UNIVERSITÀ
DI TORINO

UNIVERSITA’ DEGLI STUDI DI TORINO

Dipartimento di Scienze della Vita e Biologia dei Sistemi

TESI DI LAUREA MAGISTRALE
Evoluzione del comportamento animale e dell'uomo

Anthropogenic Disturbances and Wildlife Co-occurrence: Spatial Interactions between Wild Ungulates, Humans and Wolves in the Maritime Alps

Candidata:
Francesca Rolle
Francesca Rolle

Relatrice:
Francesca Marucco
Francesca Marucco

Correlatrice:
Maria Virginia Boiani
Maria Virginia Boiani

Anno Accademico 2021/2022

Table of Contents

1. Introduction

Different species living in shared environments often rely on similar resources, leading to complex interspecific interactions that influence their abundance and distribution (Kavčić et al., 2021; Thurman et al., 2019). These interactions can involve competitive and/or predator-prey dynamics (Berryman, 1992; Tilman, 1982), making it challenging to understand the factors that enable coexistence (Darmon et al., 2012), especially in anthropized environments where human activities can further complicate the relationships between species (Van Scoyoc et al., 2023).

Competitive interactions lead to physiological and behavioural adaptations (mainly spatial and temporal avoidance; Kneitel & Chase, 2004; Kitchen et al., 1999), which are shaped by multiple factors such as resource availability, animal density and degree of overlapping between competing species (Kavčić et al., 2021). In addition to competitive interactions, sympatric species may be exposed to predation risks, which represent another crucial variable in determining direct and indirect behavioural adaptations (Sönnichsen et al., 2013; Hebblewhite, 2005). Predators' presence can indeed alter the community structure and its internal dynamics because they perform active killing and therefore alter prey abundance (Polis & Strong, 1996). On the other hand, predators also indirectly influence the behaviour of prey, their activity patterns, habitat selection and distribution by working similarly as an environmental pressure (Hebblewhite, 2005; Schmitz et al., 1997). These non-lethal effects of predation can often be spatially and temporally structured, creating a heterogeneous "landscape of fear" (Laundré et al., 2001) that shapes animal behaviour and habitat use patterns (Wirsing et al., 2021; Suraci et al., 2019). The "landscape of fear" refers to the spatial and temporal variation in the risk of predation that prey experience in a given environment (Laundré et al., 2001). By modifying their responses to these risk factors, animals can potentially reduce their vulnerability to predation and other threats (Gaynor et al., 2019; Laundré et al., 2010). Species coexistence is facilitated when the shared habitat presents heterogeneity of resources, thus allowing sympatric species to partition in different spatial niches (Kavčić et al., 2021).

In this framework, the growing human footprint is placing significant pressure on wildlife populations worldwide, as anthropogenic activities continue to introduce multiple stressors into their environments (Montgomery et al., 2020, Bonnot et al., 2013; Boyle & Samson, 1985). In landscapes where human activities, such as farming and urbanisation, have transformed the natural environment, there has been a significant increase in spatial diversity within habitats, leading, for example, to fragmentation of forested areas. Therefore, disturbances resulting from human activities pose a risk to wildlife that is equivalent to predation (Suraci et al., 2019; Darimont et al., 2015; Frid & Dill, 2022). Some wild animals modify their movements (Tucker et al., 2018), activity or feeding patterns to avoid humans (Gaynor et al., 2018). Conversely, other species actively seek out human-associated environments to acquire resources or safety and thrive in urban areas (Newsome & Van Eeden 2017; Lowry et al., 2013).

The Western Alps present an ideal scenario to study the complexity of interspecific interactions and coexistence in a shared habitat. This ecosystem is home to several species, including predators, prey, and humans, which coexist in close proximity. The presence of multiple species of ungulates - in particular, roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), - and the only large predator in the region - wolf (*Canis lupus*) - creates an intricate web of interactions and relationships that shape the landscape and influence the behaviour of each species.

However, the social and economic crisis of the mid-19th century resulted in the colonisation by humans of many mountain areas, which were then exploited for agriculture, deforestation, and livestock grazing. Hence, the decline in forested areas, along with direct persecution and the general growth of human populations, represented the main cause of wide-spread population extinctions for both prey and predators (Palmegiani et al., 2013; Perco, 2011; Breitenmoser, 1998).

Specifically, roe deer faced extinction in the 1920s (Randi, 2005) and was later reintroduced for hunting reasons. Likewise, the red deer was also eradicated from the area but then reintroduced for hunting purposes (Mattioli et al., 2001). In contrast, the wolf, which also faced extinction in the area, naturally recolonised the western Alps from the Apennine regions (Fabbri et al., 2007).

Subsequently, in the 1960s a gradual abandonment of mountains by the human population favoured the general recovery of wild species numbers and distribution. The consequent increase in wooded areas and ecotones has improved environmental conditions for wild ungulates (Mori et al., 2017; Perco, 2011), thus leading to the return of predators that had disappeared also due to the absence of prey (Chapron et al., 2014).

Consequently, animals with broad ecological plasticity could expand their distribution range, thus encountering other mountain ungulates. The co-occurrence of red deer and roe deer, in the same area has been documented to negatively impact the latter (Borkowski et al., 2021; Richard et al., 2010). These two species show a dietary overlap that leads to resource competition (Torres et al., 2012), mostly due to red deer's more general feeding needs, which include all the plant resources roe deer relies on (Borkowski et al., 2021; Ferretti & Mori, 2020; Richard et al., 2010).

Among cervids, roe deer are highly selective herbivores (Freschi et al., 2017; Jong et al., 1995). Several studies (Borkowski et al., 2021; Freschi et al., 2017; Jong et al., 1995) showed how roe deer’s diet is limited to few major plant species even when multiple plants are available. Roe deer’s selective feeding strategy consists of browsing the most nutritious and palatable plants first (Freschi et al., 2017). Consequently, roe deer is more likely to be found in areas where high-quality food resources are available, such as woods and scrublands (Torres et al., 2012).

Moreover, roe deer are income breeders: they tend not to store fat reserves but invest them directly (Ferretti & Fattorini, 2021). This condition makes them particularly sensitive to changes in food availability (Richard et al., 2010). Accordingly, red deer’s major pressure on vegetation - due to its larger dimensions and numerosity - impacts on roe deer's forage availability (Borkowski et al., 2021), especially in winter (Richard et al., 2010). Given the high sensitivity of roe deer to interference (Ferretti & Mori, 2020; Torres et al., 2012), it has been observed that they tend to adapt by exhibiting behaviours such as temporal or spatial avoidance or utilising suboptimal resources, with this adaptation being typical of inferior species (Kavčić et al., 2021).

The rich wild ungulate community of the Alps represented an interesting topic for studies on the impact of wolf predation (Torretta et al., 2017; Marucco et al., 2008; Gazzola et al., 2005). The wolf predatory behaviour and dietary habits vary according to the ecological conditions, such as prey availability and human presence (Ferretti et al., 2019, Capitani et al., 2004; Ciucci et al., 1996). In areas where ungulate populations are abundant, wolves primarily prey on these species (Ferretti et al., 2019; Meriggi & Lovari, 1996), with cervids being the selected prey of wolves among wild ungulates in the Western Alps (Gazzola et al., 2005, 2007; Marucco et al., 2008).

However, human presence poses a challenge for both the prey and predator coexisting in the Alps. In human-dominated landscapes predator conservation becomes a complex issue as this species generates conflicts related to predation on domestic animals and perceived competition with hunters (Dressel et al., 2015). The negative perception of wolves by hunters reflects a competitive situation, where wolves are seen as a serious threat to hunting and hunting dogs (Bisi et al., 2010).

To address the conflict, data on species coexistence are necessary. In Italy, despite the ecological and hunting interest in wild ungulates, data on their abundance and distribution are scarce. Surveys are carried out only in areas interested by hunting, where an index of the population consistency is compulsory for the definition of hunting plans, or in protected areas where specific studies are conducted. At the national level the most comprehensive technical report dates back to a quadrennial document on the status of ungulates, covering the period from 2006-2010, conducted by the Italian Institute for Environmental Protection and Research (ISPRA). Roe deer reported the largest occupied territory (145,000 km^2), followed by the red deer (54,000 km^2) and chamois (42,000 km^2) (ISPRA, 2013).

Considering predators, wolf abundance has been precisely estimated for the first time at the national level in 2021 (La Morgia et al., 2022). Instead for the Alps, the wolf population size has been accurately estimated and monitored over time since the beginning of the recolonisation (Marucco et al., 2022).

The overall scarcity of data on population size estimates for ungulates may be attributed to the challenge of conducting homogeneous surveys to collect comparable data for different ungulate species, mainly due to the difficulty of coordinating a standardised sampling effort. Traditional sampling methods, such as counting or spotlight surveys, often require significant efforts in personnel and technical resources. These methods also involve inherent biases, such as observer variability and reduced detectability in dense vegetation (Jenkins & Manly, 2008).

In recent years, a novel sampling method that minimises the reliance on extensive human resources has gained increasing popularity (Rovero et al., 2013; McCallum, 2013). This method involves the use of camera traps (CTs), remotely activated devices that capture images or videos of wildlife in their natural habitats. These cameras offer an effective approach to studying different species by avoiding the need of conducting separate sampling campaigns for each species, other than major advantages of covering large areas and continuously collecting data 24/7 (Caravaggi et al., 2020; Wearn & Glover-Kapfer 2019). Furthermore, CTs can provide data on various ecological variables, such as the timing and frequency of species interactions, activity patterns, and spatial distribution (Dyck et al., 2022; Marion et al., 2022; Dorning & Harris, 2019; Rowcliffe et al., 2008; Carbone et al., 2001).

There are several methods to analyse the data obtained from CTs in ecological research. Some common methods include using capture-recapture models (Augustine et al., 2018; Royle et al., 2009), distance sampling (Harris et al., 2020; Howe et al., 2017) and occupancy models (Niedballa et al., 2015; Tobler et al., 2015). Capture-recapture models are useful when the goal is to estimate population size or density (Efford et al., 2009). This method requires identifying individuals from their unique markings or characteristics and estimating population size based on the proportion of individuals captured in successive sampling periods. Distance sampling involves estimating the distance between the camera and the animal and using this information to estimate the density of animals in the study area (Buckland et al., 2005).

Occupancy models are increasingly being used in ecological research as they allow for the estimation of species occupancy probabilities by using data on the presence or absence of a species (without needing individual identification) at a particular site over a series of sampling periods (Bailey et al., 2014; MacKenzie et al., 2002, 2003, 2004). Occupancy models are particularly useful in CT studies as they can account for detection probabilities, addressing the issue of false absences, which can occur when animals are present but not captured on camera due to various factors, such as camera placement or timing (Burton et al., 2015).

Moreover, occupancy data for multiple species can be considered in multi-species occupancy models that are particularly useful for studying species interactions in shared habitats when using CTs in large territories (Tobler et al., 2015). These models allow for the estimation of the occupancy probabilities of multiple species while accounting for the potential interactions among them, thus providing valuable insights into the co-occurrence and spatial associations of species, as well as the factors that influence these patterns (Rota et al., 2016; MacKenzie et al., 2004).

The above consideration highlights the importance of conducting a thorough analysis of species interactions in the anthropogenic environment of the Western Alps. Such an analysis can provide valuable insights into the extent to which human presence influences the spatial utilisation of animal communities and the role that inter-species relationships play in facilitating coexistence among diverse species.

1.1 Objectives of the study

This study aims to gain a deeper understanding of the co-occurrence patterns of prey and predator species in an Alpine valley environment through the deployment of camera traps, considering the complex interplay of competition, predation, and human activities. The investigated area is characterised by a complex ecological system, wherein the roe deer compete with the red deer for resources and both face predation from the now stable wolf population, with roe deer being the most used prey (Marucco et al., 2008; Rizzuto, 2012). Furthermore, the valley is home to a human population of 3,800 inhabitants that engage in activities such as tourism, agriculture and hunting, all of which may impact the occupancy of species and their interspecific relations.

Specifically, the study aims to address the following three research objectives:

1) Assessing the role of interspecific interactions in shaping the spatial distribution of species in relation to their use of habitats. This involves examining how species interactions affect the occurrence of prey and predator species in a given area, which is influenced not only by environmental factors but also by interactions within species. Specifically, I focused on the reciprocal interaction between roe deer and red deer, due to their direct competition for resources, considering effects of wolf presence, which is a common predator. Red deer are typically better competitors due to their generalist nature, which puts roe deer under significant stress since they also are the favourable prey for wolves in the area. I therefore directly tested these mechanisms.

2) Exploring the role of human activity in shaping the spatial use of different species. This second objective aims to explore the impact of human activity on species detection probability and how this eventually modifies their occupancy. Specifically, I explored whether the co-occurrence of ungulates and wolves varies in areas closer to human

habitation, taking into account relevant theories such as the "landscape of fear" hypothesis (Laundré et al., 2001). This hypothesis suggests that animals may modify their behaviour in response to the perceived risk of predation, causing them to avoid areas where predators are likely to be present, even if those areas offer abundant resources or a suitable habitat (Laundré et al., 2010). I further investigated this phenomenon to better understand the potential shift of prey species towards human settlements, also known as the "human shield" hypothesis (Berger, 2007).

3) Investigating the potential effect of the hunting season for roe deer on its competitive (i.e., red deer) and predatory (i.e., wolf) interactions. I considered roe deer in specific because it is the most frequently occurring ungulate in the study area and the only species out of the three for which hunting is permitted. Specifically, the study will examine the use of forest habitats, expecting to find a positive relation between the hunting season and roe deer's tendency to occupy woodlands as refuge areas.

1.2 The LIFE WolfAlps EU project and the wolf recolonisation process

This research is conducted in the framework of the LIFE WolfAlps EU (LIFE18 NAT/IT/000972 years: 2019-2024), a conservation project funded by the European Commission as part of the LIFE 2018 "Nature and biodiversity" program. The project aims to improve the coexistence between wolves and humans in the Alps through the development and implementation of shared conservation actions, across Italy, France, Austria, and Slovenia (www.lifewolfalps.eu). In fact, understanding the interactions among wolves, wild and domestic prey in their ecosystem is critical to support decision-making in managing both species and habitat as a whole, particularly when addressed with a population-participatory approach (including institutions, environmental association and herders, for instance).

The LIFE WolfAlps EU Project has been developed following the expansion of wolves in the Alps, after the continuous human persecution, deforestation, and reduction in prey led to the gradual decrease of wolves until the reach of total extinction in the Italian Alps at the beginning of the 20th century. Nevertheless, some isolated populations survived, all located in the Apennines, and started to naturally recolonise the southwestern portion of the Alps since the early 1990s (Marucco et al., 2022; Fabbri et al., 2007). As previously mentioned, a process of human abandonment of rural areas and Alpine valleys favoured the recolonisation of many areas by wild ungulates, including roe deer and red deer. This favourable event as well as the wolf's high ecological plasticity, high dispersal (a wolf can travel up to 1092 km; Wabakken et al., 2007) and capability to move across unfavourable habitats, contributed to the recolonisation process (Cimatti et al., 2021). As a result, the distribution range gradually expanded to the north, until the coverage of the entire Apennines and Western Alps.

The study area of this thesis is centred in the highest wolf pack density of the Alps (Marucco et al., 2022), and where the wolf settled at first in 1996 (Marucco et al., 2005). Hence, wolf presence in the study area has been documented for more than 30 years, and humans and prey had the time to adapt to such a presence.

The current LIFE WolfAlps EU project is designed to encompass a number of initiatives targeting several intervention lines and this research falls under the area of wild prey impact assessment. In Europe, there is limited understanding of how predation pressure and resource use affect the interactions between wolves, wild and domestic prey, and human stakeholders. In fact, the issue of diminished prey abundance and availability, frequently ascribed to predators, can result in extensive conflicts between wolves and hunters (Santiago-Ávila & Treves, 2022; Dressel et al., 2015; Bisi et al., 2010). The overall objective of the research is to evaluate the impact of wolves on prey, in a human-dominated landscape, in order to provide recommendations for incorporating predation into hunting management strategies (www.lifewolfalps.eu).

2. Study area

2.1 Site description and background

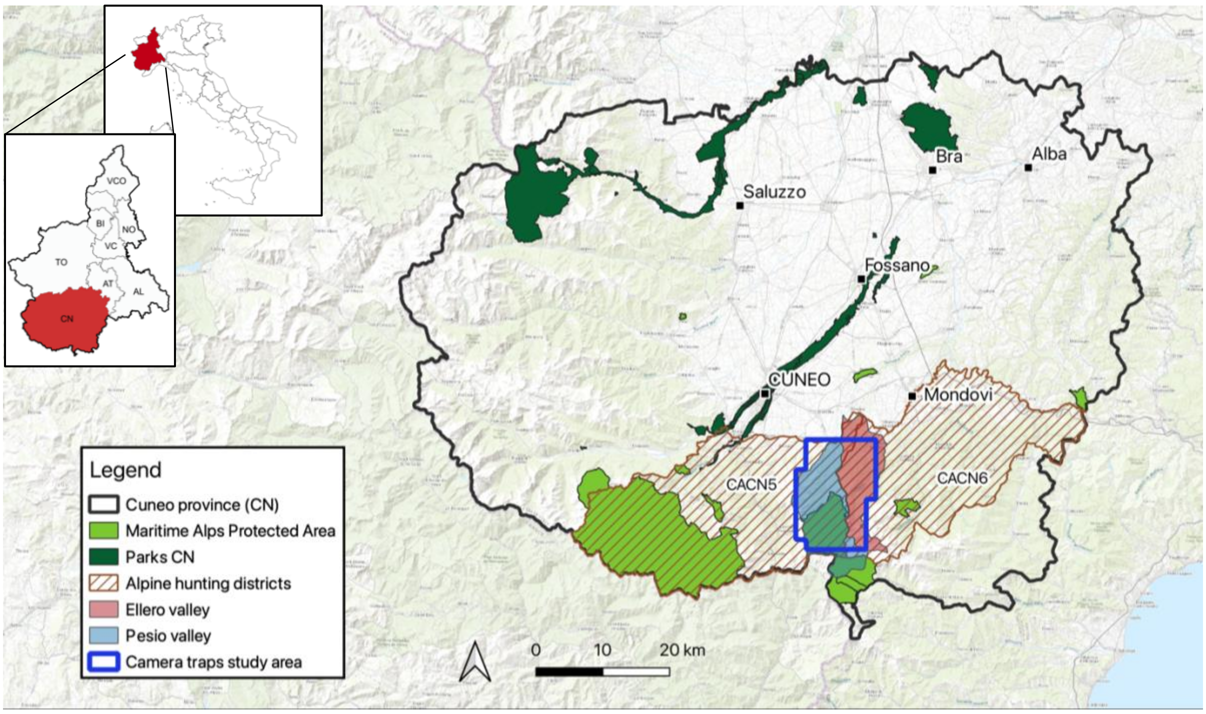

Figure 1. Cuneo (CN) province, wherein green represents the parks and protected areas (light green denotes the areas under the Maritime Alps Protected Area Institution's jurisdiction). The two hunting districts (namely CACN5 and CACN6), delineated by brown lines, completely cover the two valleys that this study concentrates on: Pesio valley (blue) and Ellero valley (red). The precise study area where the CTs were located is delineated by the blue shape.

The study area is located in the Piedmont region of the Maritime Alps in north western Italy (Figure 1). This region embraces the border that separates Italy from south western France and represents the southernmost extension of the Alpine Mountain chain.

In particular, this research was conducted within the boundaries of two mountain valleys: the Pesio valley and the Ellero valley (named after the two main rivers that flow through), which are both situated within the province of Cuneo (CN) and fall under the jurisdiction of the Maritime Alps Protected Area Institution. The Institution is responsible for the management of two natural parks (Maritime Alps Natural Park and Marguareis Natural Park) and eight natural reserves since January 1st, 2016. The two valleys cover a total area of approximately 208 km^2, with Marguareis Natural Park occupying 58 km^2, which corresponds to 74% of the park's total area. The area encompasses a variety of environments from lowlands to mountains, ranging from 750 m to 2,651 m (Marguareis Peak).

Administratively, the Pesio valley includes the municipalities of Chiusa Pesio (3,783 inhabitants), Peveragno (5,496 inhabitants), Pianfei (2,200 inhabitants), and Briga Alta (48 inhabitants), while the Ellero valley encompasses Roccaforte Mondovì (2,127 inhabitants) and Villanova Mondovì (5,838 inhabitants).

The area is also included into two hunting districts: Alpine District Cuneo 5 (CACN 5) and Alpine District Cuneo 6 (CACN 6).

2.1.1 Flora and fauna

The geological configuration of the area and its proximity to the sea contribute to the creation of a climate that allows the proliferations of an exceptional variety of plant species. In the valley, the historical forest management by the monks of the Certosa di Pesio monastery (a religious complex founded in 1173) favoured the development and maintenance of woodlands. The dominant vegetation consists of chestnut groves (*Castanea sativa*), mixed broadleaf forests and oak forests (*Quercus petraea*). At slightly higher altitudes, above 900 m, beech forests (*Fagus sylvatica*) develop, which have been utilised for centuries as a source of firewood and their spread at lower altitudes was precluded due to chestnut cultivation. As the elevation increases, coniferous forests become more prevalent, with the white fir (*Abies alba*) being dominant in the Pesio valley.

Beyond the forest limit at higher altitudes, subalpine meadows and pastures are the predominant landscape. Alpine pastures are largely artificial, created to increase the amount of feed available for livestock, that exploit the valleys during the summer. Today, the advancement of rhododendrons (*Rhododendron ferrugineum*) and alders (*Alnus viridis*) is often observed at the expense of forests and shrublands. The habitat type is represented in Figure 2, with categories derived from the Land Cover Project of Piedmont Region (Regione Piemonte, 2021), also used for later calculations in this study.

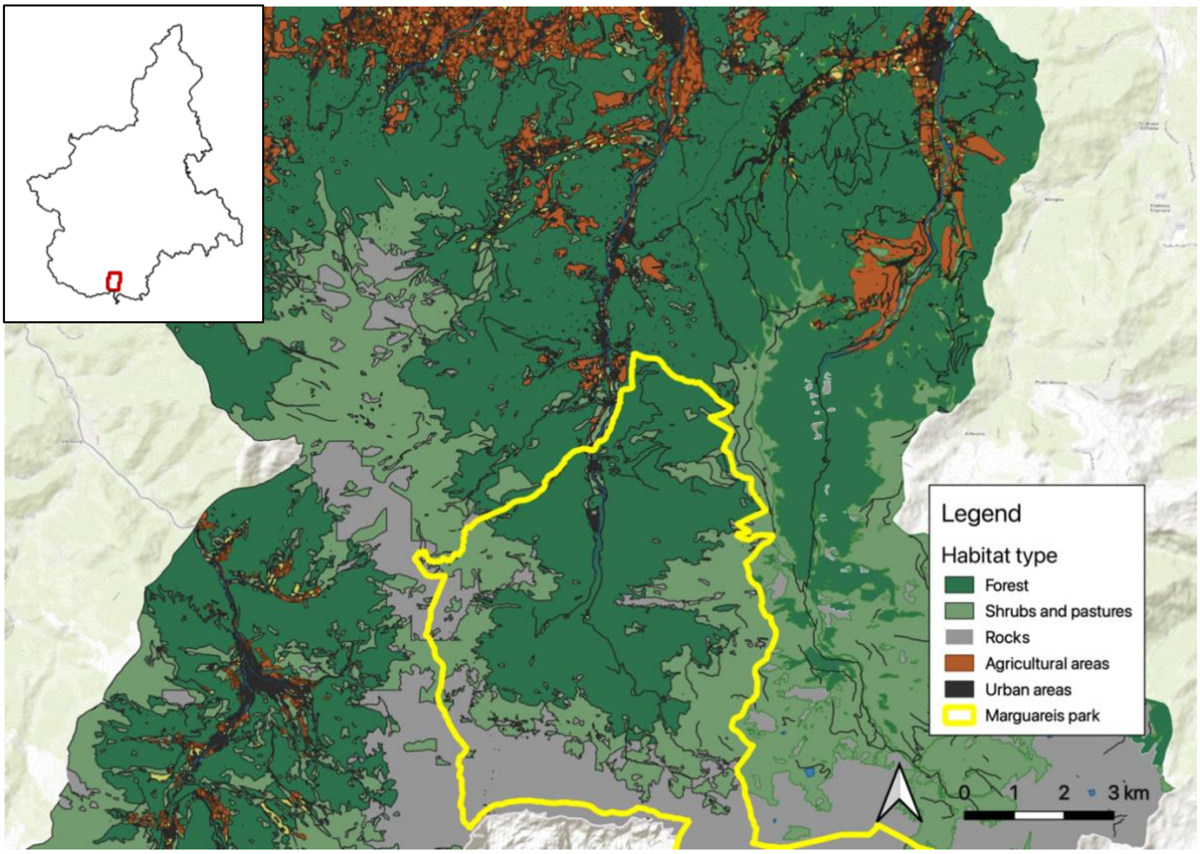

Figure 2. Habitat type classification of the study area, Pesio and Ellero valleys. The Marguareis park is highlighted in yellow. The category "Forest" includes mixed, deciduous and coniferous trees.

The area also supports a diverse array of fauna, including many species of ecological significance. It is home to several species of ungulates - including roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) - and to a large carnivore species: the wolf (*Canis lupus*), which counts 33 packs in the whole Cuneo province (Avanzinelli et al., 2022).

The roe deer, known for its adaptability, shows a strong preference for ecotonal habitats that exhibit high diversity and rich margins. The species is commonly found in areas with dense shrub vegetation, where it can effectively hide, as well as in wooded areas with clearings and undergrowth (Canalis, 2022). As a highly selective herbivore, roe deer searches for food with a high nutrient concentration by browsing buds and leaf tips (Freschi et al., 2017). The species' home range is relatively limited in comparison to other ungulates, ranging from 0.13 - 0.44 km^2 (Lovari et al., 2017).

The red deer, the largest ungulate in the Alps, exhibits considerable habitat plasticity, although it tends to favour habitats where the forest component is well-represented, with relatively low levels of rockiness, steepness and snow cover. As a predominantly grazing herbivore, the red deer is able to adjust its diet according to food availability. The size of the species' home range varies considerably based on seasonal and food availability factors (1.13 - 3.86 km^2; Georgii & Schroder, 1983). Hunting of red deer is not permitted within the local hunting districts.

The wolf is known to occupy a diverse range of habitats, with its optimal environment being large forests with minimal human disturbance. The size of wolf's home range varies depending on several factors, including food availability (Fuller, 1989), topography (Ciucci et al., 1997), wolf density (Fritts & Mech, 1981) and to some extent pack size (Peterson et al., 1984). The minimum territory occupied by a pack can vary between 100 and 600 km^2 (Ciucci et al., 1997; Mech & Boitani, 2003). When poor ecological conditions occur, the species relies on diverse food resources, such as livestock, fruit and small mammals (Meriggi et al., 1991). However, in favourable habitats, wolf primarily preys on wild ungulates, such as roe deer, red deer, wild boar, and, to a lesser extent, chamois (Canalis, 2022; Gazzola et al., 2007).

In the complex ecosystem of the area, human activities such as agriculture, livestock farming and tourism, in addition to hunting, have a significant impact on wildlife and their habitats. The region boasts a renowned network of waymarked footpaths, including the southernmost portion of the GTA (*Grande Traversata delle Alpi*), a long-distance hiking trail that spans the Piedmont Alps. Additionally, a ski facility is present within the study area.

3 Materials and methods

3.1 Field data collection

3.1.1 Camera traps: a non-invasive tool for monitoring species presence

Camera traps (CTs) are remotely activated devices used to capture images or videos of wildlife in their natural habitats. These devices consist of a camera, a motion sensor or infrared trigger, and a power source, such as batteries or solar panels. The motion sensor or infrared trigger activates the camera when an animal passes by, providing a non-invasive method for observing and studying wildlife. In particular, the camera is triggered when the passive infrared sensor detects a difference between the infrared radiation emitted by the animal in the trigger area and the infrared radiation of the surrounding environment (Moeller, 2022).

CTs are widely employed in various fields, including wildlife biology, ecology, conservation, and management. They are used to estimate and evaluate the size of animal populations, monitor species distribution and abundance over time (Rowcliffe et al., 2008; Carbone et al., 2001), track individual animals (Nipko et al., 2020; Dorning & Harris, 2019), and study animal behaviour and interactions (Marion et al., 2022; Palencia et al., 2019; Bridges et al., 2004). The data collected by CTs can thus provide valuable information for species identification, habitat use, and ecosystem health.

A discussion on the advantages and disadvantages of employing CTs in wildlife studies is hereby reported to support the selection of this sampling method in the present study, and to provide a comprehensive overview of this research approach.

The use of CTs offers several advantages over traditional methods of wildlife observation, such as direct observation or live trapping, representing a highly effective tool for wildlife surveys (Wearn & Glover-Kapfer, 2019). CTs have a low impact on wildlife, reducing the risk of disturbing or altering animal behaviour (Moeller et al., 2022). They are also cost-effective, as they can cover large areas and collect data 24/7 with relatively low effort, thus being useful for year-round studies (Caravaggi et al., 2020).

Despite their many advantages, some limitations should be noted. One of the main disadvantages is the high cost of purchasing and maintaining the equipment (Wearn &

Glover-Kapfer, 2019). Additionally, CTs can be affected by weather conditions, such as rain, snow, or dust, which can cause malfunctions or damage to the equipment. Another challenge is the potential for interference from the environmental surroundings, e.g., in forest environments branch or leaves may be present in abundance compared to other habitat types, which can trigger false activations and generate unusable data, in particular when windy conditions occur.

One of the significant challenges of using CTs is individual identification, which involves using unique physical features to distinguish between individual animals in a population. In fact, many species lack natural markings or external features that are detectable through the camera and enable individual identification, such as fur colour and patterns, body size, or unique traits (e.g., scars). As a result, studies that require individually recognisable animals, such as those using capture-mark-recapture methods, involve marking individuals when external features are unavailable, which can be invasive and impractical for many species (Green et al., 2020). However, recent methodologies are being developed to increase the reliability and precision of estimates that involve partially marked populations or partially identifiable individuals that can be classified in categories, such as sex or age (Gilbert et al., 2021b; Augustine et al., 2018). In this regard, caution is advised when making inferences about the abundance of unmarked populations (Ruprecht et al., 2021; Gilbert et al., 2021b).

Nonetheless, by combining the power of CT data with the flexibility of statistical models, it is possible to gain valuable insights into the ecology and conservation of a wide range of animal species, even in cases where individual identification is not possible, as in the case of this study. In particular, since CTs are used extensively for inventorying mammals (Kitamura et al., 2010; Rovero & De Luca, 2007), long-term monitoring of animal presence (O'Brien et al., 2010) and targeting species (Nipko et al., 2020), they can be efficiently used for species distribution models (Gilbert et al., 2021a), and have proven to be a powerful tool for understanding the distribution and ecology of wildlife species, being increasingly used by researchers and conservationists around the world (Delisle et al., 2021; Burton et al., 2015).

3.1.2 Study design: camera traps deployment

A standardised protocol was implemented to minimise variability among different cameras and ensure uniform detection opportunities.

The study area, covering a total territory of approximately 136 km^2, centred in the territory of the first wolf pack of the area, was initially divided into a grid of 60 cells of 1.5 km^2 each, through the QGIS software (version 3.16.4 - Hannover) (Figure 3). A point was randomly identified inside each cell, thus developing a set of 60 random points, to denote the theoretical position of the cameras. This sampling design was adopted due to its potential to uniformly cover the sampling territory and limit the bias induced by human decisions. Indeed, randomisation ensures that the distribution of CTs is not biased in relation to the target species (Meek et al., 2014; Rowcliffe et al., 2013). Moreover, the homogeneous coverage is intended to ensure each habitat type and environmental characteristic to be adequately sampled. Ultimately, this sampling design enables the collection of suitable data for the study of the different target species (i.e., roedeer, redder, wolves).

Access to the initially identified random point was sometimes difficult due to the challenging terrain characteristics, such as slope and steepness. To address this issue, two additional sets of random points were generated as alternative options. Nevertheless, the first point was always prioritised with a tolerance of 30 meters.

Based on the accessibility of each cell, it was evaluated whether or not to deploy the CT during the study period (corresponding to the winter season). In fact, given the altitudes which the study area covers, some locations become inaccessible in winter due to the snow coverage. For this reason, three cells of the grid turned out to be inaccessible in all the 3 random locations, thus were not included in the study. The deployment of the remaining 57 cameras - which final locations are represented in Figure 3 - started in November 2021 with priority given to those located at higher altitudes.

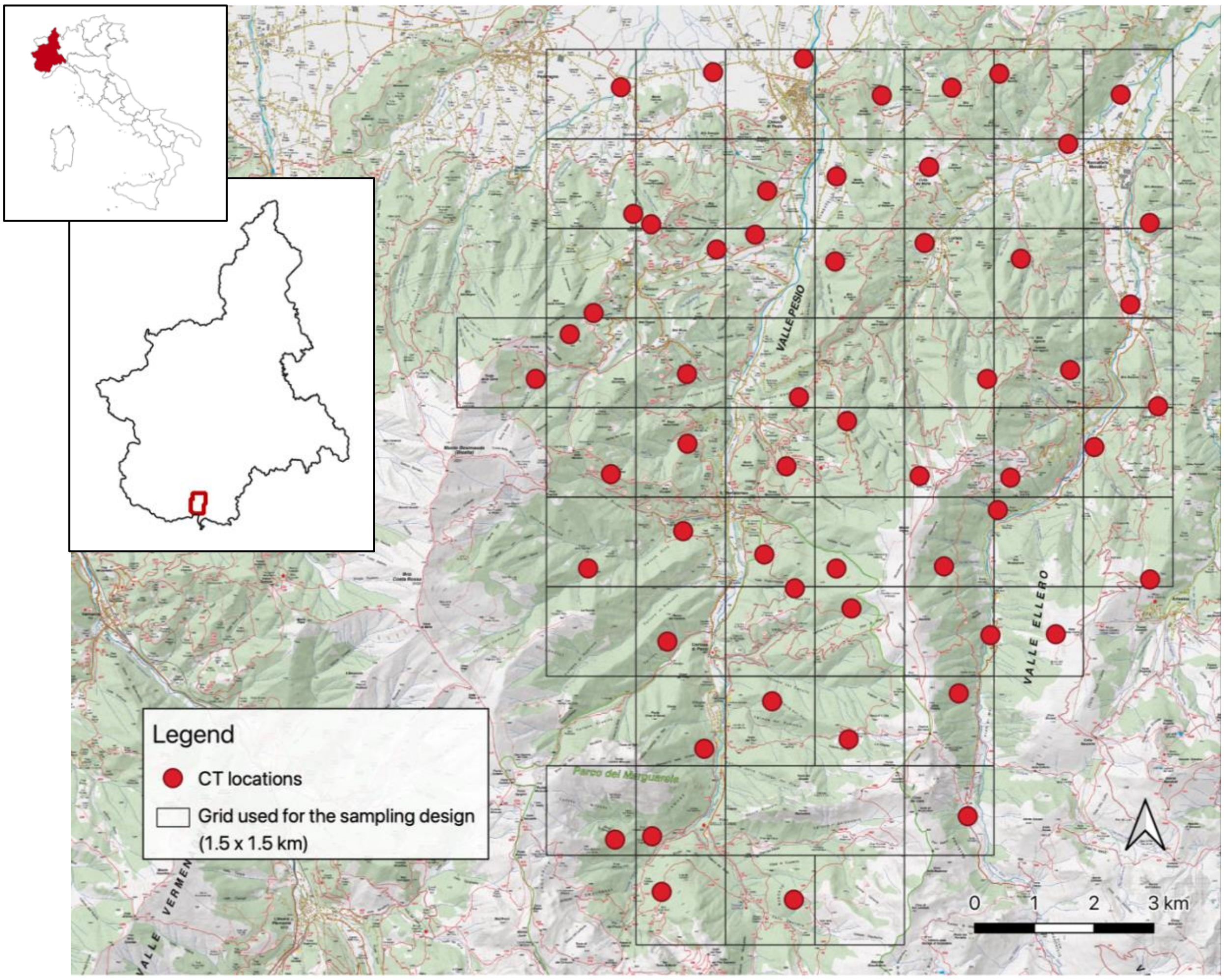

Figure 3. CT locations (red dots). The grid (black) is represented in order to illustrate how the study area was divided. Each cell is 1.5 km^2 and presents one CT in a randomly chosen location.

The CTs were installed on trees following a standardised procedure. In particular, (i) the cameras had north-facing exposure, (ii) height from ground ranged between 130 cm and 170 cm, (iii) the camera settings were constant. The northern orientation was chosen to prevent the CTs from taking blank photos due to sunlight. A minimum height of 130 cm above the ground was set to prevent snow from obscuring the camera's field of view, and a maximum height of 170 cm to prevent cameras that are too high from not capturing smaller animals. Finally, the cameras were set to be active day and night, the sensitivity was set to the highest level, the interval between shots was set to 0.1 seconds (the lowest time available) and three shots were taken for each triggering event.

The models of all cameras were either Keepguard KW696 (n = 55) or IR PLUS HD 2 UV595 (n = 2). All cameras were equipped with integrated infrared LEDs and operate completely silently when triggered to minimise disturbance to wildlife. Examples of cameras positioned on trees are reported in Figure 4.

Figure 4. Camera traps placed on trees (model Keepguard KW696).

3.1.3 Data collection

At the time of placement, environmental data were recorded to characterise the CTs' random point area.

Firstly, the following was reported:
- coordinates in WGS84 format (UTM zone 32N),
- presence/absence of snow and, if present, the snow depth,
- whether the camera was positioned on a road, trail, animal walkaway or off-trail,
- distance from intersections, mountain ridges or passes (dimensional classes: 0 m, 0-10 m, 10-50 m, >50 m)

Once the camera was installed, a visibility index was calculated to provide an assessment of the visual clarity of the camera’s field of view.

This index was determined using a chequered sheet (measuring about 42 cm x 60 cm) with black and white squares (16 in total, 8 white and 8 black), as showed in Figure 5. This chequered sheet was positioned at 6 points in the field of view of the camera at a distance of 18 m (a distance corresponding to the maximum range of the sensor of the inferior quality camera). During the index measurement, the visible squares were counted at three angles: (i) central position, (ii) maximum angle to the right and (iii) maximum angle to the left at the edges of the camera's field of view. For each angle, two measurements were undertaken: one with the chequered sheet at ground level and one at 130 cm above the ground. All visible squares were counted, regardless of whether they were black or white. The numbers were then converted in percentages so that, for example, a camera aimed at an open field reports a 100% visibility, whereas a CT aimed at a forest reports a lower percentage, depending on the trees present in the field of view.

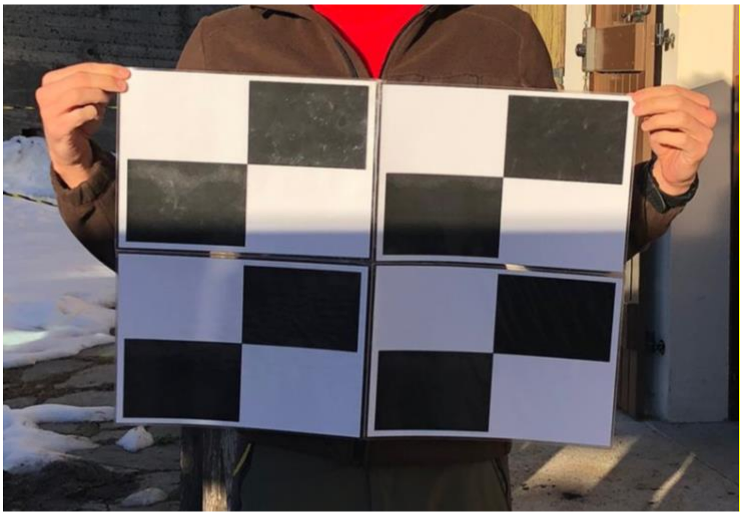

Figure 5. Chequered sheet used for calculations of CTs' visual clarity index.

In addition, environmental characterisation data were collected within a radius of 50 and 100 m around the CT to obtain accurate environmental information at the site.

In particular, if the camera was located in a forest environment, the forest was characterised in terms of the typology of trees present: Deciduous, Coniferous or Mixed. The predominant association was also indicated (e.g., beech forest) and, if possible, the type of forest management (coppice or high forest). To these data, parameters were added regarding the average distance between trees, average foliage height and the average trunk diameter (all with dimensional classes that can be estimated at sight, e.g., in the case of diameter: 0-20 cm, 20-50 cm, >50 cm). If the camera was located in an open area, this was classified as pasture, hay meadow, crop (and type), scrubland, shrubland or ecotone.

Finally, in order to quantify anthropic activities, data were collected on the presence of agricultural, pastoral (type of livestock, herd size, presence of dogs), or forestry activities (felling, deforestation or logging) in the vicinity of the camera, with an indication of the distance to the actual positioning point.

Throughout the sampling period, the CTs were checked regularly, approximately once a month. During the checks, the images were downloaded from the memory card and the batteries were changed. In Figure 6 examples of CT pictures are shown. Furthermore, data were recorded for the presence of human activity at the time of each check.

a)

b)

c)

d)

Figure 6. Examples of camera trap pictures. a) and b) roe deer, c) red deer, d) wolves.

3.2 Picture classification and dataset

Once obtained from the CTs, the images were analysed using the Timelapse Image Analyzer (Greenberg, 2019). The Timelapse software reads images from remote cameras and automatically extracts metadata (date and time), which are displayed through an interface where additional information can be added as needed in various formats (typing or selecting from a list).

For this study, the following information was recorded for each image (in addition to date and time as already specified):

- camera trap number
- temperature (°C)
- presence/absence of snow (0/1)
- animal species present in the photo
- total number of individuals
- number of new events
- sex of the animal (when recognisable for roe deer and red deer)
- other notable individual features (e.g., roe deer moulting or any malformations)

If a photograph captured individuals from two different species, the picture was duplicated to ensure that data from each species could be recorded separately.

Photos from all camera traps were manually processed according to a predefined procedure ensuring a uniform recording, and considering that 3 pictures were taken per trigger event to aid the event's discrimination. Photos of the same occasion have been grouped in a single event, defined by consecutive photos taken within the same moment and activity, close in time, as a single occurrence, as described in other studies (O'Brien et al., 2013; Rød-Eriksen et al., 2022), in order to avoid pseudo replication and guarantee independence of events. This approach allowed the classification of independent events in the case of repeated photographing of the same individual, which is particularly important to note in the case of ungulates (e.g., animals grazing or resting in front of the camera). For instance, the first image reporting an animal entering the camera's field of view was counted as one new event, and all subsequent images (such as when the animal grazes without leaving the field of view) were considered as the same event.

3.3 Statistical framework

3.3.1 Occupancy models: an overview

Wildlife studies often aim to explore changes or differences in the proportion of sites occupied by a particular species (Bailey & Adams, 2005). However, any detection bias may result in some sites where the species is actually present being classified as unoccupied, leading to inaccuracies in estimates of occupancy and other related parameters (MacKenzie et al., 2002; 2003; 2004). This imperfect detection is a common problem in wildlife studies and occupancy models provide a solution to the issue, minimising the potential bias.

Occupancy modelling is a statistical method utilised to estimate the true occupancy of a species within a specific area, based on environmental variables (Bailey et al., 2014). This method is a specific form of enhanced species distribution model, which combines species occurrence or abundance data with environmental measurements by also taking into account imperfect detection. Occupancy models were first introduced by MacKenzie et al. (2002) and have since become widely used in applied ecology, conservation, and theoretical ecology.

The sampling design for applying occupancy models involves multiple surveys at each sampling site, divided into discrete time intervals. Repeated surveys offer multiple opportunities to detect the true presence or absence of a species, thereby increasing the chances of accurately estimating its occupancy state (Bailey et al., 2014). The resulting matrix of detection/non-detection data consists of rows corresponding to the site of the surveys and columns corresponding to repeated visits, with each cell indicating the observation or non-observation of the species of interest at that site (Bailey & Adams, 2005). The non-performance of some surveys is acceptable in an occupancy modelling framework and considered as ‘NA’ (MacKenzie et al., 2002).

The repeated surveys in occupancy modelling allow the probability of a species' presence (occupancy probability) to be separately estimated from the probability of detecting it (detection probability). Occupancy probability reflects the likelihood that a species is present at a particular site, while detection probability indicates the chance of observing the species given that it is present at the same location. The combination of the two information in the occupancy hierarchical framework allows the model to assign a real occupancy probability to the sampled areas labelled as unoccupied (MacKenzie et al., 2002).

3.3.1.1 The issue of imperfect detection

The main strength of occupancy models is they account for imperfect detection, which refers to the failure to detect the species even though it is present in the sampled area, as an observed absence may occur when a species was either present at the site but undetected or genuinely absent (MacKenzie et al., 2002). This issue can result in biased estimates of occupancy and abundance, leading to incorrect conclusions about the distribution and ecology of the species (Bailey et al., 2014).

The imperfect detection issue is particularly relevant when working with CTs because these instruments have several limitations that can affect the detectability of the species, such as the field of view, the triggering mechanism, and how the cameras are placed (Burton et al., 2015). These limitations can result in missed detections.

Indeed, there are several reasons why imperfect detection can occur in occupancy models, including the limitations of survey methods, the behaviour of the species, and the environmental conditions (Devarajan et al., 2020). For example, species that are cryptic or have low densities are more difficult to be detected, and environmental variables such as weather conditions can also affect the visibility and detectability of the species. Furthermore, the choice of the survey method, such as the duration and timing of surveys, can also impact the detectability of the species. As a result, analysing detection/non-detection data as presence/absence data is inadequate due to the variation in detectability (Bailey et al., 2014).

To address the imperfect detection issue, these models operate repeated observations at each site, and incorporate the estimated detection probability in a specific observation model as a function of the site (e.g., land cover) or survey characteristics (e.g., weather conditions). Occupancy, in contrast, relates only to site characteristics (Abrams et al., 2021, Guillera-Arroita et al., 2010).

3.3.1.2 Assumptions of occupancy models

Occupancy models rely on a number of key assumptions, which are critical to their accuracy and reliability (MacKenzie et al., 2017; Bailey et al., 2014; Bailey & Adams, 2005):

(i) The occupancy state of a species is assumed to be "fixed" within the sampling season, indicating that the species remains present at occupied sites throughout the sampling season and therefore the population results closed with no births, deaths or emigrations and immigrations.

(ii) Sites are assumed to be independent, with detection of the species at one site being unrelated to its detection at other sites. However, this independence assumption may be compromised if the sites are situated too close to one another.

(iii) A species can only be detected if it truly occupies a site. In other words, it is assumed that there are no false positives.

(iv) Avoidance of unexplained heterogeneity in either occupancy or detectability is necessary. Specifically, the probability of occupancy is assumed to be uniform across all sites, or any deviations in occupancy can be accounted for by site-specific characteristics that have been quantified and incorporated into the model. Similarly, detectability is assumed to be constant across all sites and surveys, or any variations can be explained by survey or site-specific information that have been included in the model.

3.3.2 Hierarchical implementation of occupancy models

An Occupancy Model is a sophisticated version of a Logistic Regression or a Generalized Linear Model, and consists of two logistic regressions layered on top of each other (Doser et al., 2022). The first logistic regression estimates the occupancy probability as a function of site-level covariates that determine the presence or absence of a species at a certain location. In the second logistic regression, the probability of detection is modelled, which may vary across space and the various surveys. A model for the detection probability can incorporate covariance at both the site and survey levels.

The model can be mathematically represented as follows: J represents the total number of sites, and j is used to index across the sites. At each site, there are K_j replicates, and k is used to index across the replicates.

$$j = 1, \ldots, J \text{ (site)}$$

$$k = 1, \ldots, K_j \text{ (replicate)}$$

In the occupancy portion of the model (Formula 1), the true presence or absence of a species at each site J is denoted as z_j. This portion of the model is based on a Bernoulli Distribution, a discrete distribution that only has two possible outcomes: 0 and 1. These outcomes are often referred to as failure (0) and success (1) and are used to describe binary events.

The occupancy probability ψ_j is modelled using a logistic regression framework, which allows for the inclusion of various site-level covariates (X) that are believed to influence the occupancy probability. The effects of these covariates are described by a vector of regression coefficients β. The logit transformation utilises a linear combination of the covariate coefficients (which can span between ±∞) to convert them into probability values (ranging between 0 and 1).

Formula 1: Occupancy (ecological) sub-model

$$z_j \sim Bernoulli\ (\psi_j)$$

$$logit\ (\psi_j) = \beta_1 + \beta_2 \cdot X_{2,j} + \ldots + \beta_r \cdot X_{r,j}$$

The second part of the model, referred to as the detection model (Formula 2), deals with the observed data denoted as y, where $y_{j,k}$ represents the detection or non-detection of the species at site j during the k replicate survey. Similar to the occupancy model, the detection model assumes that the data arises from a Bernoulli Distribution, but it is conditional on the species actually being present at the site, as indicated by z_j. It is important to note that if the species is not present at the site, it cannot be detected, meaning that there are no false positives.

The detection probability $p_{j,k}$ varies both at the site and survey level, and is influenced by covariates (V). The effects of these covariates are described by a vector of regression coefficients α.

Formula 2: Detection (observation) sub-model

$$y_{j,k} \sim Bernoulli\ (p_{j,k} \cdot z_j)$$

$$logit\ (p_{j,k}) = \alpha_1 + \alpha_2 \cdot V_{2,j,k} + \ldots + \alpha_r \cdot V_{r,j,k}$$

This represents the fundamental single species occupancy model.

The multi-species occupancy model designates a more complex extension of this framework and focuses on modelling the community of multiple species of interest.

3.3.2.1 Multi-species occupancy models (MSOM): a description of the modelling framework

Multi-species occupancy models (MSOM) represent an advanced analytical framework that integrates diverse environmental variables and interspecific correlations to accurately estimate the factors that affect occupancy, while simultaneously accounting for imperfect detection (Rota et al., 2016). In contrast to the single-species models (SSOMs), the MSOMs aim to utilize information from multiple species to estimate the individual species' responses to environmental variables (Devarajan et al., 2020).

A MSOM is based on the key concept of incorporating multiple layers into the model structure. Instead of using a single detection-non-detection matrix, each individual species has its own matrix, which is then represented through superimposed layers (Rota et al., 2016). Specifically, the first layer corresponds to the first species, the second layer corresponds to the second species, and so on, for all species of interest within the sampled community.

MSOMs share many similarities with classical SSOMs, as both are constructed from the encounter histories of species across multiple sites in a region during repeated visits. However, MSOMs offer several key advantages over SSOMs, as they can be used to estimate species richness at both the community and metacommunity levels (Devarajan et al., 2020). This is based on the fundamental concept that a community is a complex assemblage of species that occur at a site, while a metacommunity is a broader collection of such communities. To achieve this, MSOMs integrate three levels of hierarchical organization: (i) the metacommunity level, (ii) the community level, and (iii) the individual species level.

(i) The first level is characterized by the presence or absence of each species i in the metacommunity through an indicator variable that is modelled with a Bernoulli distribution.

(ii) The second level describes the occurrence of each species i at specific sites j through a Bernoulli distribution.

(iii) The third level considers the detection process of individual species i at site j over K sampling occasions, and is modelled through a detection frequency variable (y_{ij}) and a detection probability p_{ij} for each sampling occasion k. Here, y_{ij} indicates the detection frequency and y_{ijk} is the detection/non-detection at the k^{th} sampling occasion.

$$y_{ijk} \sim Binomial\ (K,\ p_{ij}\ z_{ij})\ or\ y_{ijk} \sim Bernoulli\ (p_{ijk}\ z_{ij})$$

The Bernoulli distribution and the binomial distribution are closely related but describe slightly different phenomena. The Bernoulli distribution describes a single experiment with two possible outcomes, whereas the binomial distribution describes the number of successes in a given number of independent and identically distributed Bernoulli experiments.

Finally, the occupancy and detection probabilities can be modelled as a function of covariates in the same way as SSOMs.

The MSOM and SSOM share similar underlying assumptions including: geographic and demographic closure, independence between site in regard to occupancy and detection probability, accuracy in species identification, ecological similarity (Devarajan et al., 2020). The latter refers to the assumption that species in a community are similar.

MSOMs represent a valuable tool due to their efficiency in resource utilisation, capacity to incorporate biological interactions such as competition and predation, ability to utilise existing data, and capability to monitor entire landscapes and communities, rather than individual species. By facilitating monitoring of spatio-temporal changes in community and metacommunity size, composition and functioning, the framework enables inference at local, landscape and macro scales (Niedballa, 2017).

3.3.2.2 MSOM selection for this study

The multispecies occupancy model of Rota et al. (2016) was employed for this study, due to its capability to simultaneously model occupancy dynamics for multiple species. Previous approaches to modelling interactions between species, such as MacKenzie et al. (2004), were limited by the need for a “species interaction factor” (SIF). This ratio represented the likelihood of two species co-occurring compared to what would be expected under a hypothesis of independence and thus zero interaction (Richmond et al., 2010). However, including covariates in this model's parameterisation caused it to fail to converge when directly estimating the SIF.

To address this issue, Richmond et al. (2010) proposed a conditional two-species occupancy model that incorporated covariates. However, this model assumed asymmetric interaction between the species (one dominant over the other).

Alternative methods have been developed in recent years. For instance, Steen et al. (2014) investigated occupancy for more than two interacting species but that was achieved by fitting multiple two-species models instead of a single model that accommodates interactions.

Rota et al. (2016) proposed a generalised occupancy model that can account for two or more interacting species. This model avoids assuming asymmetric interactions by modelling the latent occupancy state as a multivariate Bernoulli variable. Furthermore, it provides conditions for interspecific independence without requiring additional parameters like the SIF. Finally, this model can successfully incorporate covariates to estimate the probability that two or more species occupy the same site.

As the aim of this study is to investigate species interactions while controlling for the effects of environmental variables, the multivariate Bernoulli model's capability represented a crucial feature. This model allows for the impact of environmental variables on one species to vary in the presence of another species. This is achieved by comparing a model that assumes the probability of one species conditional on the presence of another, is also a function of covariates.

The occupancy model of Rota et al. (2016) is implemented in R through the package *unmarked* (Fiske & Chandler, 2011).

3.4 Statistical analysis: the application of the Multi-Species Occupancy Models (MSOM)

The statistical analyses were performed on R 4.2.2, with RStudio 2022.12.0 (R Core Team, 2022).

In this study, each CT station represents a sampling site, and the time intervals for each repeated survey are grouped as one day. Diverse MSOM were fit to detection/non-detection data of roe deer, red deer and wolves obtained from CTs. A set of candidate models was applied to reflect hypotheses on the effects of interspecific interactions on occupancy and detection processes to avoid data dredging (Burnham & Anderson, 2002).

To format the data for analysis using the *unmarked* package, a set of specific procedures was followed. First, the detection/non-detection data was formatted as a list of matrices (one for each species). Next, the site-level covariates were formatted as a data frame, while the detection-level covariates were formatted as a list of data frames. Finally, the data was combined into an "*unmarkedFrameOccuMulti*" object, which was used in the model.

3.4.1 Variables

The sampling unit for the analysis is represented by the location point of each CT. Because all sites were randomly determined and could potentially be 1,5 km apart, the values used for the analysis were measured within a 200 m radius circular buffer surrounding the cameras. The buffer size ensured independence between sites and served as an index of habitat type integrity and connectivity (Cove et al., 2013).

1. The site-level covariates (occupancy) included:

(i) Measures of human disturbance:
- average daily number of people photographed at each camera trapping site, obtained from CT data directly
- distance from roads (m)
- distance from houses (m)
- distance from park border (m)

The three distances were calculated using the QGIS software - version 3.16 Hannover (QGIS.org, 2020). Vector calculations were undertaken to obtain the measurements derived from the regional layers downloaded from the online *Geoportale* catalogue of Piedmont region.

(ii) Measures of environmental variation:
- open areas in a 200 m buffer from the camera (%)
- forest in 200 m buffer from the camera (%)
- terrain ruggedness index (TRI), an indicator used to describe the roughness or irregularity of the terrain in a specific geographical area. The index accounts for terrain ruggedness using a combination of information about the slope of the terrain and the change in elevation in a specific area (Riley et al., 1999).

The three percentages were calculated using the QGIS software, relying on the data obtained from the *Land Cover Piemonte* project available on the *Geoportale* online catalogue (Regione Piemonte, 2021).
TRI was calculated through the Digital Elevation Model (DEM) of Piedmont region (scale 1:10,000), also available on the *Geoportale* catalogue (Regione Piemonte, 2008).

2. The detection-level covariates included:

- visual clarity, obtained from measurement directly undertaken at the camera site
- temperature, obtained from CT automatic measurements
- camera positioning on/off a trail or animal walkaway
- humans latent presence/absence, obtained from CT data directly
- hunting days, obtained through open access data of the hunting calendar in the area, on the website of CACN5 (www.comprensorioalpinocn5.it). Hunting occurs from the beginning of September until the end of January every day, except Tuesday and Friday.

All the variables were standardised to an average of 0 and a standard deviation of 1. The concept of standardisation is relevant when measuring continuous independent variables at very different scales (such as average number of people, ranging from 0 to 7, and distance from roads, ranging from 18 to 2061). The purpose of standardisation is to rescale an original variable to attain comparable range and/or variance (Zipkin et al., 2010).

Moreover, variables were checked for any correlation with the *VIF* function of the package *usdm* (Naimi et al., 2014) in R. In cases where a correlation was detected between two variables, only one of the variables was included in the model, with a correlation threshold of 0.6 being applied (Dormann et al., 2013). Variables above this limit were not included in the same models for the same parameter.

3.4.2 Set of models

The primary interest of this investigation was to examine the influence of inter-specific interactions on the spatial behaviour of species within an anthropogenic setting. To this end, the analysis was divided in three parts, as described in the specific objectives (par. 1.1), wherein occupancy or detection variables were selected based on prior published works

(Table 1). Table 1 provides a summary of the variables included in the candidate models and their expected effects on the respective species.

Table 1. Description and expected effect of covariates used to describe the occupancy dynamics of roe deer (Ro), red deer (Re), and wolf (W) or their interactions. If there's only one symbol (+ or -) it is referred to all species. Parameters: ψ refers to occupancy, p to detection.

Covariate	Measure	Abbreviation	Parameter	Description	Expected effect	Reference
Visual clarity	%	vs	p	Index that assesses the visual clarity of the CT's field of view	+	Rota et al., 2016
Temperature	°C	temp	p	Mean daily temperature	+	Meek et al., 2014
On/off trail	1/0	trail	p	Whether the CT is positioned on or off a trail	+W	Callaghan, 2002; Musiani et al., 1998
Human presence/absence	1/0	human	p	Record of presence or absence of humans each day	-	Oberosler et al., 2017
Hunting days	1/0	hunting	p	Record of the days in which hunting was active	-Ro	Bonnot et al., 2013; Benhaïem et al., 2008
Forest cover	%	forest	ψ	Percentage of deciduous, coniferous or mixed forest cover	+Ro +Ro/Re	Mori et al., 2021;
Terrain ruggedness index	%	TRI	ψ	Percentage of roughness or irregularity of the terrain	-	Wevers et al., 2021; Falcucci et al., 2013; Whittington et al., 2005
Distance to the closest road	m	dist road	ψ	Minimal distance between CT and primary/secondary/tertiary roads	-Ro -Re	Petridou et al., 2023; Bonnot et al., 2013; Coulon et al., 2008
Distance to the closest house	m	dist house	ψ	Minimal distance between CT and a habitation	-Ro -Re +Ro/Re	Henderson et al., 2022; Bonnot et al., 2013
Number of people per day	people/ day	avg people	ψ	Average number of people captured by a CT per day	-W	Whittington et al., 2005; Theuerkauf et al. 2003

The modelling framework is divided in three sections, that follow the three objectives of the study, as described in section 1.1. The first objective of the study, which comprises a set of 3 models, aims to evaluate the extent to which interactions play a role in shaping inter-specific communities (ch. 3.4.2.1). The second objective, also comprising three models, aims to explore the impact of human activity on species detection probability and how this eventually modifies the occupancy effect (ch. 3.4.2.2). Lastly, the third objective of the study introduces hunting to explore the variation of competition and predation issues within a focal species, the roe deer - the most frequent in the study area and only species for which hunting is permitted among the three (ch. 3.4.2.3).

3.4.2.1 Species interactions

The aim of the first set of models (M1, M2, M3) is to examine the role of inter-specific interactions in shaping the spatial distribution of species in relation to their use of habitats.

Here, human pressure is modelled with variables indicating permanent disturbance, such as roads or houses and an index of the average number of people visiting the sites that do not vary within surveys.

The three models are summarized in Table 2.

M1, M2, M3 all assume species-specific detection probabilities as a function of the visual clarity of the camera (Rota et al., 2016), the temperature (Meek et al., 2014) and whether the camera was on or off a trail (Oberosler et al., 2017, Rota et al., 2016), as indices of the camera functioning. Conversely, occupancy variables vary according to the species of interest.

Table 2. Specification of the detection and occupancy formulas for the 3 candidate models M1, M2, M3 aimed at examining the role of inter-specific interactions among roe deer, red deer and wolf.

Model	Species	Detection formulas	Occupancy formulas
M1	Roe deer	vs + temp + trail	forest + TRI + dist roads
	Red deer	vs + temp + trail	TRI + dist houses
	Wolf	vs + temp + trail	TRI + avg people
M2	Roe deer	vs + temp + trail	forest + TRI + dist roads
	Red deer	vs + temp + trail	TRI + dist houses
	Wolf	vs + temp + trail	TRI + avg people
	Roe & Red		1
	Roe & Wolf		1
	Red & Wolf		1
M3	Roe deer	vs + temp + trail	forest + TRI + dist roads
	Red deer	vs + temp + trail	TRI + dist houses
	Wolf	vs + temp + trail	TRI + avg people
	Roe & Red		forest + dist houses
	Roe & Wolf		TRI + dist roads
	Red & Wolf		TRI + dist roads

Model M1 reflects the hypothesis that all three species occur independently and that marginal occupancy probabilities for each species are a function of habitat type (percentage of forest and/or TRI; Mori et al., 2021; Wevers et al., 2021) and a distinctive human disturbance covariate, identified on the basis of previous research works that highlighted an effect.

Roe deer marginal occupancy was modelled as a function of forest, TRI (one of the primary factors to lead habitat use in roe deer according to the findings of Wevers et al. (2021) and

Lone et al. (2014)), and the distance from roads, which serves as an indicator of a major disturbance to the species, as road accidents are the primary cause of deaths in similar Western Alps valleys (Gazzola et al., 2005). Red deer marginal occupancy was also modelled as a function of TRI and the distance from houses (Henderson et al., 2022). Finally, wolf marginal occupancy was modelled as a function of TRI (Dyck et al., 2022; Falcucci et al., 2013) and the average number of hikers, since wolves usually tend to minimise their probability of encountering people (Whittington et al., 2005; Theuerkauf et al., 2003).

Model M2 assumes that occupancy probabilities of the single species are a function of habitat type and human disturbance, as defined in M1, and further incorporates the hypothesis of constant pairwise dependence among species (i.e., without any covariate). This is achieved with the addition of the *MaxOrder* argument in the modelling framework (here, *MaxOrder* = 2).

Model M3 incorporates the hypothesis that the association between human disturbance and the likelihood of occupancy for individual species differs in the presence or absence of other species. This time, the pairwise dependence among species is not considered as constant, but is modelled with covariates. When modelling the probability of co-occurrence between two species, it can be challenging to determine which variables to use, as this represents a unique aspect of the MSOM used in this study that lacks clear guidance in scientific literature (Rota et al., 2016). The modelling for each pairwise interaction includes at least one environmental factor and one human disturbance factor, in order to evaluate their single or combined impact.

The probability that roe deer and red deer occur together is modelled as a function of forest and distance from houses, because human settlements can create edges or boundaries in the landscape, which have been generally proven to offer a suitable habitat for ungulates, due to the supplemental feeding areas (Etter et al., 2002, Porter et al., 2004). The probability that both roe deer and wolves and red deer and wolves occur together is modelled as a function of TRI and distance from roads. The TRI is used as a proxy for terrain complexity, as all species are expected to more likely inhabit less rugged terrains (Wevers et al., 2021; Falcucci et al., 2013; Whittington et al., 2005), while roads are used as the index of human disturbance that could affect all species, to address the framework of the “landscape of fear” (Laundré et al., 2001).

3.4.2.2 The impact of human presence

M4, M5, M6 (Table 3) reflect the same set of hypotheses regarding the occupancy process outlined for models M1, M2, M3 respectively but now assume that detection probability is also a function of the latent presence/absence of humans (i.e., varying across surveys). Humans are potentially competitively superior to animal species so they may alter detectability of interacting species when present. In particular, human disturbance was revealed to play a significant role in influencing the detection probability of prey and predator in a study by Oberosler et al. (2017). Moreover, several studies (Reimoser, 2012; Cederlund, 1981; Jeppesen, 1989) showed that roe deer are habitually active during the day, similar to humans, an important evaluation which allows for a more accurate comparison in this study, where temporal patterns were not included. Therefore, adding this variable is likely to show a negative effect of human presence on the detectability of all species.

This set of models still includes three options as it is necessary to confirm the first hypothesis regarding the role of interactions in shaping the community.

Table 3. Specification of the detection and occupancy formulas for the 3 candidate models M4, M5, M6 aimed at examining the role of human presence on roe deer, red deer and wolf detectability.

Model	Species	Detection formulas	Occupancy formulas
M4	Roe deer	vs + temp + trail + human	forest + TRI + dist roads
	Red deer	vs + temp + trail + human	TRI + dist houses
	Wolf	vs + temp + trail + human	TRI + avg people
M5	Roe deer	vs + temp + trail + human	forest + TRI + dist roads
	Red deer	vs + temp + trail + human	TRI + dist houses
	Wolf	vs + temp + trail + human	TRI + avg people
	Roe & Red		1
	Roe & Wolf		1
	Red & Wolf		1
M6	Roe deer	vs + temp + trail + human	forest + TRI + dist roads
	Red deer	vs + temp + trail	TRI + dist houses
	Wolf	vs + temp + trail	TRI + avg people
	Roe & Red		forest + dist houses
	Roe & Wolf		TRI + dist roads
	Red & Wolf		TRI + dist roads

3.4.2.3 The effects of hunting

The final objective of the study was to explore the potential effect of hunting on the target species, with an investigation on how competitive and predatory interactions vary during the hunting season. In particular, a focus applies to roe deer as it is the most widespread species in the study area and the only one that can be legally hunted. In order to address this issue, roe deer detectability was modelled in relation to hunting days, as in Bonnot et al. (2013) it was observed that the onset of the hunting season had an impact on roe deer's habitat use. Additionally, the study examined the forest habitat expecting to find a positive relation with roe deer marginal occupancy, since Benhaïem et al. (2008) found that roe deer's spatial behaviour is influenced by the perceived risk of open landscapes compared to wooded areas and, Bonnot et al. (2013) confirmed that during the open season, regardless of the time of day, roe deer tend to spend more time in woodlands.

M7 is summarized in Table 4.

Table 4. Specification of the detection and occupancy formulas for the model M7, aimed at examining the effects of the hunting season on roe deer and its result on shaping ungulates and prey-predator interactions.

Model	Species	Detection formulas	Occupancy formulas
M7	Roe deer	VS + temp + trail + human + hunting	forest + TRI + dist roads
	Red deer	VS + trail + hunting	TRI + dist houses
	Wolf	temp + trail +hunting	TRI + avg people
	Roe & Red		forest + dist houses
	Roe & Wolf		TRI + dist roads
	Red & Wolf		TRI + dist roads

The candidate models were evaluated using the Akaike Information Criterion (AIC). The AIC is a widely used criterion in statistics that balances the trade-off between identifying the model with the best combination of variables while keeping the number of variables as little as possible, in accordance with the principle of parsimony (Burnham & Anderson, 2002). It can be defined as:

$$AIC = 2\delta - 2\ ln(L)$$

Where δ represents the number of estimated parameters in the model, and L represents the maximum value of the likelihood function of the model.

4. Results

4.1 Descriptive analysis of the dataset

A total of 58 CTs were deployed. Out of all the positioned cameras, 62% were positioned at the first random location, 28% at the second, and only 10% at the third. Data collection was carried out for a total of six months, from November 2021 to April 2022 and the majority of the cameras (80%) were positioned during the initial two months of the sampling period (November and December; Figure 7). Once positioned they run until the end of the study. Out of the total cameras, 4 were stolen during the entire sampling period. 20% of the total CTs are located inside the Marguareis Natural Park, where hunting is prohibited and car access restricted.

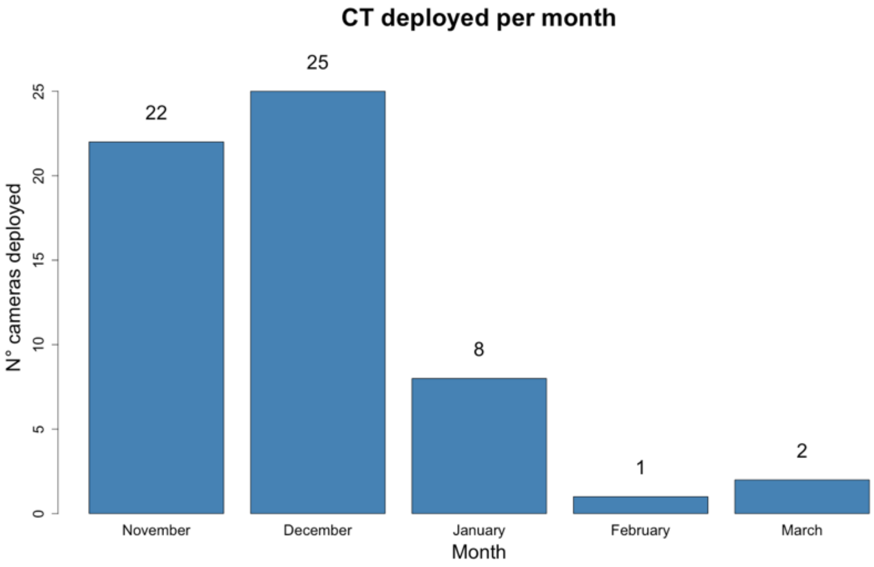

Figure 7. Number of cameras deployed per month. 80% of the cameras were positioned during the first two months of the sampling period (November-December). Once positioned they run until the end of the study.

One camera did not work properly due to technical issues so it was excluded from the study. As a result, the entire dataset consisted of 57 CT sites and 6,288 trap days. The most long active camera was continuously active for 162 days and the least lasting camera was active for 23 days. The mean of trap days for the cameras was 112 ± 38 days.

The dataset includes a total number of 45,525 pictures, cleaned from false triggers (i.e., blank photos due to bad weather conditions, strong wind, over-illumination or camera's malfunctioning).

Table 5 presents a summary of the total number of pictures and events per species in the study area, highlighting in bold the species relevant to this research. The category "Other" includes species with less than 1% of detections, comprising: mustelids, cats, birds, squirrels, hares, livestock, and unidentifiable animals (i.e., out of focus or of low quality).

Among the species identified, the roe deer exhibited the highest frequency of pictures, accounting for 42% of the total, and also had the greatest number of recorded events, amounting to 31% of the total. Notably, there was a 13% difference in events between roe deer and the second most detected species, the wild boar. Humans were the third most commonly captured species, accounting for 16% of total photographs and 21% of total events. Red deer ranked fifth with 6% of photographs and 4% of events, while the wolf was identified as the ninth most frequent species, with a representation of 1% of total photographs and 1% of total events.

Table 5. Total number of pictures and total number of events per species in the study area. The category "Other" includes species with <1% detections. Highlighted in grey are the species of interest for this research.

Species	Pictures	Events
Roe deer (*Capreolus capreolus*)	18967 (42%)	2581 (31%)
Wild boar (*Sus scrofa*)	6421 (14%)	1474 (18%)
Human (*Homo sapiens*)	7327 (16%)	1096 (21%)
Fox (*Vulpes vulpes*)	3288 (7%)	691 (8%)
Red deer (*Cervus elaphus*)	2852 (6%)	332 (4%)
Badger (*Meles meles*)	2319 (5%)	462 (6%)
Chamois (*Rupicapra rupicapra*)	1039 (2%)	111 (1%)
Dog (*Canis lupus familiaris*)	845 (2%)	200 (2%)
Wolf (*Canis lupus*)	580 (1%)	123 (1%)
Other (<1%)	1887 (4%)	529 (6%)
TOTAL	45525	8257

As far as the focus species are concerned, we obtained 2581, 1096, 332 and 123 detections (i.e., events) of roe deer, human, red deer and wolf, respectively, at 52, 27, 21 and 23 sites, respectively (Figure 8).

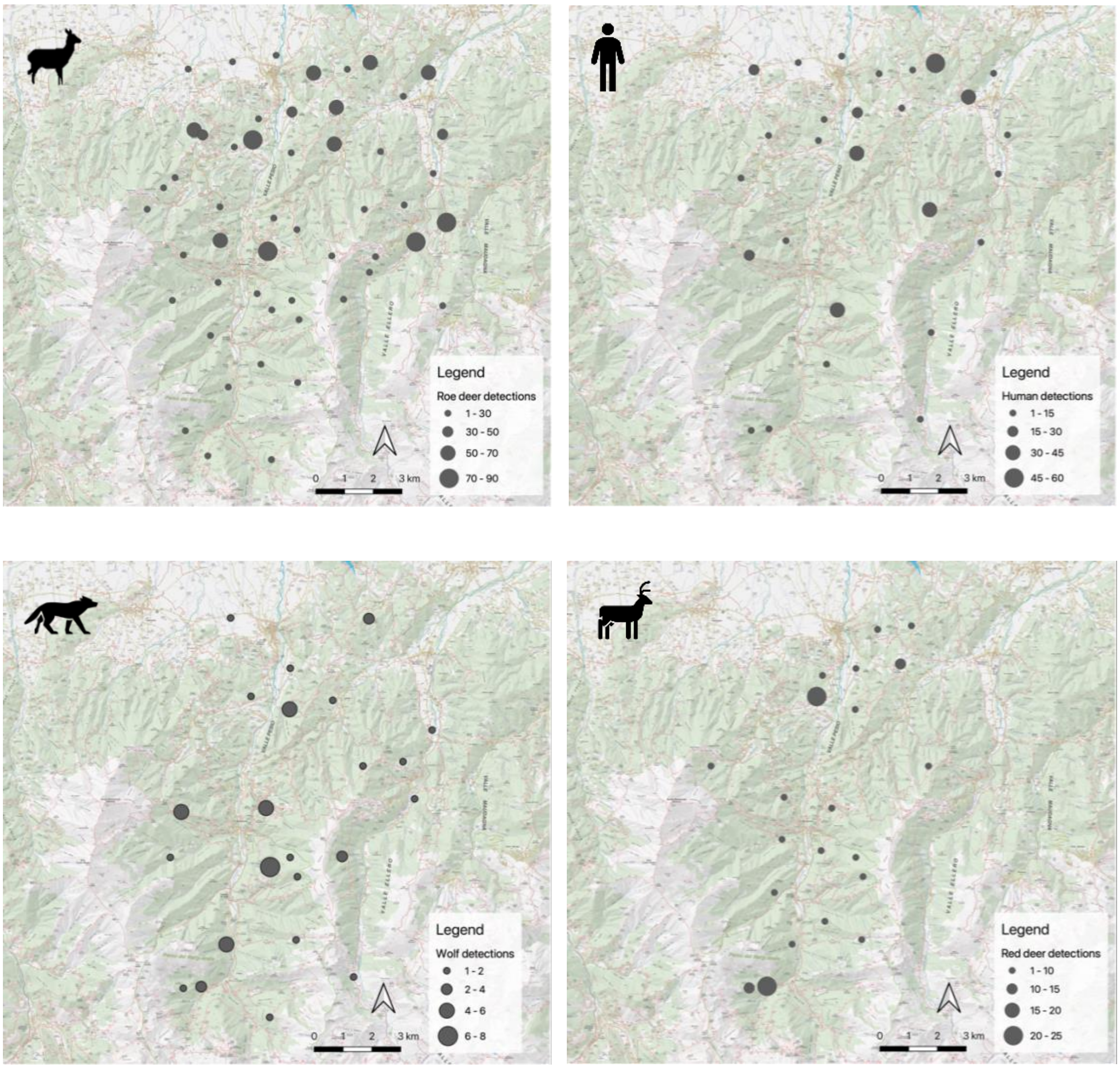

Figure 8. Number of detections for each species. Roe deer (top left) is the most widespread species, with detections at 91% of the cameras. Humans (top right) were detected at 47% of the cameras, wolf (bottom left) at 40% and red deer (bottom right) at 37%.

4.2 Model selection

Overall, the model selection process provided evidence of interspecific dependence among the three observed species and the influence of human presence. The models compared with the Akaike Information Criterion (AIC) are displayed in Table 6.

Table 6. AIC model ranks. Δ AIC is the difference of each model's AIC.

Model	AIC	Δ AIC
M7	3796	0
M6	3802	6
M4	3807	11
M5	3812	16
M3	3813	17
M1	3815	19
M2	3820	24

4.2.1 Species interactions

The best model among the first set, M3, accounted for interspecific interactions, dependent on covariates. The results of the three models are presented in Table 7.

Table 7. MSOMs results, evaluating: independent occurrence of the three species (M1), constant pairwise dependence among species (M2) and pairwise dependence modelled with covariates (M3). Statistically significant results are highlighted with an asterisk (*) at P < 0.05.

		M1			**M2**			**M3**		
Species	**Variable**	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value
Roe deer	*Intercept p*	*-1.225*	*0.075*	*<0.001**	*-1.225*	*0.075*	*<0.001**	*-1.225*	*0.075*	*<0.001**
	VS	0.517	0.059	<0.001*	0.517	0.059	<0.001*	0.493	0.060	<0.001*
	temp	0.043	0.009	<0.001*	0.043	0.009	<0.001*	0.040	0.009	<0.001*
	trail	-0.454	0.049	<0.001*	-0.455	0.049	<0.001*	-0.518	0.053	<0.001*
	Intercept ψ	*5.570*	*2.225*	*0.012**	*3.474*	*3.900*	*0.373*	*23.070*	*11.43*	*0.043**
	forest	0.086	0.816	0.916	-0.182	0.903	0.840	0.877	1.660	0.597
	TRI	-4.187	1.992	0.036*	-4.447	2.031	0.028*	-10.161	6.570	0.122
	dist roads	1.815	1.082	0.093	1.621	1.018	0.111	10.269	4.760	0.031*
Red deer	*Intercept p*	*-3.616*	*0.269*	*<0.001**	*-3.639*	*0.271*	*<0.001**	*-3.710*	*0.257*	*<0.001**
	VS	0.556	0.205	0.007*	0.561	0.204	0.006*	0.657	0.211	0.002*
	temp	0.024	0.027	0.379	0.024	0.027	0.377	0.019	0.027	0.475
	trail	-0.874	0.319	<0.001*	-0.881	0.214	<0.001*	-0.845	0.208	<0.001*
	Intercept ψ	*-0.038*	*0.536*	*0.943*	*-1.121*	*2.077*	*0.589*	*25.565*	*12.21*	*0.036**
	TRI	0.097	0.520	0.853	0.512	0.863	0.553	7.914	5.720	0.167
	dist houses	-1.752	0.732	0.017*	-1.822	0.791	0.021*	-1.422	2.580	0.581

Wolf	*Intercept p*	*-3.874*	*0.318*	*<0.001**	*-3.828*	*0.322*	*<0.001**	*-3.683*	*0.293*	*<0.001**
	VS	0.433	0.292	0.138	0.386	0.284	0.175	0.222	0.288	0.441
	temp	-0.080	0.043	0.063	-0.077	0.043	0.072	-0.078	0.043	0.067
	trail	0.438	0.154	0.004*	0.414	0.151	0.006*	0.424	0.148	0.004*
	Intercept ψ	*1.688*	*0.953*	*0.077*	*1.153*	*3.000*	*0.701*	*20.453*	*10.790*	*0.058*
	TRI	0.675	1.040	0.516	1.628	1.261	0.197	13.144	7.920	0.097
	avg people	0.378	1.066	0.723	4.156	3.776	0.271	7.172	3.320	0.031*
Roe - Red	*Intercept ψ*				*1.746*	*2.193*	*0.426*	*-16.113*	*8.560*	*0.059*
	forest							2.494	1.790	0.164
	dist houses							-8.892	4.230	0.036*
Roe - Wolf	*Intercept ψ*				*1.815*	*4.071*	*0.656*	*-6.352*	*6.080*	*0.296*
	slope							0.901	5.170	0.861
	dist roads							-4.107	2.430	0.091
Red - Wolf	*Intercept ψ*				*-0.532*	*1.975*	*0.788*	*-12.530*	*7.190*	*0.081*
	slope							-14.994	6.960	0.031*
	dist roads							7.721	2.730	0.005*

Regarding marginal occupancy, distance from roads had a significant positive effect on roe deer independent occupancy (M3, z = 2.159, p = 0.031), while forest and slope did not show any significant effect. This result differs from M1 that did not report an effect of roads when roe deer were considered independent of relations with other species and M1 also reported a negative effect of slope (M1, z = -2.102, p = 0.036) that fades when interactions are present in M3. Red deer occupancy was not significantly influenced by any of the identified variables. Wolf occupancy was positively influenced by the average number of people per day (M3, z = 2.160, p = 0.031).

In terms of co-occurrences (M3), roe deer and red deer were more likely to be found together as distance from houses decreased (z = -2.101, p = 0.036), with no significant effect of forest. The co-occurrence of roe deer and wolf was not significantly influenced by slope or distance from roads. However, wolf and red deer co-occurrence showed significant results for both the environmental and human-related variables identified. Specifically, slope had a negative influence on their co-occurrence (z = -2.154, p = 0.031) and distance from roads had a positive effect (z = 2.832, p = 0.005).

Regarding the detection section of the best model of this part (M3), the visual clarity of the camera had a positive effect on detection for roe deer (z = 8.730, p < 0.001) and red deer (z = 3.107, p = 0.002), while it had no effect on wolf. Temperature had a positive effect on roe deer detection (z = 4.623, p < 0.001) but had no influence on red deer or wolf. Finally, animal trail influenced the detection probability of each species (Figure 9), with a negative influence on roe deer (z = -9.232, p < 0.001) and red deer (z = -4.068, p < 0.001) and a positive influence on wolf (z = 2.865, p = 0.004).

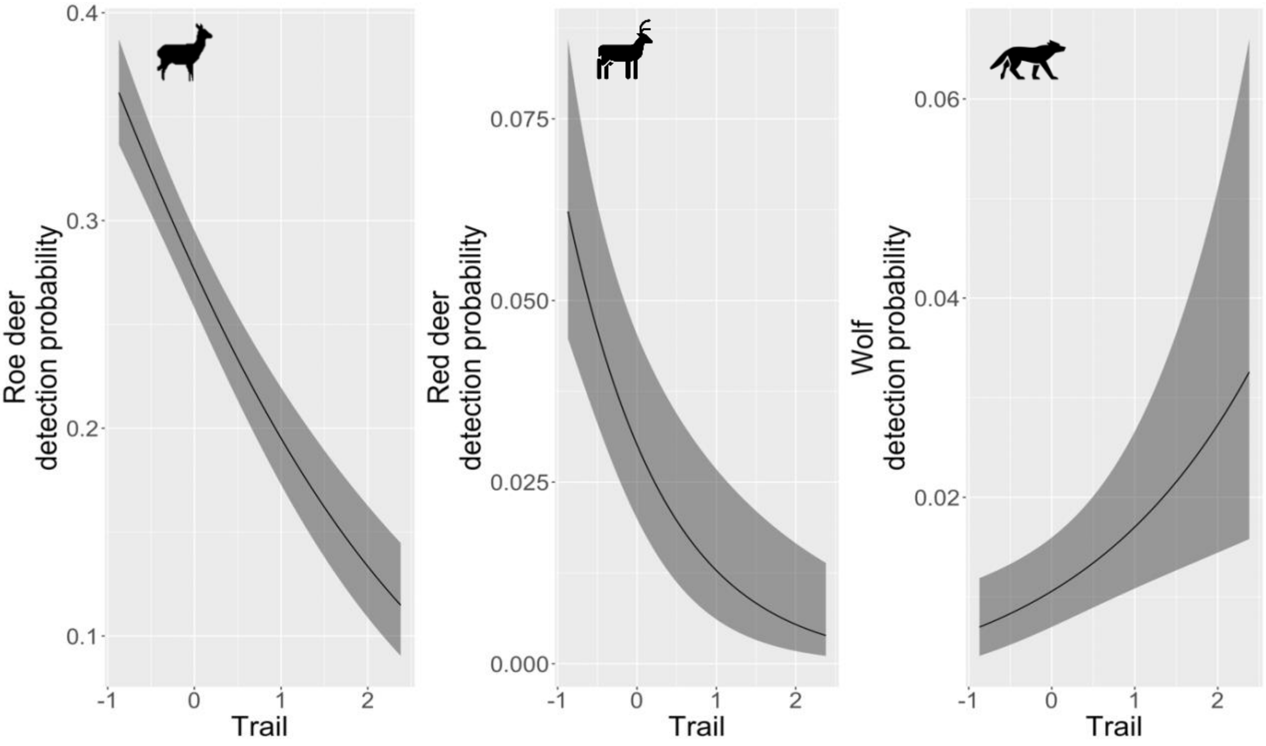

Figure 9. Detection probability of roe deer (left), red deer (central) and wolf (right) in relation to trails. Solid lines represent the mean posterior distribution and grey ribbons envelop 95% credible intervals. Roe deer and red deer were more likely detectable off-trail, while wolves show an opposite trend, being more likely detectable on trails.

4.2.2 The impact of human presence

All three models of the second set (M4, M5, M6) reported a lower AIC compared to the first set (M1, M2, M3), with Δ AIC > 10 among the best models of the two sets. These values suggest that the latent presence/absence of humans is an important factor in determining the detectability of the species. The best model among the three, M6, found a significant positive influence of human presence on the detectability of roe deer (z = 3.637, p < 0.001). The total results are presented in Table 8.

Table 8. MSOMs results, with species detection probability modelled as a function of the latent presence/absence of humans, evaluating: independent occurrence of the three species (M4), constant pairwise dependence among species (M5) and pairwise dependence modelled with covariates (M6). Statistically significant results are highlighted with an asterisk (*) at $P < 0.05$.

		M4			**M5**			**M6**		
Species	**Variable**	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value
Roe deer	*Intercept p*	*-1.269*	*0.076*	*<0.001**	*-1.267*	*0.076*	*<0.001**	*-1.268*	*0.076*	*<0.001**
	VS	0.493	0.060	<0.001*	0.493	0.060	<0.001*	0.493	0.060	<0.001*
	temp	0.040	0.009	<0.001*	0.040	0.009	<0.001*	0.040	0.009	<0.001*
	trail	-0.517	0.053	<0.001*	-0.518	0.053	<0.001*	-0.518	0.053	<0.001*
	human	0.592	0.163	<0.001*	0.593	0.163	<0.001*	0.593	0.163	<0.001*
	Intercept ψ	*5.577*	*2.226*	*0.012**	*2.809*	*4.004*	*0.483*	*22.792*	*11.26*	*0.043**
	forest	0.061	0.825	0.941	-0.182	0.904	0.840	0.882	1.680	0.598
	TRI	-4.198	1.994	0.035*	-4.531	2.032	0.026*	-10.002	6.430	0.120
	dist roads	1.836	1.077	0.088	1.599	1.004	0.111	10.210	4.720	0.031*
Red deer	*Intercept p*	*-3.610*	*0.270*	*<0.001**	*-3.634*	*0.271*	*<0.001**	*-3.710*	*0.257*	*<0.001**
	VS	0.570	0.207	0.006*	0.574	0.206	0.005*	0.655	0.211	0.002*
	temp	0.026	0.028	0.343	0.026	0.028	0.344	0.019	0.027	0.475
	trail	-0.852	0.215	<0.001*	-0.872	0.216	<0.001*	-0.845	0.208	<0.001*
	human	-0.356	0.630	0.572	-0.331	0.630	0.599			
	Intercept ψ	*-0.034*	*0.534*	*0.949*	*-0.981*	*2.092*	*0.639*	*25.428*	*12.12*	*0.036**
	TRI	0.089	0.519	0.863	0.562	0.848	0.508	7.967	5.72	0.164
	dist houses	-1.732	0.727	0.017*	-1.826	0.796	0.021*	-1.434	2.57	0.577
Wolf	*Intercept p*	*-3.841*	*0.313*	*<0.001**	*-3.892*	*0.330*	*<0.001**	*-3.685*	*0.293*	*<0.001**
	VS	0.351	0.288	0.222	0.341	0.286	0.233	0.221	0.288	0.443
	temp	-0.079	0.043	0.064	-0.080	0.043	0.061	-0.078	0.043	0.067
	trail	0.375	0.159	0.018*	0.374	0.160	0.019*	0.425	0.148	0.004*
	human	0.368	0.485	0.448	0.427	0.491	0.384			
	Intercept ψ	*2.286*	*1.460*	*0.117*	*1.179*	*3.039*	*0.698*	*20.241*	*10.620*	*0.058*
	TRI	1.437	0.939	0.126	1.943	1.560	0.213	13.280	7.900	0.092
	avg people	3.366	2.266	0.137	4.979	4.220	0.238	7.185	3.320	0.030*
Roe - Red	*Intercept* ψ				*1.823*	*2.218*	*0.411*	*-15.980*	*8.490*	*0.060*
	forest							2.457	1.770	0.165
	dist houses							-8.829	4.200	0.035*
Roe - Wolf	*Intercept* ψ				*2.613*	*4.231*	*0.537*	*-6.155*	*5.910*	*0.297*
	slope							0.769	5.080	0.880
	dist roads							-4.088	2.410	0.091
Red - Wolf	*Intercept* ψ				*-0.763*	*1.887*	*0.686*	*-12.506*	*7.160*	*0.081*
	slope							-15.001	6.940	0.031*
	dist roads							7.695	2.720	0.005*

The three graphs presented below illustrate the relationship between the marginal occupancy probability of each species and a specific environmental or human-related variable that was regarded as important to describe their occupancy (roe deer-TRI: Figure 10, red deer-houses: Figure 11 and wolf-people: Figure 12).

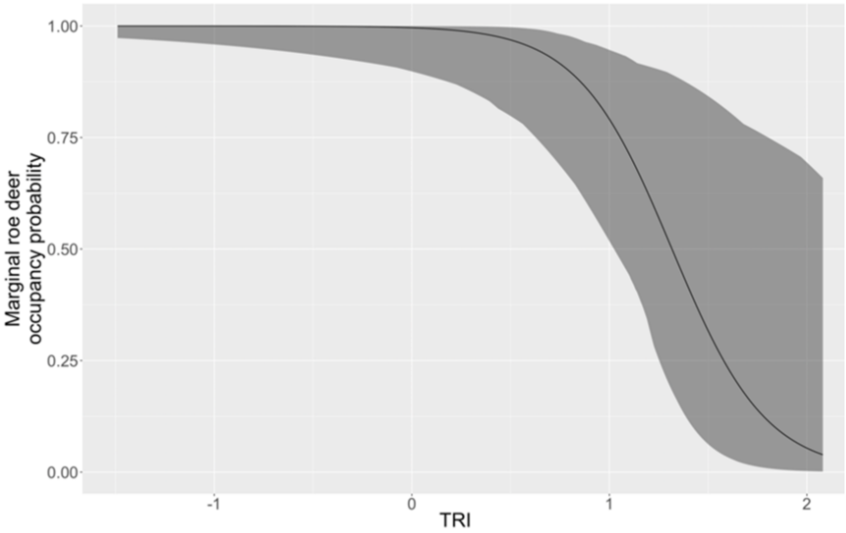

Figure 10. Marginal occupancy probability of roe deer as a function of the terrain ruggedness index (TRI). Solid lines represent the mean posterior distribution and grey ribbons envelop 95% credible intervals. The graph shows how roe deer tend to occupy with maximum likelihood areas with a gentler terrain ruggedness, and, as this increases, it tends to be less likely for them to occupy the site.

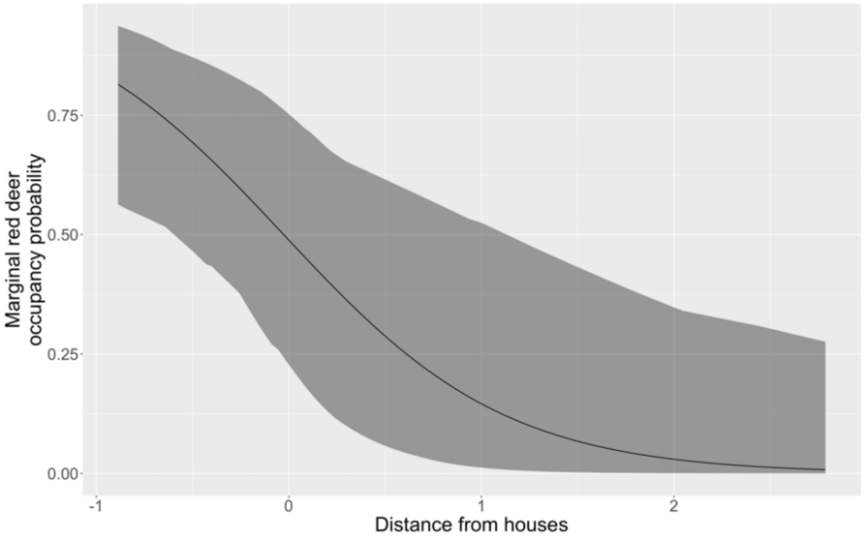

Figure 11. Marginal occupancy probability of red deer as a function of the distance from the closest human habitation. Solid lines represent the mean posterior distribution and grey ribbons envelop 95% credible intervals. Red deer are more likely to occupy sites which are closer to human habitations.

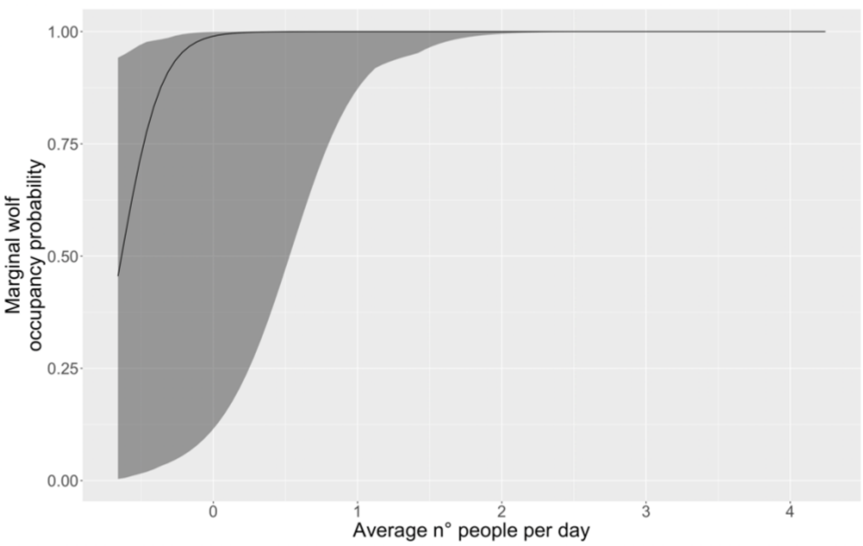

Figure 12. Marginal occupancy probability of wolf as a function of the average number of people per day. Solid lines represent the mean posterior distribution and grey ribbons envelop 95% credible intervals. Wolf occupancy shows a strong relation with the average daily number of people occupying a site, reporting a maximum likelihood occupancy even when low values of people passage are concerned.

4.2.3 The effects of hunting

M7, the model with the best overall AIC, reported a significant value of hunting days on roe deer detection highlighting a negative relation (z = -3.424, p < 0.001). Moreover, hunting days did not show a significant effect on both red deer and wolf detection probabilities. Forest had no significant effect on roe deer marginal occupancy and co-occurrence with red deer. Distance from houses reported a negative significant effect on ungulates co-occupancy probability (z = -2.107, p = 0.035). The total results are presented in Table 9.

Table 9. MSOM results, with species detection probability modelled as a function of the latent presence/absence of humans and the hunting period, evaluating pairwise dependence among species modelled with covariates (M7). Statistically significant results are highlighted with an asterisk (*) at P < 0.05.

		M7		
Species	**Variable**	Estimate	SE	p-value
Roe deer	*Intercept p*	*-1.174*	*0.080*	*<0.001*
	VS	0.503	0.060	<0.001*
	temp	0.036	0.009	<0.001*
	trail	-0.522	0.053	<0.001*
	human	0.585	0.164	<0.001*
	hunting	-0.428	0.125	<0.001*
	Intercept ψ	*23.889*	*11.67*	*0.041**
	forest	0.976	1.690	0.563
	TRI	-10.452	6.590	0.113
	dist roads	10.538	4.810	0.028*

Red deer	*Intercept p*	*-3.692*	*0.267*	*<0.001**
	VS	0.664	0.212	0.002*
	temp	0.018	0.027	0.500
	trail	-0.843	0.208	<0.001*
	hunting	-0.095	0.361	0.792
	Intercept ψ	*25.862*	*12.33*	*0.036**
	TRI	7.490	5.64	0.184
	dist houses	-1.525	2.59	0.555
Wolf	*Intercept p*	*-3.671*	*0.306*	*<0.001**
	VS	0.222	0.288	0.441
	temp	-0.079	0.043	0.064
	trail	0.424	0.148	0.004*
	hunting	-0.053	0.459	0.907
	Intercept ψ	*20.329*	*10.700*	*0.057*
	TRI	12.926	7.860	0.099
	avg people	7.151	3.290	0.029*
Roe - Red	*Intercept ψ*	*-16.766*	*8.760*	*0.056*
	forest	2.596	1.810	0.152
	dist houses	-8.920	4.230	0.035*
Roe - Wolf	*Intercept ψ*	*-6.541*	*5.910*	*0.297*
	slope	0.909	5.080	0.880
	dist roads	-4.175	2.410	0.091
Red - Wolf	*Intercept ψ*	*-12.233*	*7.090*	*0.084*
	slope	-14.769	6.890	0.032*
	dist roads	7.782	2.740	0.004*

5. Discussion

In recent years, camera traps have gained considerable recognition as an effective tool to monitor animal presence and offer a potential substitute for conventional, labour-intensive survey techniques (Gilbert et al., 2021b; Burton et al., 2015). According to the findings of Wearn and Glover-Kapfer (2019), comparative analyses of CTs with alternative survey methods generally support the view that CTs are a highly effective tool for conducting wildlife surveys. Specifically, their efficiency concerns the ability to detect a diverse range of species and record a large number of detections of targeted species.

In light of the benefits afforded by CTs in monitoring wildlife populations, the current study was conducted to examine patterns of co-occurrence between ungulates and wolves in mountain valleys where they coexist with human populations.

The camera trap network installed in the research area indicated the roe deer to be the most frequently detected species, accounting for approximately one-third of all recorded events and, especially, this species reported detections across more than 90% of the cameras. Notably, this species exhibited significantly higher detection numbers compared to the other three species, as humans were captured at almost half of the cameras (47%), while wolves and red deer were comparably detected on less than half of the cameras (40% and 37% respectively).

The aim of this study did not involve determining species abundance, and therefore it is not possible to ascertain which species is more numerous. However, valuable insights can be gained by examining spatial utilisation and identifying factors that explain the high incidence of roe deer detections across the study area.

The habitat within the study area is predominantly wooded due to the altitudinal range it covers, with limited expansion of areas with scarce vegetation or pastures. Roe deer has been identified as a wood-dependent species (Morellet et al., 2011; Lovari & San Josè, 1997; Hewison et al., 2001) and its small body size and shape (averaging 27.7 kg for males and 26.7 kg for females; Loison, 1999) are suitable for moving through densely vegetated habitat conditions (Hansson, 1994).

Deciduous woodland with thick underwood (typically found at low altitudes in our study area), especially if mixed and uneven in age, plays a pivotal role in providing roe deer with food and shelter (Ferretti et al., 2011; Pellerin et al., 2010; Lovari & San Josè, 1997). This role increases in importance in fragmented habitats, such as those found at lower altitudes where forests are interrupted by cultivated fields, where woodland patches appear to be particularly relevant for roe deer (Morellet et al., 2011). Due to their highly selective herbivorous diet, roe deer prefer to occupy woodlands and scrublands where they can easily access high-quality food resources (Freschi et al., 2017; Torres et al., 2012; Jong et al., 1995).

Thus, the area where the study was conducted represented an optimal environment for roe deer and justifies their widespread detections. Moreover, it is noteworthy that the study sites did not encompass higher altitude habitats where roe deer are less abundant due to unfavourable terrain conditions such as steepness, rocks, and food scarcity (Wevers et al., 2021). In fact, roe deer exhibit considerable variation in their spatial behaviour depending on resource availability and snow cover, particularly in mountain areas (Lamberti et al., 2004; Mysterud, 1997).

However, the sampling period precluded access to these higher altitude areas where the expected detection of roe deer would have been lower, given the unsafe snow conditions during the winter season.

Although no claims on consistency are possible, the other ungulate of interest, red deer, may be less abundant in our study area given that its detections were slightly more than one-tenth of those of roe deer. However, red deer are overall less widely distributed in the Western Alps, as opposed to roe deer that are present with substantial continuity of population (ISPRA, 2013). This is partly because red deer were reintroduced later compared to other ungulates in the same region, with the Italian and French Park Systems initiating the reintroduction of roe deer (along with chamois and wild boar) in the 1980s, while red deer were reintroduced towards the end of the 1990s (Marucco et al., 2008). However, red deer is recently expanding at the Alpine scale (ISPRA, 2013).

The predator, wolf, was detected at 40% of the total sites, but the detections were considerably lower than those of roe deer (one twentieth) and red deer (less than half). Nonetheless, this is consistent with the wolf's lower density compared to ungulates, typical of large carnivores which move over large areas (Mech & Boitani, 2003), and its use of space as the species is known to travel in packs (Mech, 2000; Fuller & Keith, 1980; Peterson, 1977) and a single pack's territory can occupy an entire valley. Therefore, wolves' home range is significantly larger than that of their prey (wolf: 100 - 600 km^2, Ciucci et al., 1997, Mech & Boitani, 2003; red deer: 1.13 - 3.86 km^2, Georgii & Schroder, 1983; roe deer: 0.13

- 0.44 km^2, Lovari et al., 2017). Currently, the wolf population in the study area is reported to be stable (Avanzinelli et al., 2022).

5.1 Influences of detection probability

One important aspect of the occupancy models used in this study is their ability to include the estimated detection probability, which takes into account the unique conditions of each site or survey (MacKenzie et al., 2002). This is essential to ensure that the results are not biased by imperfect detection, and allows for a more accurate assessment of the presence or absence of different species in the study area (Bailey et al., 2014).

Temperature, which is known to impact camera functioning (Meek et al., 2014), was found to be an important factor driving roe deer detectability but not those of other species, such as red deer. The sensitivity of the passive infra-red sensors of the cameras is affected by weather, particularly extreme heat and cold conditions. The reliability of CTs tends to decrease as the temperature difference between the moving animal and ambient background decreases, since the sensors function by detecting a change of temperature between the background and a passing object (Meek et al., 2012). Therefore, the difference in detectability between the two ungulates can be explained by the remarkable difference in body size (red deer average weight ranges from 107.5 kg for females to 160.0 kg for males and roe deer ranges from females 26.7 kg to males 27.7 kg; Loison et al., 1999). Therefore, red deer are more likely to be detected even in situations where camera performance is lower, because of the greater change between background temperature and the passing animal, due to body size.

To improve estimates of detection, a visual clarity index was calculated for each camera, which provided a measure of the visibility of the camera's field of view. This index was found to be relevant for roe deer and red deer, but not for wolf detectability, which appeared to be unaffected by the clarity of the camera view. Wolves may be less likely to be obstructed by vegetation or other obstacles due to their tendency to move along linear features such as hiking trails (Whittington et al., 2005; Thurber et al., 1994), as also confirmed by the results presented in the following paragraph, while ungulates tend to occupy the underwood in search of food and cover (Freschi et al., 2017; Jong et al., 1995).

Finally, another interesting value for detectability regards the type of point in which the camera was positioned. CTs placed on trails were more likely to detect wolves but less likely to detect ungulates, which were, conversely, more likely to be detected at off-trail cameras. This finding is consistent with current knowledge on wolves moving strategies. As already mentioned, many studies (Dickie et al., 2017; Callaghan, 2002; James & Stuart-Smith, 2000) report that wolves use linear features as travel routes, such as hiking trails, which offer convenient travel itineraries across the territory (Whittington et al., 2005).

This result could explain the positive relationship emerged between wolf occupancy probability and human passage at a given site. In fact, the relationship is due to wolves' tendency to utilize trails as their travel routes, which, given the study area, coincides with the patterns of human movement along these same routes. Hence, this preference for the same type of passage has to be attributed to a shared preference for trail-based movement, which is particularly relevant in this mountainous area with a vast network of hiking trails, and not to a surrounding high-quality habitat for wolves (Whittington et al., 2005).

However, the current study did not explore the hypothesis of temporal segregation, as temporal patterns were not investigated. Previous studies have examined the temporal patterns of wolves, revealing that the species is predominantly active at night, while humans tend to be active during the day, enabling wolves to utilize areas that are heavily used by humans, trails included, at different times (Petridou et al., 2023; Kusak et al., 2005; Ciucci et al., 1997).

5.2 Species interactions

Both the first and second parts of the modelling analysis demonstrated that species interactions improved model performance beyond what could be explained by single species modelling alone. This supports the expectation that interactions among species play a crucial role in shaping habitat utilisation, outweighing the impact of individual species' effects. While single species models showed some influence on the marginal probability of each species occupying a site, they did not fully capture the complex ways in which species interact with each other. The combined effect of these interactions was found to significantly affect model outcomes.

Rota et al. (2016) asserted that species occurrence in a given area is often determined not only by biotic and abiotic factors, but also by interactions with other species. This highlights the significance of using a multi-species model, which enables simultaneous analysis of detection/non-detection data for multiple species and can identify evidence of species interactions across different environmental conditions.

The ability to model the probability of co-occurrence between two species as a function of covariates has provided valuable insights into the factors driving marginal occupancy probabilities that might have otherwise been overlooked. This is particularly evident in the case of roe deer occupancy. When modelled independently of interactions, roe deer appear to be primarily influenced by TRI, as previously suggested by other studies that have reported a positive association with gentle slopes (Wevers et al., 2021) and avoidance of rugged terrain (Lone et al., 2014). This could reflect a movement strategy aimed at maximizing energy efficiency (Petridou et al., 2023). Nevertheless, when interactions are taken into account in the analysis, the influence of slope on roe deer occupancy weakens, and distance to roads emerges as the most influential variable determining roe deer marginal occupancy. Specifically, occupancy increases with greater distance from roads. This finding is consistent with previous studies that have reported roe deer avoidance of roads across various landscape contexts (Coulon et al., 2008).

Interestingly, when considered individually, roe deer tend to be more likely found distant from roads. However, when examining the relationship between red deer and roe deer, the two ungulates were more likely to co-occur as the distance from houses decreased. One possible explanation for this pattern is that human settlements can create edges or boundaries in the landscape, which may offer a more suitable habitat for both species (Etter et al., 2002, Porter et al., 2004). For instance, houses may create areas with greater vegetation or access to water, which can attract ungulates. Additionally, the disturbances caused by human activity may create openings in the forest canopy that trigger a transition to younger and smaller plants (McDowell et al., 2020), which can provide browsing and foraging opportunities. This aligns with the findings of Bonnot et al. (2013), which suggest that the effects of infrastructures on roe deer occupancy can be influenced by the immediate environment, as roe deer can tolerate high proximity to settlements by staying within protective forested habitats during the day.

Since the effect of roads on roe deer emerged when interactions were added to the model, it is possible that also wolf incoming in the scene plays a role in shaping ungulates spatial use.

In particular, a relevant hypothesis is that concerning the landscape of fear. This definition refers to the spatial and temporal variation in the risk of predation that prey experience in a given environment (Laundré et al., 2001). By modifying their responses to these risk factors, animals can potentially reduce their vulnerability to predation, as they may alter their behaviour in response to the perceived risk, avoiding areas where predators are likely to be present even if those areas provide abundant resources or a suitable habitat (Gaynor et al., 2019; Laundré et al., 2010).

However, the co-occurrence of roe deer and wolves could not be explained by any of the chosen variables, and similarly, results on roe deer marginal occupancy did not allow for an explanation of effects ascribable to wolf presence, and therefore, the insights into the landscape of fear hypothesis cannot be confirmed for roe deer. This could be due to the vast detection of roe deer through the study area, which impede to find variables that could fully explain this complex situation. In addition, a recent study by Palmer et al. (2022) identified time as a crucial dimension in landscapes of fear, since risk varies both in space and time but static spatial models implicitly assume that risk is constant and this study did not include temporal variations.

On the other hand, the co-occurrence of red deer and wolves increased as the distance from roads increased. In addition, they tended to be detected together more frequently in areas with gentler slopes, suggesting a preference for such terrain for more efficient movements. Although co-occupancy effects were present, individual red deer occupancy did not appear to change in relation to wolf presence. In this case, as opposed to roe deer, the reason could lay in the fact that red deer are not the primary prey used by wolves in the region of interest (Regine, 2008), so they may be less impacted by the predator's attacks. In addition, the study period did not coincide with red deer reproductive season, which may have affected the results, since fawns may become a favourable prey (Torretta et al., 2017; Smietana & Klimek, 1993).

5.3 The impact of human presence

The second major hypothesis concerned human disturbance. In fact, in some areas, human activity is reported to affect herbivores more than habitat or natural predators (Bonnot et al., 2020; Ciuti et al., 2012).

The study aimed to investigate the role of human presence in influencing species detectability. All three models considering human disturbance yielded better results than the first set, indicating that the latent presence or absence of humans is a crucial factor in determining species detectability. However, contrary to expectations, only roe deer exhibited a significantly positive effect and other variables did not change their effects upon the introduction of humans. A possible explanation of the positive outcome is that hikers (intended as general people variably occupying the mountains) may enhance roe deer detectability through their activity and noise, as they could disturb the animals, causing them to flee or move more than they usually do, and eventually making them more easily detectable.

Roe deer are particularly sensitive to human disturbance, such as human presence, vehicles, dogs, and livestock and often avoid sources of disturbance such as roads (as also confirmed in this study), houses, agricultural land and recreational activities (Petridou et al., 2023; Bonnot et al., 2013). On the other hand, red deer and wolves may not have been affected by human disturbance due to their more crepuscular/nocturnal temporal habits (Kusak et al., 2005; Carranza et al., 1991), conducting to a limited temporal overlap with hikers in respect to roe deer (Oberosler et al., 2017).

5.4 The effects of hunting

In human-dominated landscapes, habitat fragmentation leads to greater proximity and accessibility of humans to natural areas, resulting in increased conflicts between humans and wildlife (Bonnot et al., 2013). The presence of wolves in the study area poses a challenge for predator conservation, as this species has been generally known to generate conflicts with hunters who perceive them as competitors (Dressel et al., 2015). The negative perception of wolves by hunters reflects a competitive situation, where wolves are seen as a serious threat to hunting and hunting dogs (Bisi et al., 2010).

Out of the three species examined, roe deer is the only one legally hunted in the area. Previous studies have reported that hunting has a significant impact on this ungulate. Benhaïem et al. (2008) demonstrated that the selection of feeding sites was affected, as roe deer no longer based their choices solely on food availability but also depended on risk perception. In addition, Bonnot et al. (2013) found that vigilance levels increased during the hunting season.

The investigation into the effects of hunting in this study area produced interesting findings. Adding hunting days as a variable revealed that the likelihood of capturing roe deer was significantly lower during the hunting season. However, the presence of hunting did not affect either red deer or wolf. This can be attributed to the fact that roe deer are the only game species among the three and therefore are more sensitive to hunting periods. Moreover, the lower detection probability of roe deer during the hunting season can be attributed to their reduced movement, since moving across patches in fragmented habitats is highly risky (Cote et al., 2017). As mentioned, during hunting season, roe deer have to make a trade-off between security and other needs, particularly food resources. This constraint on their movement during the day increases the need to explore more during the night to locate food resources (Martin et al., 2018). For this reason, investigating temporal patterns would be beneficial in gaining a better understanding of how roe deer cope with hunters.

It was expected that a different effect of environmental variables would be found in comparison to other models, as previous research has demonstrated an impact. For example, Bonnot et al. (2013) found that roe deer respond to the hunting threat by decreasing their daytime use of high-crops, which offer both shelter and food resources but are often targeted by hunters with dogs during the open season. Consequently, roe deer adjust their habitat usage by concentrating on open forage-rich areas at night. Similarly, Benhaiem et al. (2008) observed that hunting risk influences vigilance behaviour, resulting in higher overall levels during the hunting season, particularly in the more open areas of the landscape. However, these effects were not detected by examining the significance of the variables in this study This could be due to the major fact that both of the aforementioned studies included time in their analysis, allowing for a distinction between habitat usage during the day (when hunters are active) and at night (when roe deer can move without the risk of being shot).

6. Conclusion

This study aimed to investigate the co-occurrence patterns of Alpine species in a mountain valley environment in the Western Italian Alps, where a complex interplay of competition, predation, and human activities is present. Camera traps were employed for data collection, which is an increasingly effective tool for monitoring species presence, given the parallel development of statistical methods for managing this type of data.

The results suggest that the use of habitat by wildlife should not only be examined in relation to site-specific variables (e.g., environmental variables such as terrain roughness or forests, or human disturbance variables such as houses or roads), because species are in close interaction with each other, and this interaction cannot be overlooked, given its primary role in modifying habitat use. Additionally, humans (e.g., residents, tourists, hikers, cyclists) resulted to exert a significant influence on shaping the community, as the sharing of habitat makes them fully involved in the predator-prey interaction mechanisms. Finally, the most sensitive species to hunting risk, the roe deer, resulted to be impacted in its detectability by the hunting season, making this additional anthropogenic disturbance fundamental in describing species-environment and species-specific interactions.

An interesting element of the study concerned the detection of roe deer in almost all of the sampling sites. The occupancy of roe deer was found to be widespread throughout the valley, hence, despite the relevant anthropogenic impact, this does not prevent a good expansion of the species, although quantitative studies on abundance are needed. The habitat type of the study area is suitable for roe deer (deciduous forests with undergrowth and abundant food resources), which undoubtedly contributes to their ability to withstand competitive interaction with red deer, predation by wolves and human disturbance. Moreover, the fact that the study area has a relatively small human population, limited to the valley floor, leaves the higher parts of the mountains and the forests free from continuous intense disturbance, as could be caused by a city or a larger urban area.

In conclusion, the investigated area exhibits a complex ecological system, wherein ungulates compete for resources, face predation from wolves, and share their habitat with humans engaging in diverse activities. It is evident that the study of such a community of species, which is typical in the Western Alps, cannot disregard the inclusion of the interactions that occur between prey, predators and human activities, being those fundamental in shaping species habitat use. This study gives important insights of such interactions, particularly relevant for guiding management decision and for indicating good practices to minimise human impacts for developing sustainable approaches in complex predator-prey systems.

Acknowledgments

I would like to thank my supervisor, Professor Francesca Marucco for the time she dedicated to review the drafts of this thesis and the treasured comments she provided. Moreover, her passion for the study of wildlife has been truly inspiring during the whole project.
I wish to thank Virginia Boiani for the helpful insights and her qualified and enthusiastic support. I also wish to thank Dr Achaz von Hardenberg for the kind recommendations.

I am most grateful to the park rangers of the Maritime Alps Protected Area for their support during my stay in Chiusa Pesio. I would also like to extend my special thanks to Davide Sigaudo for his proficiency and dedication.
Finally, I would like to thank my family for the endless support during my academic journey and my friends for being an exceptional team.

7. References

Abrams, J. F., Sollmann, R., Mitchell, S. L., Struebig, M. J., & Wilting, A. 2021. Occupancy-based diversity profiles: capturing biodiversity complexities while accounting for imperfect detection. *Ecography*, 44(7), 975-986. DOI: 10.1111/ecog.05577

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In B. N. Petrov & F. Caski (Eds.), *Proceedings of the Second International Symposium on Information Theory*, 267–281. Budapest: Akademiai Kiado.

Augustine, B.C., Royle, A.J., Kelly, M.J., Satter, C.B., Alonso, R.S., Boydston, E.E., & Crooks, K.R. 2018. Spatial capture–recapture with partial identity: An application to camera traps. *Annals of Applied Statistics*, 12 (1), 67 - 95. DOI: 10.1214/17-AOAS1091

Avanzinelli E., D. Perrone, A. Menzano, P. Bertotto, R. Bionda, M. V. Boiani, G. Ferraro, L. Martinelli, I. Russo, Friard O., & Marucco F. 2022. Il lupo in regione Piemonte 2020/2021. Relazione tecnica dell'attività di monitoraggio nazionale nell'ambito del Piano di Azione del lupo ai sensi della Convenzione ISPRA MITE e nell'ambito del Progetto LIFE 18 NAT/IT/000972 WOLFALPS EU.

Bailey, L., & Adams, M. J. 2005. Occupancy models to study wildlife, 2005-3096. US Geological Survey. DOI: 10.3133/fs20053096

Bailey, L. L., MacKenzie, D. I., & Nichols, J. D. 2014. Advances and applications of occupancy models. *Methods in Ecology and Evolution*, 5(12), 1269-1279. DOI: 10.1111/2041-210X.12100

Barbato, M., Hailer, F., Orozco-terWengel, P., Kijas, J., Mereu, P., Cabras, P., Mazza, R., Pirastru, M., & Bruford, M. W. 2017. Genomic signatures of adaptive introgression from European mouflon into domestic sheep. *Scientific Reports*, 7(1), 1-13. DOI:10.1038/s41598-017-07382-7

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M., Morellet, N. & Verheyden, H. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour*, 76, 611-618.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology letters*, 3(6), 620-623. DOI: 10.1098/rsbl.2007.0415

Berryman, A. A. 1992. The origins and evolution of predator-prey theory. *Ecology*, *73*(5), 1530-1535. DOI: 10.2307/1940005

Bisi, J., Liukkonen, T., Mykrä, S., Pohja-Mykrä, M., & Kurki, S. 2010. The good bad wolf—wolf evaluation reveals the roots of the Finnish wolf conflict. *European Journal of Wildlife Research*, 56, 771-779. DOI: 10.1007/s10344-010-0374-0

Boitani, L. 2018. Canis lupus (Europe assessment) (errata version published in 2019). *The IUCN Red List of Threatened Species* 2018: e.T3746A144226239. Accessed on 16 February 2023.

Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., & Hewison, A. M. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European journal of wildlife research*, 59, 185-193. DOI: 10.1007/s10344-012-0665-8

Bonnot, N. C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J. E., Gehr, B., Heurich, M., Kjellander, P., Kröschel, M., Morellet, N., Sönnischen, & Hewison, A. M. 2020. Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. *Journal of Animal Ecology*, 89(1), 132-145. DOI: 10.1111/1365-2656.13161

Borkowski, J., Banul, R., Jurkiewicz-Azab, J., Hołdyński, C., Święczkowska, J., Nasiadko, M., & Załuski, D. 2021. There is only one winner: The negative impact of red deer density on roe deer numbers and distribution in the Słowiński National Park and its vicinity. *Ecology and Evolution*, 11(11), 6889-6899. DOI: 10.1002/ece3.7538

Boyle, S. A., & Samson, F. B. 1985. Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin (1973-2006)*, 13(2), 110-116.

Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. *Biological conservation*, 83(3), 279-289. DOI: 10.1016/S0006-3207(97)00084-0

Bridges, A. S., Vaughan, M. R., & Klenzendorf, S. 2004. Seasonal variation in American black bear Ursus americanus activity patterns: quantification via remote photography. *Wildlife Biology*, 10(4), 277-284. DOI: 10.2981/wlb.2004.033

Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. 2005. Distance sampling. *Encyclopedia of biostatistics*, 2. DOI: 10.1002/0470011815.b2a16019

Burnham, K.P. & Anderson D.R. 2002. Model Selection and Multimodel Inference, Ed 2. Springer, New York

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52(3), 675-685. DOI: 10.1111/1365-2664.12432

Callaghan, C. J. 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the central Rocky Mountains, Canada. Dissertation. University of Guelph, Guelph, Ontario, Canada.

Canalis L., 2022. I mammiferi delle Alpi - come riconoscerli, dove e quando osservarli. Il Castello srl, Cornaredo, Milano.

Capitani, C., Bertelli, I., Varuzza, P., Scandura, M., & Apollonio, M. 2004. A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. *Mammalian biology*, *69*(1), 1-10. https://doi.org/10.1078/1616-5047-112

Caravaggi, A., Burton, A. C., Clark, D. A., Fisher, J. T., Grass, A., Green, S., Hobaiter, C., Hofmeester, T.M., Kalan, A.K., Rabaiotti, D., & Rivet, D. 2020. A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conservation Science and Practice*, 2(8), e239. DOI: 10.1111/csp2.239

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J. R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D.J.L., Tilson, R., & Shahruddin, W. W. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. In *Animal Conservation forum,* 4(1), 75-79, Cambridge University Press. DOI: 10.1017/S1367943001001081

Carnevali, L., Lovari, S., Monaco, A., & Mori, E. 2016. Nocturnal activity of a “diurnal” species, the northern chamois, in a predator-free Alpine area. *Behavioural processes*, 126, 101-107. DOI: 10.1016/j.beproc.2016.03.013

Carranza, J., de Trucios, S. J. H., Medina, R., Valencia, J., & Delgado, J. 1991. Space use by red deer in a Mediterranean ecosystem as determined by radio-tracking. *Applied Animal Behaviour Science*, 30(3-4), 363-371. DOI: 10.1016/0168-1591(91)90141-J

Cederlund, G. 1981. Daily and seasonal activity pattern of roe deer in a boreal habitat. Swedish Wildlife Research, 11, 315–347.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balciauskas, L., Balys, V., Bedo, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremi, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Maji, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Myslajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunovi, M., Persson, J., Potocnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Vána, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., & Boitani, L. 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. *Science,* 346, 1517–1519. DOI: 10.1126/science.1257553

Cimatti, M., Ranc, N., Benítez-López, A., Maiorano, L., Boitani, L., Cagnacci, F., Čengić, M., Ciucci, P., Huijbregts, M. A. J., Krofel, M., López-Bao, J. V., Selva, N., Andren, H., Bautista, C., Cirovic, D., Hemmingmoore, H., Reinhardt, I., Marenče, M., Mertzanis, Y., Pedrotti, L., Trbojević, I., Zetterberg, A., & Santini, L. 2021. Large carnivore expansion in Europe is associated with human population density and land cover changes. *Diversity and Distributions*, 27(4), 602-617. DOI: 10.1111/ddi.13219

Ciucci, P., Boitani, L., Pelliccioni, E. R., Rocco, M., & Guy, I. 1996. A comparison of scat-analysis methods to assess the diet of the wolf Canis lupus. *Wildlife biology*, 2(1), 37-48. DOI: 10.2981/wlb.1996.006

Ciucci, P., Boitani, L., Francisci, F., & Andreoli, G. 1997. Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology*, 243, 803–819. DOI: 10.1111/j.1469-7998.1997.tb01977.x

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PloS one*, *7*(11), e50611. DOI: 10.1371/journal.pone.0050611

Comprensorio Alpino CN5. Periodi di caccia. https://www.comprensorioalpinocn5.it. Accessed on 16/2/22.

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D., & Baguette, M. 2017. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography*, 40(1), 56-73. DOI: 10.1111/ecog.02538

Cove, M.V., Spínola, R.M., Jackson, V.L., Sáenz, J. C., & Chassot, O. 2013. Integrating occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor. *Tropical Conservation Science*, 6(6), 781-795. DOI:10.1177/194008291300600606

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.M., Hewison, A.J.M. 2008. Inferring the effects of landscape structure on roe deer (*Capreolus capreolus*) movements using a step selection function. Landscape Ecology, 23, 603–614. DOI: 10.1007/s10980-008-9220-0

Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. 2015. The unique ecology of human predators. *Science*, *349*(6250), 858-860. DOI: 10.1126/science.aac4249

Darmon, G., Calenge, C., Loiso, A., Jullien, J.M., Maillard D., & Lopez, J.F. 2012. Spatial distribution and habitat selection in coexisting species of mountain ungulates. *Ecography* 35:44–53. DOI: 10.1111/j.1600-0587.2011.06664.x

Delisle, Z. J., Flaherty, E. A., Nobbe, M. R., Wzientek, C. M., & Swihart, R. K. 2021. Next-generation camera trapping: systematic review of historic trends suggests keys to expanded research applications in ecology and conservation. *Frontiers in Ecology and Evolution*, 9, 617996. DOI: 10.3389/fevo.2021.617996

Devarajan, K., Morelli, T. L., & Tenan, S. 2020. Multi-species occupancy models: Review, roadmap, and recommendations. *Ecography*, 43(11), 1612-1624. DOI: 10.1111/ecog.04957

Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, 54(1), 253-263. DOI: 10.1111/1365-2664.12732

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B.,. Skidmore, A.K., Zurell, D., & Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27-46. DOI: 10.1111/j.1600-0587.2012.07348.x

Dorning, J., & Harris, S. 2019. The challenges of recognising individuals with few distinguishing features: Identifying red foxes *Vulpes vulpes* from camera-trap photos. *PloS one*, 14(5), e0216531. DOI: 10.1371/journal.pone.0216531

Doser, J. W., Finley, A. O., Kéry, M., & Zipkin, E. F. 2022. spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, 13(8), 1670-1678. DOI: 10.1111/2041-210X.13897

Dressel, S., Sandström, C., & Ericsson, G. 2015. A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. *Conservation Biology*, *29*(2), 565-574. DOI: 10.1111/cobi.12420

Dyck, M.A., Iosif, R., Promberger–Fürpass, B., & Popescu, V.D. 2022. Dracula's ménagerie: A multispecies occupancy analysis of lynx, wildcat, and wolf in the Romanian Carpathians. *Ecology and Evolution*, 12(5), e8921. DOI: 10.1002/ece3.8921

Efford, M.G., Borchers, D.L., Byrom, A.E. 2009. Density Estimation by Spatially Explicit Capture–Recapture: Likelihood-Based Methods. In: Thomson, D.L., Cooch, E.G., Conroy, M.J. (eds) Modeling Demographic Processes In Marked Populations. *Environmental and Ecological Statistics*, vol 3. Springer, Boston, MA. DOI: 10.1007/978-0-387-78151-8_11

Etter, D. R., Hollis, K. M., Van Deelen, T. R., Ludwig, D. R., Chelsvig, J. E., Anchor, C. L., & Warner, R. E. 2002. Survival and Movements of White-Tailed Deer in Suburban Chicago, Illinois. *The Journal of Wildlife Management*, 66(2), 500–510. DOI: 10.2307/3803183

Fabbri, E., Miquel, C., Lucchini, V., Santini, A., Caniglia, R., Duchamp, C., Weber, J.M., Lequette, B., Marucco, F., Boitani, L., Fumagalli, L., Taberlet, P., & Randi, E. 2007. From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (*Canis lupus*) population. *Molecular ecology*, 16(8), 1661-1671. DOI: 10.1111/j.1365-294X.2007.03262.x

Fabbri, E., Caniglia, R., Kusak, J., Galov, A., Gomerčić, T., Arbanasić, H., Huber, D., & Randi, E. 2014. Genetic structure of expanding wolf (*Canis lupus*) populations in Italy and Croatia, and the early steps of the recolonization of the Eastern Alps. *Mammalian Biology*, 79, 138-148. DOI: 10.1016/j.mambio.2013.10.002

Falcucci, A., Maiorano, L., Tempio, G., Boitani, L., & Ciucci, P. 2013. Modeling the potential distribution for a range-expanding species: Wolf recolonization of the Alpine range. *Biological conservation*, 158, 63-72. DOI: 10.1016/j.biocon.2012.08.029

Ferretti, F., Sforzi, A. & Lovari, S. 2011. Behavioural interference between ungulate species: roe are not on velvet with fallow deer. *Behavoral Ecology and Sociobiology*, 65, 875–887. DOI: 10.1007/s00265-010-1088-8

Ferretti, F., Lovari, S., Mancino, V., Burrini, L., & Rossa, M. 2019. Food habits of wolves and selection of wild ungulates in a prey-rich Mediterranean coastal area. *Mammalian Biology*, 99, 119–127. DOI: 10.1016/j.mambio.2019.10.008

Ferretti, F., & Mori, E. 2020. Displacement interference between wild ungulate species: does it occur?, *Ethology Ecology & Evolution*, 32:1, 2-15. DOI: 10.1080/03949370.2019.1680447

Ferretti, F., & Fattorini, N. 2021. Competitor densities, habitat, and weather: effects on interspecific interactions between wild deer species. *Integrative Zoology*, 16(5), 670-684. DOI: 10.1111/1749-4877.12470

Ferretti, F., Lazzeri, L., & Fattorini, N. 2023. A test of motion-sensitive cameras to index ungulate densities: group size matters. *Journal of Wildlife Management,* e22356. DOI: 10.1002/jwmg.22356

Fiske, I., & Chandler, R. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software*, 43(10), 1-23. URL DOI: 10.18637/jss.v043.i10

Freschi, P., Fascetti, S., Riga, F., Cosentino, C., Rizzardini, G., & Musto, M. 2017. Diet composition of the Italian roe deer (*Capreolus capreolus italicus*) (Mammalia: Cervidae) from two protected areas. *The European Zoological Journal*, 84(1), 34-42. DOI: 10.1080/11250003.2016.1268655

Frid, A., & Dill, L. 2002. Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, 6(1). http://www.jstor.org/stable/26271862

Fritts, S. H., & Mech, L. D. 1981. Dynamics, Movements, and Feeding Ecology of a Newly Protected Wolf Population in Northwestern Minnesota. *Wildlife Monographs*, 80, 3–79. http://www.jstor.org/stable/3830611

Fuller, T. K., & Keith, L. B. 1980. Wolf Population Dynamics and Prey Relationships in Northeastern Alberta. *The Journal of Wildlife Management*, 44(3), 583–602. DOI: 10.2307/3808006

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Central Minnesota. *Wildlife Monographs*, 105, 3–41. http://www.jstor.org/stable/3830614

Gaudiano, L., Pucciarelli, L., & Mori, E. 2021. Livestock grazing affects movements and activity pattern of Italian roe deer in Southern Italy. *European Journal of Wildlife Research*, 67(4), 66. DOI: 10.1007/s10344-021-01506-1

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. 2019. Landscapes of fear: spatial patterns of risk perception and response. *Trends in ecology & evolution*, 34(4), 355-368. DOI: 10.1016/j.tree.2019.01.004

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. 2018. The influence of human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232-1235. DOI: 10.1126/science.aar7121

Gazzola, A., Bertelli, I., Avanzinelli, E., Tolosano, A., Bertotto, P., & Apollonio, M. 2005. Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *Journal of Zoology*, 266(2), 205-213. DOI: 10.1017/S0952836905006801

Gazzola, A., Avanzinelli, E., Bertelli, I., Tolosano, A., Bertotto, P., Musso, R., & Apollonio, M. 2007. The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps. *Italian Journal of Zoology*, 74(3), 297-307. DOI: 10.1080/11250000701447074

Georgii B, & Schroder W. 1983. Home range and activity patterns of male red deer (Cervus elaphus L.) in the alps. *Oecologia*. 58(2):238-248. DOI: 10.1007/BF00399224

Gilbert, N. A., Pease, B. S., Anhalt-Depies, C. M., Clare, J. D., Stenglein, J. L., Townsend, P. A., Van Deelen, T.R., & Zuckerberg, B. 2021a. Integrating harvest and camera trap data in species distribution models. *Biological Conservation*, 258, 109147. DOI: 10.1016/j.biocon.2021.109147

Gilbert, N. A., Clare, J. D., Stenglein, J. L., & Zuckerberg, B. 2021b. Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology*, 35(1), 88-100. DOI: 10.1111/cobi.13517

Green, A. M., Chynoweth, M. W., & Şekercioğlu, Ç. H. 2020. Spatially explicit capture-recapture through camera trapping: a review of benchmark analyses for wildlife density estimation. *Frontiers in Ecology and Evolution*, 8, 563477. DOI: 10.3389/fevo.2020.563477

Greenberg, S., Godin, T., & Whittington, J. 2019. Design patterns for wildlife-related camera trap image analysis. *Ecology and Evolution*, 9(24), 13706-13730. DOI: 10.1002/ece3.5767

Guillera-Arroita, G., Ridout, M. S., & Morgan, B. J. 2010. Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, 1(2), 131-139. DOI: 10.1111/j.2041-210X.2010.00017.x

Hansson, L. 1994. Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. *Landscape Ecology*, 9, 105–115. DOI: 10.1007/BF00124377

Harris, G.M., Butler, M.J., Stewart, D.R., Rominger, E.M., & Ruhl, C.Q. 2020. Accurate population estimation of Caprinae using camera traps and distance sampling. *Scientific Reports*, 10, 17729. DOI: 10.1038/s41598-020-73893-5

Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., ... & Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, 86(8), 2135-2144. DOI: 10.1890/04-1269

Henderson, R., Mosher, B., Watters, R., Jal, T., & Murdoch, J. 2022. Human disturbance influences occupancy of red deer in Mongolia. *Mongolian Journal of Biological Sciences*, 20(2), 3-12. DOI:10.22353/mjbs.2022.20.10

Henrich, M., Niederlechner, S., Kröschel, M., Thoma, S., Dormann, C. F., Hartig, F., & Heurich, M. 2020. The influence of camera trap flash type on the behavioural reactions and trapping rates of red deer and roe deer. *Remote Sensing in Ecology and Conservation*, 6(3), 399-410. DOI: 10.1002/rse2.150

Henrich, M., F. Hartig, C. F. Dormann, H. S. Kühl, W. Peters, F. Franke, T. Peterka, P. Šustr, and M. Heurich. 2022. Deer behavior affects density estimates with camera traps, but is outweighed by spatial variability. *Frontiers in Ecology and Evolution*, 10, 881502. DOI: 10.3389/fevo.2022.881502

Hewison, A.J.M., Vincent, J.P., Joachim, J., Angibault, J.M., Cargnelutti, B., Cibien, C. 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. *Canadian Journal of Zoology*, 79(4), 679–689. DOI: 10.1139/z01-032

Howe, E. J., Buckland, S. T., Després-Einspenner, M. L., & Kühl, H. S. 2017. Distance sampling with camera traps. *Methods in Ecology and Evolution*, 8(11), 1558-1565. DOI: 10.1111/2041-210X.12790

ISPRA, 2013. Linee guida per la gestione degli ungulati. Cervidi e bovidi. *Manuali e Linee Guida*, 91/2013.

James, A.R.C., & Stuart-Smith, A.K. 2000. Distribution of Caribou and Wolves in Relation to Linear Corridors. *The Journal of Wildlife Management*, 64(1), 154–159. DOI: 10.2307/3802985

Jenkins, K.J., & Manly, B.F.J. 2008. A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. *Journal of Applied Ecology*, 45, 1339-1348. DOI: 10.1111/j.1365-2664.2008.01512.x

Jeppesen, J.L. 1989. Activity patterns of free-ranging roe deer (*Capreolus capreolus*) at Kalø. *Danish Review of Game Biology*, 13, 1–32.

Jong, C. B., Gill, R.M.A., Van Wieren, S.E., & Burlton, F.W.E. 1995. Diet selection by roe deer *Capreolus capreolus* in Kielder Forest in relation to plant cover. *Forest ecology and management*, 79(1-2), 91-97. DOI: 10.1016/0378-1127(95)03622-9

Kavčić, K., Palencia, P., Apollonio, M., Vicente, J., & Šprem, N. (2021). Random encounter model to estimate density of mountain-dwelling ungulate. *European Journal of Wildlife Research*, 67(5), 87. DOI: 10.1007/s10344-021-01530-1

Kitamura, S., Thong-Aree, S., Madsri, S., & Poonswad, P. 2010. Mammal diversity and conservation in a small isolated forest of southern Thailand. *Raffles Bulletin of Zoology*, 58(1).

Kitchen, A.M., Gese, E.M., & Schauster, E.R. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *Canadian Journal of Zool*ogy, 77, 1645-1656. DOI:10.1139/z99-143

Kneitel, J.M., & Chase J.M. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Lett*ers, 7, 69-80. DOI:10.1046/j.1461-0248.2003.00551.x

Kusak, J., Skrbinšek, A.M. & Huber, D. 2005. Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *European Journal of Wildlife Research*, 51, 254–262. DOI: 10.1007/s10344-005-0111-2

La Morgia V., Marucco F., Aragno P., Salvatori V., Gervasi V., De Angelis D., Fabbri E., Caniglia R., Velli E., Avanzinelli E., Boiani M.V., Genovesi P., 2022. Stima della distribuzione e consistenza del lupo a scala nazionale 2020/2021. Relazione tecnica realizzata nell’ambito della convenzione ISPRA-Ministero della Transizione Ecologica “Attività di monitoraggio nazionale nell’ambito del Piano di Azione del lupo”.

Lamberti, P., Mauri, L., & Apollonio, M. 2004 Two distinct patterns of spatial behaviour of female roe deer (*Capreolus capreolus*) in a mountainous habitat. *Ethology Ecology & Evolution*, 16:1, 41-53, DOI: 10.1080/08927014.2004.9522653

Laundré, J. W., Hernández, L., & Altendorf, K. B. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, 79(8), 1401-1409. DOI: 10.1139/z01-094

Laundré, J. W., Hernández, L., & Ripple, W. J. 2010. The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, 3(1). DOI: 10.2174/1874213001003030001

LIFE WolfAlps EU. 2020. Azioni coordinate per migliorare la coesistenza fra lupo e attività umane a livello di popolazione alpina. Valutazione dell’impatto del lupo sulle prede selvatiche. https://www.lifewolfalps.eu. Accessed on 16/2/22.

Loison, A., Gaillard, J-M., Pélabon, C., & Yoccoz, N.G. 1999. What factors shape sexual size dimorphism in ungulates. *Evolutionary Ecology Research,* 1, 611–633.

Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D., Odden, J., Remmen, J., & Mysterud, A. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos*, 123(6), 641-651. DOI: 10.1111/j.1600-0706.2013.00938.x

Lovari, S., & San José, C. 1997. Wood dispersion affects home range size of female roe deer. *Behavioral Processes*, 40, 239–241.

Lovari, S., Serrao, G., & Mori, E. 2017. Woodland features determining home range size of roe deer. *Behavioural processes*, 140, 115-120. DOI: 10.1016/j.beproc.2017.04.012

Lowry, H., Lill, A., & Wong, B. B. 2013. Behavioural responses of wildlife to urban environments. *Biological reviews*, 88(3), 537-549. DOI: 10.1111/brv.12012

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., & C. A. Langtimm. 2002. Estimating site occupancy rates when detection prob- abilities are less than one. *Ecology*, 83, 2248-2255. DOI: 10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., & Franklin, A.B. 2003. Estimating site occupancy, colonization and local extinction probabilities when a species is detected imperfectly. *Ecology,* 84, 2200-2207. DOI: 10.1890/02-3090

MacKenzie, D.I., Bailey, L.L., & Nichols, J.D. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, 73, 546-555. DOI: 10.1111/j.0021-8790.2004.00828.x

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., & Hines, J.E. 2017. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, 146.

Marion, S., Demšar, U., Davies, A. L., Stephens, P. A., Irvine, R. J., & Long, J. A. 2022. Red deer behavioural response to hiking activity: A study using camera traps. *Journal of Zoology*, 317(4), 249-261. DOI: 10.1111/jzo.12976

Marucco, F., Avanzinelli E., & Gazzola, A. 2005. Il lupo in Piemonte: azioni per la conoscenza e la conservazione della specie, per la prevenzione dei danni al bestiame domestico e per l'attuazione di un regime di coesistenza stabile tra lupo ed attività economiche - Stato, distribuzione, e dieta della popolazione di lupo in regione Piemonte. Report 2005 - Progetto Lupo Regione Piemonte, Torino.

Marucco, F., Pletscher, D. H., & Boitani, L. 2008. Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. *Journal of Mammalogy*, 89(3), 665-673. DOI: 10.1644/07-MAMM-A-005R3.1

Marucco F., Avanzinelli, E., Boiani, M.V., Menzano, A., Perrone, S., Dupont, P., Bischof,R., Milleret, C., von Hardenberg, A., Pilgrim, K., Friard, O., Bisi, F., Bombieri, G., Calderola, S., Carolfi, S., Chioso, C., Fattori, U., Ferrari, P., Pedrotti, L., Righetti, D., Tomasella, M., Truc, F., Aragno, P., La Morgia, V., & Genovesi, P. 2022. La popolazione di lupo nelle regioni alpine Italiane 2020-2021. Relazione tecnica dell'Attività di monitoraggio nazionale nell'ambito del Piano di Azione del lupo ai sensi della Convenzione ISPRA- MITE e nell'ambito del Progetto LIFE 18 NAT/IT/000972 WOLFALPS EU.

Marucco, F., Pilgrim, K. L., Avanzinelli, E., Schwartz, M. K., & Rossi, L. 2022. Wolf dispersal patterns in the Italian Alps and implications for wildlife diseases spreading. *Animals*, 12(10), 1260. DOI: 10.3390/ani12101260

Mattioli, L., Capitani, C., Avanzinelli, E., Bertelli, I., Gazzola, A., & Apollonio, M. 2004. Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. *Journal of Zoology*, 264(3), 249-258. DOI:10.1017/S095283690400576X

McCallum, J. 2013. Changing use of camera traps in mammalian field research: habitats, taxa and study types. *Mammal Review*, 43(3), 196-206. DOI: 10.1111/j.1365-2907.2012.00216.x

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G., Jackson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., & Xu, C. 2020. Pervasive shifts in forest dynamics in a changing world. *Science*, 368(6494), eaaz9463. DOI: 10.1126/science.aaz9463

Martin, J., Vourc'h, G., Bonnot, N., Cargnelutti, B., Chaval, Y., Lourtet, B., Goulard, M., Hoch, T., Plantard, O., Hewison, A.J.M, & Morellet, N. 2018. Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape. *Landscape Ecology*, 33, 937–954. DOI: 10.1007/s10980-018-0641-0

Mech, L.D., Leadership in Wolf, *Canis lupus*, Packs. 2000. USGS Northern Prairie Wildlife Research Center. 384. http://digitalcommons.unl.edu/usgsnpwrc/384

Mech, L.D., & Boitani, L. 2003. Wolf Social Ecology. *USGS Northern Prairie Wildlife Research Center*. 318, 2-34. https://digitalcommons.unl.edu/usgsnpwrc/318

Meek, P.D., Ballard, G. & Fleming, P. 2012. An Introduction to Camera Trapping for Wildlife Surveys in Australia. PestSmart Toolkit publication. *Invasive Animals Cooperative Research Centre*, Canberra, Australia.

Meek, P.D., Ballard, G., Claridge, A., R. Kays, Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D.E., Tobler, M., & Townsend, S. 2014. Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation,* 23, 2321–2343. DOI: 10.1007/s10531-014-0712-8

Meriggi, A., Rosa, P., Brangi, A., & Matteucci, C. 1991. Habitat use and diet of the wolf in northern Italy. *Acta theriologica*, 36(1-2), 141-151.

Meriggi, A., & Lovari, S.1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? Journal of Applied Ecology, 33, 1561–1571. DOI: 10.2307/2404794

Moeller, A. K., Waller, S. J., DeCesare, N. J., Chitwood, M. C., & Lukacs, P. M. 2022. Best practices to account for capture probability and viewable area in camera-based abundance estimation. *Remote Sensing in Ecology and Conservation*, 9(1), 152-164. DOI: 10.1002/rse2.300

Montgomery, R. A., Macdonald, D. W., & Hayward, M. W. 2020. The inducible defences of large mammals to human lethality. *Functional Ecology*, 34(12), 2426-2441. DOI: 10.1111/1365-2435.13685

Morellet, N., Van Moorter, B., Cargnelutti, B. Angibault, J.M, Lourtet, B., Merlet, J., Ladet, S., & Hewison, A.J.M. 2011. Landscape composition influences roe deer habitat selection at both home range and landscape scales. Landscape Ecololgy 26, 999–1010. DOI: 10.1007/s10980-011-9624-0

Mori, E., Benatti, L., Lovari, S., & Ferretti, F. 2017. What does the wild boar mean to the wolf?. *European Journal of Wildlife Research*, 63, 9. DOI: 10.1007/s10344-016-1060-7

Mori, E., Cicero, M., Lovari, Zaccaroni, M., Salomoni, S., Vendramin, A., & Augugliaro, C. 2021. Occupancy and activity rhythms of the Siberian roe deer. *Biologia* 76, 2991–2999. DOI: 10.1007/s11756-021-00790-1

Musiani, M., Okarma, H., & Jędrzejewski, W. 1998. Speed and actual distances travelled by radiocollared wolves in Białowieża Primeval Forest (Poland). *Acta Theriologica,* 43(4), 409-416.

Mysterud, A., Bjornsen, B.H., & Ostbye, E. 1997. Effects of snow depth on food and habitat selection by roe deer Capreolus capreolus along an altitudinal gradient in south-central Norway. Wildlife Biology, 3, 27–33.

Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K., Toxopeus, A.G. 2014. Where is positional uncertainty a problem for species distribution modelling. *Ecography*, 37, 191-203. DOI:10.1111/j.1600-0587.2013.00205.x

Newsome, T. M., & Van Eeden, L. M. 2017. The effects of food waste on wildlife and humans. *Sustainability*, 9(7), 1269. DOI: 10.3390/su9071269

Niedballa, J., Sollmann, R., Mohamed, A., Bender, J., & Wilting, A. 2015. Defining habitat covariates in camera-trap based occupancy studies. *Scientific Reports*, 5, 17041. DOI: 10.1038/srep17041

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. 2016. camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7(12), 1457-1462. DOI: 10.1111/2041-210X.12600

Niedballa, J. 2017. *Managing and Analysing Camera Trapping Data: An Advanced Toolbox* (Doctoral dissertation).

Nipko, R.B., Holcombe, B.E., & Kelly, M.J. 2020. Identifying individual jaguars and ocelots via pattern-recognition software: comparing HotSpotter and Wild-ID. *Wildlife Society Bulletin*, 44(2), 424-433. DOI: 10.1002/wsb.1086

Oberosler, V., Groff, C., Iemma, A., Pedrini, P., & Rovero, F. 2017. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mammalian Biology*, 87, 50-61. DOI: 10.1016/j.mambio.2017.05.005

O'Brien, T. G., Baillie, J. E. M., Krueger, L., & Cuke, M. 2010. The Wildlife Picture Index: monitoring top trophic levels. *Animal Conservation*, 13(4), 335-343. DOI: 10.1111/j.1469-1795.2010.00357.x

O'Brien, T., Kinnaird, M., & Wibisono, H. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation Forum*, 6(2), 131-139. DOI:10.1017/S1367943003003172

Pagon, N., Grignolio, S., Pipia, A., Bongi, P., Bertolucci, C., & Apollonio, M. 2013. Seasonal variation of activity patterns in roe deer in a temperate forested area. *Chronobiology International*, 30(6), 772-785. DOI: 10.3109/07420528.2013.765887

Palencia, P., Vicente, J., Barroso, P., Barasona, J. Á., Soriguer, R. C., & Acevedo, P. 2019. Estimating day range from camera-trap data: the animals' behaviour as a key parameter. *Journal of Zoology*, 309(3), 182-190. DOI: 10.1111/jzo.12710

Palmegiani, I., Gazzola, A., & Apollonio, M. 2013. Wolf diet and its impact on the ungulates community in a new recolonized area of Western Alps: Gran Paradiso National Park. *Folia Zoologica*, 62(1), 59-66. DOI: 10.25225/fozo.v62.i1.a9.2013

Palmer, M.S., Gaynor, K.M., Becker, J.A., Abraham, J.O., Mumma, M.A., & Pringle, R.M. 2022. Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends in Ecology & Evolution*, 37(10), 911-925. DOI: 10.1016/j.tree.2022.06.007

Parco Naturale Marguareis. https://www.parcomarguareis.it. Accessed on 16/2/22.

Pellerin, M., Calenge, C., Saïd, S., Gaillard, J.M., Fritz, H., Duncan, P., & Van Laere, G. 2010. Habitat use by female western roe deer (Capreolus capreolus): influence of resource availability on habitat selection in two contrasting years. *Canadian Journal of Zoology*. 88(11): 1052-1062. DOI: 10.1139/Z10-070

Perco, F. 2011. Fauna selvatica, biologia e gestione. Il capriolo. Edizioni Il Piviere, Gavi, Piemonte.

Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. *United States National Park Service Scientific Monograph Series*, 11 :1- 210.

Peterson, R.O., Woolington, J.D., & Bailey, T.N. 1984. Wolves of the Kenay peninsula, Alaska. *Wildlife Monograph,* 88, 1-52.

Petridou, M., Benson, J. F., Gimenez, O., & Kati, V. 2023. Spatiotemporal Patterns of Wolves, and Sympatric Predators and Prey Relative to Human Disturbance in Northwestern Greece. *Diversity*, 15(2), 184. MDPI AG. DOI: 10.3390/d15020184

Polis, G.A., & Strong, D.R. 1996. Food web complexity and community dynamics. *American Naturalist* 147, 813–846. DOI: 10.1086/285880

Porter, W. F., Underwood, H.B., & Woodard, J.L. 2004. Movement behavior, dispersal, and the potential for localized management of deer in a suburban environment. *Journal of Wildlife Management*, 68,247-256. DOI: 10.2193/0022541X(2004)068[0247:MBDATP]2.0.CO;2

QGIS.org. 2020. QGIS Geographic Information System. QGIS Association. URL http://www.qgis.org/.

Randi, E. 2005. Management of Wild Ungulate Populations in Italy: Captive-Breeding, Hybridisation and Genetic Consequences of Translocations. Veterinary Research Communications, 29(2), 71–75. DOI: /10.1007/s11259-005-0025-1

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ražen, N., Brugnoli, A., Castagna, C., Groff, C., Kaczensky, P., Kljun, F., Knauer, F., Kos, I., Krofel, M., Luštrik, R., Majić, A., Rauer, G., Righetti, D., & Potočnik, H. 2016. Long-distance dispersal connects Dinaric-Balkan and Alpine grey wolf (*Canis lupus*) populations. *European journal of wildlife research*, 62, 137-142. DOI: 10.1007/s10344-015-0971-z

Regine, D. 2008 Ecologia alimentare del lupo in sistemi multi-preda: tre anni di studio sulle Alpi Occidentali. Tesi di laurea. Università degli Studi di Roma “La Sapienza”.

Regione Piemonte. 2008. Modello digitale del terreno da CTRN 1:10000 (passo 10 m) - STORICO. www.geoportale.piemonte.it

Regione Piemonte. 2021. Land Cover Piemonte. www.geoportale.piemonte.it

Reimoser, S. 2012. Influence of anthropogenic disturbances on activity, behavior and heart rate of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), in context of their daily and yearly patterns. In: *AA Cahler, JP Marsten. Deer: Habitat, Behavior and Conservation*, New York, USA: Nova Science Publishers Inc, 1, 1-87.

Richard, E., Gaillard, JM., Saïd, S., Hamann, J.L., Klein, F. 2010. High red deer density depresses body mass of roe deer fawns. *Oecologia* 163, 91–97. DOI: 10.1007/s00442-009-1538-z

Richmond, O. M., Hines, J. E., & Beissinger, S. R. 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, 20(7), 2036-2046. DOI: 10.2307/25741366

Riley, S.J., DeGloria, S.D., & Elliot, R. 1999. Index that quantifies topographic heterogeneity. *Intermountain Journal of sciences*, 5(1-4), 23-27.

Rizzuto, M. 2012. Interazioni preda-predatore: ecologia alimentare del Lupo (C. lupus) e comportamento anti-predatorio del Camoscio (R. Rupicapra) nelle Alpi Marittime. Università di Torino.

Rød-Eriksen, L., Killengreen, S. T., Ehrich, D., Ims, R. A., Herfindal, I., Landa, A. M., & Eide, N. E. 2022. Predator co-occurrence in alpine and Arctic tundra in relation to fluctuating prey. *Journal of Animal Ecology*. DOI: 10.1111/1365-2656.13875

Rota, C.T., Ferreira, M.A., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W., & Millspaugh, J.J. 2016. A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7(10), 1164-1173. DOI: 10.1111/2041-210X.12587

Rovero, F., & De Luca, D.W. 2007. Checklist of mammals of the Udzungwa Mountains of Tanzania. *Mammalia*, 71(1-2), 47-55. DOI: 10.1515/MAMM.2007.015

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. 2013. "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, the Italian Journal of Mammalogy, 24(2), 148-156. DOI: 10.4404/hystrix-24.2-8789

Ruprecht, J. S., Eriksson, C. E., Forrester, T. D., Clark, D. A., Wisdom, M. J., Rowland, M. M., Johnson, B.K., & Levi, T. 2021. Evaluating and integrating spatial capture–recapture models with data of variable individual identifiability. *Ecological Applications*, 31(7), e02405. DOI: 10.1002/eap.2405

Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 1228-1236. DOI: 1/j.l365-2664.2008.01473.x

Rowcliffe J.M., Kays R., Carbone C. & Jansen P.A. 2013. Clarifying assumptions behind the estimation of animal density from camera trap rates. *The Journal of Wildlife Manage*ment, 77, 876. DOI: 10.1002/jwmg.533

Royle, J. A., Karanth, K. U., Gopalaswamy, A. M., & Kumar, N. S. 2009. Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. *Ecology*, 90(11), 3233-3244. DOI: 10.1890/08-1481.1

Santiago-Ávila, F.J., & Treves, A. 2022. Poaching of protected wolves fluctuated seasonally and with non-wolf hunting. *Scientific Reports*, 12, 1738. DOI: 10.1038/s41598-022-05679-w

Schmitz, O. J., A. P. Beckerman, & K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78, 1388–1399. DOI: 10.1890/0012-9658(1997)078[1388:BMTCEO]2.0.CO;2

Smietana, W., & Klimek, A. 1993. Diet of wolves in the Bieszczady Mountains, Poland. *Acta theriologica*, *38*(3), 245-251.

Sönnichsen, L., Bokje, M., Marchal, J., Hofer, H., Jędrzejewska, B., Kramer-Schadt, S., & Ortmann, S. 2013. Behavioural Responses of E uropean Roe Deer to Temporal Variation in Predation Risk. *Ethology*, 119(3), 233-243. DOI: 10.1111/eth.12057

Steen, D.A., McClure, C.J.W., Brock, J.C., Craig Rudolph, D., Pierce, J.B., Lee, J.R., Humphries, J.W., Gregory, B.B., Sutton, W.B., Smith, L.L., Baxley, D.L., Stevenson, D.J., & Guyer, C. 2014. Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. *Journal of Animal Ecology*, 83, 286–295. DOI: 10.1111/1365-2656.12121

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology letters*, 22(10), 1578-1586. DOI: 10.1111/ele.13344

Theuerkauf, J., Jedrzejewski, W., Schmidt, K., & Gula, R. 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). *Journal of Wildlife Management* 67 (4), DOI: 706– 716. 10.2307/3802677

Thurber, J. M., Peterson, R. O., Drummer, T. D., & Thomasma, S. A. 1994. Gray Wolf Response to Refuge Boundaries and Roads in Alaska. *Wildlife Society Bulletin* (1973-2006). 22(1), 61–68. http://www.jstor.org/stable/3783224

Thurman, L.L., Barner, A.K., Garcia, T.S., & Chestnut, T. 2019. Testing the link between species interactions and species co-occurrence in a trophic network. *Ecography*, 42(10), 1658-1670. DOI: 10.1111/ecog.04360

Tilman, D. 1982. *Resource competition and community structure*. 17, Princeton university press, 296.

Tobler, M. W., Zúñiga Hartley, A., Carrillo-Percastegui, S. E., & Powell, G. V. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology*, 52(2), 413-421. DOI: 10.1111/1365-2664.12399

Torres, R. T., Virgós, E., Santos, J., Linnell, J. D., & Fonseca, C. 2012. Habitat use by sympatric red and roe deer in a Mediterranean ecosystem, *Animal Biology*, 62(3), 351-366. DOI: 10.1163/157075612X631213

Torretta, E., Serafini, M., Imbert, C., Milanesi, P., & Meriggi, A. 2017. Wolves and wild ungulates in the Ligurian Alps (Western Italy): prey selection and spatial-temporal interactions. *Mammalia*, 81(6), 537-551. DOI: 10.1515/mammalia-2016-0066

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A.H., Allen, A.M., Attias, N., ... & Mueller, T. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359(6374), 466-469. DOI: 10.1126/science.aam9712

Van Scoyoc, A., Smith, J. A., Gaynor, K. M., Barker, K., & Brashares, J. S. 2023. The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology*, 00, 1-11. DOI: 10.1111/1365-2656.13892

Wabakken, P., Sand, H., Kojola, I., Zimmermann, B., Arnemo, J. M., Pedersen, H. C., & Liberg, O. 2007. Multistage, long-range natal dispersal by a global positioning system-collared Scandinavian wolf. *The Journal of Wildlife Management*, 71(5), 1631-1634. DOI: 10.2193/2006-222

Wearn, O. R., & Glover-Kapfer, P. 2019. Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *Royal Society open science*, 6(3), 181748. DOI: 10.1098/rsos.181748

Wevers, J., Beenaerts, N., Casaer, J., Zimmermann, F., Artois, T., & Fattebert, J. 2021. Modelling species distribution from camera trap by-catch using a scale-optimized occupancy approach. *Remote Sensing in Ecology and Conservation*, 7(3), 534-549. DOI: 10.1002/rse2.207

Whittington, J., St. Clair, C. C., & Mercer, G. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological applications*, 15(2), 543-553. DOI: 10.1890/03-5317

Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P., & Schmitz, O. J. 2021. The context dependence of non-consumptive predator effects. *Ecology Letters*, 24(1), 113-129. DOI: 10.1111/ele.13614

Zipkin, E. F., Royle, J. A., Dawson, D. K., & Bates, S. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, 143(2), 479-484. DOI: 10.1016/j.biocon.2009.11.016