3 m

APPENDIX S3 – Model selection

Table S3.1 Model selection for dependence of contact detection distance on logger type, height from ground and radio transmission power.

Model	AIC
Height*power*device	2122.7
Height*power+device	2339.5
Height+power*device	2396.9
Power*device	2465.9
Power+height*device	2467.3
Power+height+device	2487.3
Power+ logger_type	2545.1
Power*height	2571.2
Power+height	2673.3
Power	2715.7
Height*device	2866.7
Height+device	2877.2
Logger_type	2905.9
Height	2943.9
Intercept only	2972.8

Table S3.2 Comparison of a suite of models where we evaluated the dependence of the GPS success rate on the number of agents used for the tests (Actors) and the radio transmission power. Legend: '*' indicates two-way interaction

Model	**AIC**
Actors+ Power	30.38
Actors	33.96
Power*Actors	34.06
Power	49.83
Intercept	52.21

APPENDIX S4

Full set of replicates for test 1, given by the combination among logger type, radio transmission power, and height of loggers from ground. The number of trials is lower for the type "Wildscope naked" due to the malfunctioning of two loggers during the test.

Observation_ID	Logger Type	Power	Height from ground	Number trials
1	Sirtrack	0	100 - 100	20
2	Sirtrack	0	20 - 20	20
3	Sirtrack	0	100 - 20	20
4	Sirtrack	16	100 - 100	20
5	Sirtrack	16	20 - 20	20
6	Sirtrack	16	100 - 20	20
7	Sirtrack	31	100 - 100	20
8	Sirtrack	31	20 - 20	20
9	Sirtrack	31	100 - 20	20
10	Wildscope naked	3	100 - 100	14
11	Wildscope naked	3	20 - 20	14
12	Wildscope naked	3	100 - 20	14
13	Wildscope naked	7	100 - 100	12
14	Wildscope naked	7	20 - 20	12
15	Wildscope naked	7	100 - 20	14
16	Wildscope naked	15	100 - 100	12
17	Wildscope naked	15	20 - 20	12
18	Wildscope naked	15	100 - 20	12
19	Wildscope naked	27	100 - 100	12
20	Wildscope naked	27	20 - 20	12
21	Wildscope naked	27	100 - 20	12
22	Wildscope caged	3	100 - 100	20
23	Wildscope caged	3	20 - 20	20
24	Wildscope caged	3	100 - 20	20

25	Wildscope caged	7	100 - 100	20
26	Wildscope caged	7	20 - 20	20
27	Wildscope caged	7	100 - 20	20
28	Wildscope caged	15	100 - 100	20
29	Wildscope caged	15	20 - 20	20
30	Wildscope caged	15	100 - 20	20
31	Wildscope caged	27	100 - 100	20
32	Wildscope caged	27	20 - 20	20
33	Wildscope caged	27	100 - 20	20

FIGURE S1

Image of the deployment of the Test 1. The loggers are kept at height 100 cm – 100 cm (equal high) (adapted from Drewe et al. 2012).

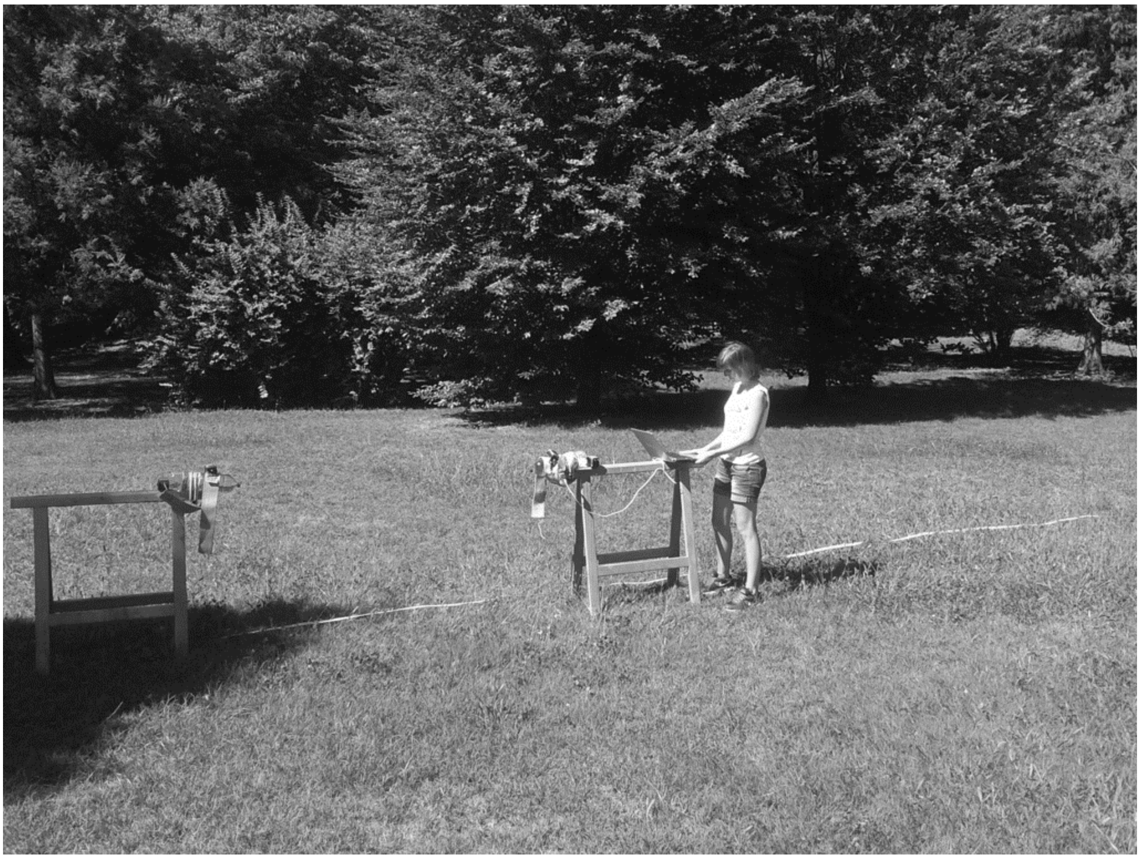


FIGURE S2

Image of the deployment of Test 2. Two agents move the mobile loggers on an established path to simulate a pair of individuals moving side by side. To note that the loggers are fixed on the same supports used in the Test 1.

FIGURE S3

Image of the deployment of the Test 3. The loggers, fixed on easily removable collars, are fitted on horses.

FIGURE S4

Image of the deployment of Test 4. The deer in the picture is equipped with a mobile logger, whilst the fixed logger is deployed on the feeding station close to the photographer' position (not shown in the picture).

CHAPTER 3.2

Spatiotemporal databases and animal tracking data: an attempt to infer spatial relationships under limiting conditions

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ABSTRACT

The perturbation of resource distribution under limiting conditions generated by supplemental feeding practices can lead to unusual concentration of individuals in proximity of feeding sites. This tendency to gather might have negative consequences for animal welfare, e.g. by increasing stress due to competition to access the food or transmission of pathogens. Regardless of the importance of these issues for wildlife preservation and management, the evaluation of the effect of feeding stations on spatial relationships between individuals remains so far widely unknown, probably because of technical constraints associated with the establishment of encounter rates between individuals. I present here the first attempt, to my knowledge, to apply a spatiotemporal database, SECONDO, for inferring spatial relationships between individuals from trajectory data. Relying on the data collected within the EURODEER database, I describe the technical steps to compute the distance between roe deer dyads from their individual trajectory, in relation to their proximity to a feeding station. I then discuss the potential use of this outcome to infer the effect of proximity of feeding stations on patterns of spatial relationships between individuals. I lastly present the perspectives and challenges associated with the applicability of SECONDO spatiotemporal database to investigate other ecological patterns in roe deer and other GPS radio-tracked species.

INTRODUCTION

Patchy spatiotemporal distribution of high quality food resources can lead to unusual concentration of individuals around those food sources, thus creating localized areas of high population density (Cooper et al. 2006). Supplemental feeding stations represent a perfect example of such resources, especially in those areas where winter is the limiting season. Indeed supplemental feeding stations have been found to be attraction points towards which individuals concentrate their movements (see e.g. Van Beest et al. 2010, Guillet et al. 1996). Although feeding stations are usually set with the aim of helping the target supplemented individuals to overwinter (Putman and Staines 2004), there is growing attention focused on the effective impact of feeding on wild populations health (Brown and Cooper 2006) and ecological processes (Cooper et al. 2006). The increase of intra- and inter-specific interactions at feeding sites (e.g. Fagan et al. 2007, Jerina 2012, Campbell et al. 2013) can give rise to competition (Putman and Staines 2004), especially in animals like ungulates that are known to segregate into stable, social groups with dominance hierarchies (Clutton-Brock and Guinness 1982). Competitive feeding behaviour (Ceacero et al. 2012) with the exclusion of subordinates from productive foraging sites (Thouless 1990) can induce stress development in grouping living animals, with negative consequences for population health (Wal et al. 2012). Even more importantly, the increased concentration at feeding sites can enhance the direct or indirect pathogen transmission (Conner and Miller 2004, Kenkre et al. 2007, Thompson et al. 2008, Sorensen et al. 2014). Indeed connectance between individuals is one of the main factors affecting transmission rate of wildlife diseases (Perkins et al. 2009). These issues are of particular relevance in a species as roe deer (*Capreolus capreolus*), which is an important host of several zoonosis (see e.g. Carpi et al. 2009). Supplemental feeding has been found to affect roe deer space use tactics, acting as central places towards which the individuals tend to converge (Guillet et al. 1996). However, the analysis of the effect of the feeding stations from an inter-individual perspective, i.e. looking at the spatial relationships between individuals, has received much less attention.

The lack of knowledge on this topic is certainly affected by the technical challenges associated with the assessment of spatial relationships between individuals, which require to conjugate the spatial and temporal information from individuals. In this sense, the recent development of proximity loggers (see e.g. Prange et al. 2006, and the Chapter 3 of this thesis for further details) represents a valid way to investigate contact rate between individuals. However, the use of proximity loggers is so far limited. As an alternative, it is possible to infer spatial relationships between individuals from their movement trajectories, i.e. using the data collected by Global Position System loggers (GPS) (see e.g. Schauber et al. 2007, Kjaer et al. 2008, Habib et al. 2011).

Although the accuracy of the inferred spatial relationships is fatally limited by the intrinsic position error of GPS devices (D'Eon and Delparte 2005), the amount of available location data for analysis is huge, especially if compared to the data collected by contact loggers. GPS data could thus be used at least to infer trends of occurring spatial relationships between individuals, acknowledging the limited precision of the data and consequently limiting the biological inferences of the observed patterns.

A valuable tool to work involves spatiotemporal databases, i.e. which conjugate spatial and temporal information on moving objects. To our knowledge, these management tools have almost never been applied to animal tracking data. Indeed spatiotemporal databases may represent the way to go for next generation data management in movement ecology (Urbano et al. 2010). SECONDO is a spatiotemporal database recently developed (Guting et al. 2005), which allows investigation of moving objects both in a spatial and temporal dimension. In SECONDO semantic, animal trajectories are moving objects that can be analyzed in pairs to detect the distance between the animals at each time, and ultimately extrapolate information on the spatial relationships between individuals. Assuming a threshold distance between individuals to define them 'in contact', it is possible to exploit SECONDO capabilities to infer contact rates among individuals.

From the biological perspective, the spatial relationships between individuals inferred from SECONDO application represent a valuable information that can be used to address important ecological issues, such as, for instance, the influence of aggregation on contact rate and on disease transmission patterns in wild populations.

On the other side, SECONDO has not yet been applied to tracking animal data. Therefore, even from the perspective of SECONDO database developers, the challenge to transform biological questions in SECONDO spatiotemporal queries represent a step forward for the extension of the applicability of this spatiotemporal database.

This collaborative work, which involved biologists and IT people, represents therefore a perfect example of sharing reciprocal scientific knowledge to enhance the quality of the final outcome.

In this work, I firstly aimed at evaluating whether SECONDO spatiotemporal database could work with GSP data that are collected at relatively long time intervals. In fact SECONDO has been used to infer spatiotemporal patterns of moving objects, which are continuously tracked (e.g. cars, planes, trains…) while animals are often tracked at scheduled interval times that range from a few minutes to several hours, to trade-off between information acquisition and saving GPS battery.

Then, I wanted to explore the patterns of spatial relationships between roe deer in proximity of feeding stations, across a wide latitudinal and altitudinal gradient, relying on the data collected within the EURODEER scientific collaborative project (www.eurodeer.org). In particular, I wanted to exploit the features of SECONDO to determine the distances occurring between pairs of individuals, in relation to the distance from the closest feeding station and its management. In perspective, these data could then be used to infer inter-individual relationships between individuals in proximity of feeding stations, thus constituting a valuable proxy to evaluate the potential negative effect of supplemental feeding practice on welfare of roe deer populations.

MATERIALS AND METHODS & PRELIMINARY RESULTS

Data collection

I used for the analyses the GPS data collected and stored within the EURODEER database (www.eurodeer.org) (see the main section on Material and Methods for an extensive description of the database). In particular, for the biological purposes of this work, I selected the GPS data from the nine study areas where supplemental feeding is practiced (see chapter 1 above for a detailed description of the study areas). Moreover, I discarded from the analyses those individuals which were monitored for less than 60 consecutive days, or whose monitoring period did not overlap the activation of feeding stations (i.e. which were not monitored during wintertime, see chapter 1 above for further details). As a result, the sample size included more than 1.5 million GPS locations, from 281 individuals, with a pretty balanced sex ratio (161 females and 120 males).

In parallel, I collected the data on the management of feeding stations in these areas, which included their position and dates of activation (i.e. the period in which the feeding stations are filled with food by managers), and several other covariates related to their management (described in details in chapter 1).

Processing of spatial data in SECONDO database

The process from import of raw GPS locations to determination of the distance between the locations of a pair of individuals is a process that involves several steps, which are described in detail here after. Within SECONDO, as well as in other database relational systems, a table is defined as a 'relation', in that the data it contains can be joined with information stored in other tables. Accordingly, this will be the terminology used in this section to describe the processing of data within SECONDO database.

Data import and standardization

The GPS raw data, the information on the individuals (sex, age, study area) and the supplemental feeding management data were imported in three empty relations within the database that had been previously created. The GPS data within the EURODEER database are often scheduled at different sampling intervals, according to the needs of any research group. Moreover, missed locations are common, due to technical issues related to this technology (e.g. malfunctioning, failure of retrieving the data from individuals, etc…). Since trajectory standardization is an important issue to consider when analyzing movement data, I imposed a filter to keep only locations occurring at 3 hours interval frequency or more. I also excluded from analysis those parts of trajectories where the interval between subsequent relocations exceeded 24 hours: from a biological perspective, I considered this gap as too long to infer any biological pattern based on linear interpolation between the relocations.

From raw data to objects for distance computation

SECONDO database allows spatiotemporal queries on moving objects to be done, which are issued from raw location data. A moving object is by definition an object that changes its position in space and time. SECONDO creates moving objects from the location data, based on linear interpolation between subsequent relocations. Specifically it starts this operation from the first position data (individual relocation) until the last one available. As such, each individual trajectory is transformed in a moving object, which can be used to query spatiotemporal patterns of proximity with other moving objects.

I used SECONDO also for the management of feeding stations. These resources, in a spatiotemporal database perspective, can indeed be considered as objects that are fixed in the space but temporary dynamic (according to their activation state, which in turn depends from supplemental feeding management). SECONDO associates the spatial position of feeding stations to moving bools, which define the status of an object in the time. The moving bool was set to be true in the case the feeding station was supplemented at a specific time, or false in the opposite. This operation allowed analysing spatiotemporal patterns between individuals (moving objects) in relation to the proximity and activation state of the feeding stations (moving boolean).

Computing distances in SECONDO

For each pair of moving objects, SECONDO computes a '*moving real*', i.e. their distance at each instant in which these objects are defined. In the most of the instants the position of an object is not real but derived from linear interpolation. I was interested in computing the distance between a generic object 'A' and another object 'B' only at real positions (i.e. GPS locations) of the individual 'A'. In fact the ancillary information (e.g. land cover, snow cover, temperature, precipitation…), which are commonly used to infer the biological motivation of an individual for being in a given position, are related to a real GPS location, and cannot be extended to any interpolated point. As such, I forced SECONDO to compute only the distance between the real locations of a moving object 'A' and the locations (true or interpolated) of a moving object 'B'. I thus defined, for each pair of moving objects, a series of distances, true or interpolated. Specifically, I defined 'true distances' as those which were computed between a real location of the moving object 'A' and real locations of a moving object 'B' as those which fell within a ten minutes buffer from the real location of moving object 'A'. Alternatively, the distances between a real location of the moving object 'A' and interpolated locations of the moving object 'B' were classified as 'interpolated distances'. This process was run only for pairs of synchronous moving objects closer than 70 kilometers; this threshold was chosen to avoid meaningless computation of distances between individuals living in different study areas. I thus obtained a relation including over 7 million rows, each recording the identity of the two individuals, the length and type of computed distance (true or interpolated), and the time instant in which the distance was computed.

I applied a similar procedure to compute the distance between individuals and the closest feeding station. Firstly, I programmed SECONDO to query the distance between the real position of a given individual (moving object) and the position of the feeding stations, taking in account their activation state. Then, I selected the lowest among all the computed distances between a real position of the moving object and the feeding stations.

Associating distances with ancillary information on animals, environment and feeding management

The information on distance between two individuals *per se* is not particularly informative on animal state, and scarcely permits to infer biological motivations underlying the observed movement pattern. To elucidate the main drivers of spatial relationships between individuals, it is necessary to associate ancillary information on environmental conditions, biological features of the animals and management of feeding stations to the records on the distances between individuals or between an individual and a given feeding station. These data are then analyzed with appropriate statistical tools to derive relevant biological conclusions on the patterns found. In this respect, I associated the records of each distance between a generic pair of individuals 'A' and 'B' with information on their sex and age at the specific time in which the spatial relationship was measured. Then, I also joined the ancillary environmental data relative to the position of the individual 'A' of the pair considered (snow cover, land cover, temperature, topography…). Since I was interested in assessing the effect of proximity to feeding stations on the spatial relationships between individuals, I also joined the distance between the individual 'A' and the closest feeding station, which was computed at the same time as the distance between the two individuals. Lastly, I associated to the final data the information on the management characteristics of the specific feeding station, including its activation state. The ancillary data collected are summarized in Table 1.

DISCUSSION AND PERSPECTIVES

I demonstrated that SECONDO spatiotemporal database can be applied to the analysis of spatial relationships between radio-tracked individuals. The periodicity with which the GPS data are collected was not a major technical concern, and the data could be easily imported within SECONDO database and processed as illustrated above.

The association of the data on spatial relationships between individuals with a series of biological, environmental and management related covariates should now permit to link the observed patterns with the factors that drive them. However, statistical models to work in this direction are not trivial to apply. A promising approach would come from multivariate statistics, and in particular multivariate matrix analysis (Johnson et al. 2002). This modelling approach might permit to quantify variation of spatial relationships between individuals in relation to the distance from the closest feeding station, which in turns is expect to depend from other environmental and management related covariates. To our knowledge, this kind of analysis would thus allow to infer for the first time the effect of feeding stations on roe deer from an inter-individual perspective, opening exciting perspectives to evaluate the importance of these sites on dynamics of disease transmission, e.g. by means of Social Network Analysis (Krause et al. 2007).

Given the easiness to compute the distance between individual pairs within SECONDO spatiotemporal database, such approach could be extended to the investigation of other relevant biological patterns in any GPS or VHF radio-tracked species. Limited to the case of roe deer, it might be worth to assess whether the spatial relationships between individuals in winter ranges concur to affect migration patterns, under a density dependence hypothesis (Mysterud et al. 2011). Other relevant topics that might be investigated are the spatiotemporal variation of relationships between neighbor males during territoriality phase (Hoem et al. 2007), or the parental care of females during the first months of life of fawns (this would require radio-tracking data of roe deer fawns, which have been collected in some study areas).

The huge potential for SECONDO application to wildlife investigation also poses some relevant technical challenges and interesting perspectives. First, since SECONDO outcomes are generally quite big datasets, high computational power machines are required to run the desired analyses. Second, it still has to come the implementation of raster layers within SECONDO database. Raster data are commonly used to run spatial analysis in ecology; their information can conspicuously improve the quality of the analyses performed. For instance, the implementation of Digital Elevation Models (DEM) raster might permit to compute distances between individuals in a three-dimensional space, a quite relevant aspect to consider when working with animals in mountainous areas. Lastly, it would be interesting to connect SECONDO to other already existing database, such as EURODEER. The creation of a network between these databases might allow the direct computation of spatiotemporal queries within the EURODEER environment, thus fastening the processes above described to infer spatial relationships between individuals. All these perspectives described aim at better exploiting the raw data on individual locations locally collected, improving the quality of the scientific outcomes that can help scientists to increase their knowledge on biological patterns under investigation.

A brief demo on the functionality of SECONDO spatiotemporal database is available at http://www.youtube.com/watch?v=GWbdc1BZQ_A&list=UUJrt_PkHUvf9JWGovpG0c4Q.

TABLES

Table 1. Description of the data associated with the distance between a pair of generic individuals ‘A’ and ‘B’ in a given instant of time T.

General information field	Data collected
Spatial relationship between individuals	Distance between individual ‘A’ and individual ‘B’
	Type of computed distance (true or interpolated)
	Instant time ‘T’ in which the distance is computed
Attributes of the individuals	Sex and age class individual ‘A’
	Sex and age class individual ‘B’
Environmental context (at location of individual ‘A’)	Land cover
	Snow cover
	Topography (altitude, slope, esposition)
Feeding station management	Distance location ‘A’ to the closest feeding station at time ‘T’
	Activation state of the feeding station
	Quality of food provided
	Presence of competitors at feeding station
	Typology of feeding station (proper feeding or box trap)

CONCLUSIONS

The assessment of roe deer space use patterns in winter clearly demonstrated the importance of adverse environmental conditions on shaping individual movements. As a consequence of its low morphological and physiological adaptations to winter severity (Holand et al. 1998), and of its income breeder tactic (Andersen et al. 2000), roe deer display movement patterns that are highly sensitive to the lack of resources and to winter severity (expressed by deep snow cover and low temperature). Indeed, my work shows that roe deer use of feeding stations does not match temporally with the availability of resources. Instead, my results support the hypothesis of 'environmental triggering' of feeding station use, which nicely accounts for the selective feeding behavior of roe deer. The importance that environmental conditions have on shaping roe deer movement patterns underlines the relevance of acquiring robust data on the environmental covariates that are expected to influence the observed movement patterns (Maher et al. 2012). Accurate data on temperature variation and snow cover patterns are required because these climatic variables are likely the most important drivers of roe deer (and other ungulates) winter movement patterns in mountain and northern environments. My large-scale analysis identified a marked role of temperature but not of snow cover in the use of feeding stations and ultimately for shaping roe deer movement patterns. However, the snow cover affects roe deer winter resource selection in the Alps, where accurate data empirically collected on snow conditions could be used to explain reliably individual movement patterns. I recognize the logistic unfeasibility to couple empirical collection of detailed snow cover data with large-scale patterns assessment. However, recent progresses in Remote Sensing provide detailed data on the spatial distribution of these environmental covariates (e.g. MODSCAG for snow cover assessment, Rittger et al. 2013; surface temperature: Metz et al. 2014). Applying these data for ecological investigation of large-scale movement patterns, for which the empirical collection of data is logistically impossible, would greatly increase the quality of the results obtained (Maher et al. 2012).

Supplemental feeding is pervasively practiced throughout most of European countries (Putman et al. 2011). My research highlights the importance of this perturbation of natural systems as a component of roe deer winter habitat. Therefore, the distribution of feeding stations should be considered when modeling movement patterns of individuals living in those areas where supplemental feeding occurs. According to Mysterud (2010), supplemental feeding represents a form of semi-domestication of ungulates, i.e. of partial control on space use patterns resulting from human actions that aim at increasing the potential economic (or other) profit from a species management (Clutton-Brock 1999). In this sense, supplemental feeding is a perfect example of human-induced modification of a natural system, which we cannot ignore when analyzing movement ecology issues of supplementary fed species. In other words, ecologists should move their focus onto the analysis of an 'anthropogenic bioma' (*sensu* Ellis and Ramankutty 2008), in which human-induced alterations such as feeding stations are an inside part of the system to analyze and not an external component to it. This is a crucial issue to consider for sustainable management of ecosystems affected by human impact. For example, Jones et al. (2014) recently found that migration in red deer (*Cervus elaphus*) could be substantially altered by modification of resource distribution due to supplemental feeding. In the case of roe deer, the distribution of feeding stations was not considered when analyzing partial migration (Cagnacci et al. 2011), but based on my results that feeding stations affect individual movement patterns, it might be worthy to reconsider roe deer migration patterns in relation to the distribution of feeding stations. In particular, it would be interesting to assess whether supplemental feeding management influences migration patterns in space (e.g. distance of migration, use of stopover sites) and time (linking the timing of migration with the management of the feeding stations).

The relationship between roe deer use of supplemental feeding and winter severity suggests that this management practice provides to individuals an 'emergency feeding to buffer climate extremes' (Mysterud 2010). Under this scenario, it is crucial to investigate the effect of ongoing environmental alterations due to climate change (Alley et al. 2003) on patterns of use of feeding stations and, ultimately, on individual movement patterns. Indeed, climate change is inducing an increase of temperatures (Iones et al. 2013), with the consequence of increasing freezing level (IPCC 2007) and, as such, distribution of snow cover at low and intermediate altitude (Steger et al. 2013, O'Gorman 2014). In turn, alteration of snow depth and snow melting time has important implications for plant phenology and re-growth (Wipf et al. 2009), thus affecting the spatiotemporal distribution of natural resources (Post and Stenseth 1999). If the motivation for management of feeding sites is to buffer extreme winter conditions, the change in climate should lead to a reassessment of this management practice.

A potential way to investigate in this direction is by mapping 'critical areas' for roe deer in winter, where supplemental feeding might be justified (but see below for more general considerations on the drawback of this practice). In this sense, the first requirement is the determination of tolerance threshold of temperature and snow cover, over which we can assume that roe deer face an energetic crisis caused by the combined costs of thermoregulation and hampered locomotion. In this regard, I found a threshold of snow tolerance around thirty centimetres during a not excessively snowy winter. To my knowledge, the determination of a critical threshold of temperature (e.g. by relating air temperature to the amount of use of supplemental food as proxy of energetic expenditure) was lacking up to now. The next step to determine critical areas implies the retrieving of predictive distribution maps of snow cover and temperatures, which could be reclassified in categorical maps of roe deer 'tolerance' or 'avoidance' for snow and temperatures, according to the determined thresholds. Predictive maps providing information on expected variation of temperature and snow cover are available, due to massive research on climate change (e.g. Metz et al. 2014; Lawrence and Slater 2010). Lastly, the interpolation of these data could permit to generate predictive maps of 'overwinter suitability' for roe deer. The overlap with distribution of feeding stations might allow identifying those sites where this practice might be no more justified in future – assumed that the supplemental feeding is indeed managed to buffer climatic extremes.

Beyond considering supplemental feeding practice as a matter of fact that has to be included in movement ecology investigations, or questioning on future perspectives regarding the way to manage such resources, a central question remains open to debate: is supplemental feeding a correct practice for ungulates management? Researchers need to focus on the trade-off between benefits and costs of supplemental feeding to help wildlife managers to take the right decision for roe deer, as well as for other ungulates. Besides providing an alternative food resource under limiting conditions, there are several other motivations associated to the use of supplemental feeding (Putman and Staines 2004). These include the maintenance of high individual densities and the enhancement of males' trophies for game purposes; the reduction of browsing on young stems to preserve forest; or the alteration of migration patterns to limit impacts on human activity (e.g. car accidents). In this sense, the effectiveness of supplemental feeding practice is still controversial: in the case of roe deer, as well as for other large ungulates, we indeed lack evidence about the need to feed animals (Putman and Staines 2004). Comparing individual performance between fed and unfed individuals living under similar environmental conditions might provide a valuable way to investigate this topic. However, even if such researches have found that roe deer individual performance take benefit from supplemental food, we should consider the potential drawbacks of this activity, which might act at different temporal scales. On the long-term, supplemental feeding may risk to create populations that are fully dependent on this food resource (Mysterud 2010), and eventually can lead to the alteration of fundamental evolutionary processes like natural selection (Schmidt and Hoi 2002; Mysterud 2010). The aggregation of individuals in proximity of feeding sites is a more immediate pitfall of supplemental feeding, which can give rise to intra- or inter-specific competition, and especially enhance the risk of disease transmission (see e.g. Blanco et al. 2011, Sorensen et al. 2014). Empirical assessment of contact rates at feeding sites may represent one of the first steps to be accomplished to investigate that topic. Indeed the determination of contact patterns may permit to investigate the consequences of supplemental feeding practice on animal welfare (e.g. by means of Social Network Analysis approach (Krause et at. 2007)), an issue of particular relevance for a species like roe deer, which is an important host of several zoonoses (e.g. Carpi et al. 2009).

In spite of the relevance of the issues here discussed, and of the pervasiveness of supplemental feeding practice across Europe, well-documented cases investigating the effects of feeding sites on ungulates ecology remain surprisingly few (Mysterud 2010). In this thesis, I tried to set the basis for future investigation in this direction for roe deer, providing evidence of a link between the distribution of these resources and individual movement patterns in winter limiting conditions. I am aware that investigating in this direction may provide inconvenient results for wildlife managers and hunters, which may have to revisit their management habits. However, time has come for ecologists to accept the challenge and fairly investigate in this direction, in order to acquire robust knowledge to preserve successfully the (limited) natural systems that we aim to defend.

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