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Mammal communities is the Anthropocene: systematic camera-trapping to study wildlife responses to anthropogenic pressures

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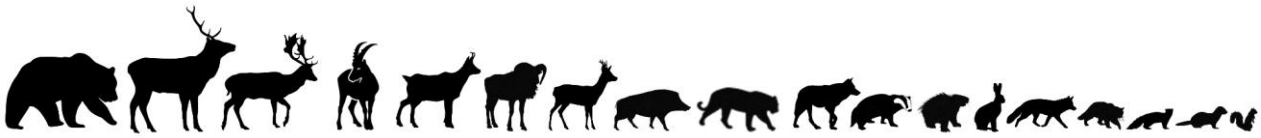

Ph.D. Thesis

Marco Salvatori

“Tutti gli esseri viventi sono fenomeni diversi di un'unica sostanza universale;
traggono dalla stessa radice metafisica, e la loro differenza è quantitativa, non qualitativa.”

“All living beings are different phenomena of one universal substance;
they derive from the same metaphysical root, and their difference is quantitative, not qualitative.”

Giordano Bruno

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Abstract

The current epoch is unique in the history of planet Earth, for one single species, *Homo sapiens*, is changing profoundly and rapidly the habitats of all other living beings. In the Anthropocene, the impoverishment of the biosphere with loss of individuals and populations of non-human animals is not sparing wild mammals, whose biomass has decreased 85% compared to pre-human times. Mammals are crucial species within ecosystems, providing numerous ecological functions like vegetation structure modification, predation and prey regulation, trophic cascades, seed dispersal and the facilitation of tree establishment, scavenging and carcass removal, increase in soil complexity through burrowing, spatial niche creation, and nutrient cycling. Yet, about one quarter of the 6,500 species of mammals are currently under threat of extinction. Habitat destruction is recognized as the major driver of mammalian decline worldwide, with infrastructure networks then fragmenting and isolating the remaining habitats. Overharvesting, poaching, and wildlife trading are other important impacts on mammalian communities, especially in the southern hemisphere. Beyond these well-known impacts, new emergent threats to wildlife communities are recently rising: particular concern is roused by competition with domesticated animals and human disturbance from outdoor recreational activities, both of which are among the most reported threats in protected areas (PAs) of the northern hemisphere. These two emerging threats on mammalian communities are the two main topics of this thesis, addressed respectively in part 1 and 2. In both cases I tested ecological hypotheses by utilising systematic camera-trapping as sampling technique, a non-invasive method that allows the collection of large amounts of data on multiple species over large areas at relatively low cost. I coupled this technique with a range of analytical approaches, primarily hierarchical modelling, that allowed me to estimate important community metrics, such as spatial co-occurrence between species and multi-year trends in occurrence while accounting for the pervasive issue of imperfect detection. Furthermore, through generalised linear models I assessed the behavioural responses of species and communities to anthropogenic pressures.

In Part1, chapter 1 and 2, I explored the spatio-temporal relationships between wild and domesticated mammals in four Central Asian grasslands located in the Altai mountains of western Mongolia, reconstructing potential interspecific interactions under livestock encroachment into PAs. Demand for animal products is growing globally, and also in Central Asia livestock numbers have strongly increased after the fall of the Soviet Union and the

globalisation of the Cashmere wool market. Domestic herbivores have consequently become several orders of magnitude more abundant than wild ones, with indirect repercussions also on carnivores. I used two different analytical approaches to uncover the network of potential relationships that bind mammals of these communities, explicitly including the widespread presence of livestock. In part 2, chapter 3 and 4, I assessed the behavioural responses of mammalian communities in Italian mountainous PAs to the increasing trend of outdoor recreation in natural habitats. As typical in recent European environmental history, Italy has seen a natural re-expansion of forests following socio-economic changes, that coupled with legal protection and lowered persecution has allowed the re-establishment of previously rare or locally extinct medium and large mammals. Yet, the increasingly urbanised population is engaging in sports and recreational activities within natural areas, with potential disturbance on the wildlife inhabiting them, underscoring the need of monitoring the responses of animals to this human frequentation. In particular, in chapter 3 I took advantage of a long-term dataset collected with my contribution in and around an Alpine PA of western Trentino, north-eastern Italy, to estimate temporal trends in occurrence of 8 mammalian species and their spatio-temporal use of habitat under intense outdoor recreation and tourist activity. I then broadened the spatial scale of analysis in chapter 4 by targeting four PAs of the European Natura 2000 Network, and studied responses of wildlife site use to human presence in three different temporal slots, diurnal, crepuscular and nocturnal, for four mammalian communities with different species compositions.

Riassunto

L'epoca in cui viviamo è unica nella storia del pianeta Terra, poiché una sola specie, l'*Homo sapiens*, sta cambiando profondamente e rapidamente gli habitat di tutti gli altri esseri viventi. Nell'Antropocene, l'impoverimento della biosfera con la perdita di individui e popolazioni di animali non umani non risparmia i mammiferi selvatici, la cui biomassa è diminuita dell'85% rispetto all'epoca preumana. I mammiferi sono specie cruciali all'interno degli ecosistemi, dato che svolgono numerose funzioni ecologiche come la modifica della struttura della vegetazione, la predazione e la regolazione dell'abbondanza delle prede, le cascate trofiche, la dispersione dei semi e la facilitazione dell'insediamento degli alberi, la rimozione delle carcasse, l'aumento della complessità del suolo attraverso l'attività di scavo, la creazione di nicchie spaziali e il ciclo dei nutrienti. Tuttavia, circa un quarto delle 6.500 specie di mammiferi è attualmente a rischio di estinzione. La distruzione dell'habitat è riconosciuta come il principale fattore di declino dei mammiferi in tutto il mondo, con l'espansione urbana come primario cambiamento di uso del suolo a livello globale e la deforestazione che è concentrata soprattutto nelle aree tropicali. Una

rete di infrastrutture sempre più fitta poi frammenta e isola gli habitat rimanenti, impedendo il movimento degli animali e il flusso genico. La caccia eccessiva, il bracconaggio e il commercio di animali selvatici sono altri impatti importanti sulle comunità di mammiferi, soprattutto nell'emisfero meridionale. Oltre a ciò, di recente stanno emergendo nuove minacce per le comunità di animali selvatici all'interno delle aree naturali e protette: particolare preoccupazione suscitano la competizione con gli animali domestici e il disturbo umano derivante dalle attività ricreative all'aperto, entrambe tra le minacce più segnalate nelle aree protette (AP) dell'emisfero settentrionale. Queste due pressioni emergenti sulle comunità di mammiferi sono i due argomenti principali di questa tesi, che affronto rispettivamente nella parte 1 e 2. In entrambi i casi ho testato le mie ipotesi ecologiche attraverso la tecnica del foto-trappolaggio sistematico, un metodo non invasivo che permette di raccogliere una grande quantità di dati su più specie in aree estese e a costi relativamente bassi.

Nella Parte 1, capitoli 1 e 2, ho esplorato le relazioni spazio-temporali tra mammiferi selvatici e domestici in quattro praterie dell'Asia centrale situate nei monti Altai della Mongolia occidentale, ricostruendo le potenziali interazioni interspecifiche in un contesto di sistematica intrusione del bestiame nelle AP. Il consumo di prodotti di origine animale è in crescita a livello globale, ed anche in Asia centrale il numero di capi di bestiame è fortemente aumentato a seguito della caduta dell'Unione Sovietica e la globalizzazione del mercato della lana di cashmere. Di conseguenza, gli erbivori domestici sono diventati di diversi ordini di grandezza più abbondanti di quelli selvatici, con ricadute indirette anche sui carnivori. Ho utilizzato due diversi approcci analitici per ricostruire la complessa rete di potenziali relazioni che collegano i mammiferi di queste comunità, includendo esplicitamente la presenza diffusa del bestiame. Nella seconda parte, capitoli 3 e 4, ho valutato le risposte comportamentali delle comunità di mammiferi nelle AP montane italiane all'aumento delle attività ricreative negli habitat naturali. Seguendo una dinamica tipica della recente storia ambientale europea, l'Italia ha assistito a una naturale ri-espansione delle foreste in seguito a cambiamenti socioeconomici, che, unitamente alla protezione legale e alla diminuzione della persecuzione, ha permesso il ristabilimento di mammiferi precedentemente rari o estinti. Tuttavia, la popolazione sempre più urbanizzata è alla ricerca di opportunità per praticare attività sportive e ricreative all'interno delle aree naturali, con un potenziale disturbo per la fauna selvatica che le abita. Per questi motivi è particolarmente importante studiare e monitorare nel tempo le risposte dei mammiferi a questa crescente frequentazione umana dei loro habitat. In particolare, nel capitolo 3 ho sfruttato una serie di dati a lungo termine che ho contribuito a raccogliere in un'area alpina del

Trentino occidentale, nel nord-est dell'Italia, per stimare le tendenze temporali di presenza di 8 specie di mammiferi e il loro uso spazio-temporale dell'habitat in condizioni di intensa attività ricreativa e turistica. Nel capitolo 4 ho poi ampliato la scala spaziale dell'analisi, includendo altre tre AP della Rete Natura 2000 europea, e ho studiato le risposte nell'uso dei siti da parte della fauna selvatica alla presenza umana in tre diverse fasce temporali, diurna, crepuscolare e notturna, per quattro comunità di mammiferi con diverse composizioni di specie.

General introduction

Millions of years of biological evolution have generated, with Charles Darwin words, 'endless forms most beautiful and wonderful', shaping an impressively complex and rich tree of life. Current estimates point to more than eight million of species existing on the planet (Mora et al., 2011), yet this striking diversity is currently risking to disappear or to soon become only a pale image of its original luxuriance, under the increasing anthropization of the Earth (Venter et al., 2016). The unrelenting modification of the Earth's biological and geochemical systems by an increasingly numerous humanity has required to propose a new geological epoch, the Anthropocene. Despite some disagreement on when Anthropocene should start, with a range of historic events proposed as possible beginning of the human-dominated epoch, such as Pleistocene megafauna extinctions, Neolithic agricultural revolution, XIX century industrial revolution, atomic weaponry development in the mid XX century, the scientific community agrees on the uniqueness of such age (Steffen et al., 2015). Biodiversity in the Anthropocene is undergoing great turmoil: not only species are going extinct at a rate up to 100 times higher than normal extinction rates (Ceballos et al., 2015), but populations, including those of non-threatened species, are plummeting, with a 70% decline estimated since 1970 (Living Planet Index, 2022). Among taxonomic groups, mammals have already experienced anthropogenic mass extinction events when *Homo sapiens* hunter-gatherers wiped away half of mammalian megafauna species during Late Pleistocene (Bartlett et al., 2015; Barnosky et al., 2008) and again later when humans shifted from hunting and gatherings to farming (Braje et al., 2013). Currently, under the ongoing technological revolution, the biomass of humanity has expanded dramatically, concomitantly decreasing that of wild mammals: humans now make up 36 % of total mammalian biomass, while wild species account for only the 4% (the rest being constituted by domestic mammals), resulting from an estimated 85% biomass decline since pre-human times (Barnosky et al., 2008; Smil, 2011; Bar-On et al., 2018).

Nonetheless, the importance of wild mammals for ecological processes and ecosystem services to humanity is widely recognised (Lacher et al., 2019; Sinclair, 2003). The largest terrestrial animals of present time are found among mammalian herbivores, omnivores, and carnivores, that often, due to high energetic and spatial demands, constitute primary forces in the energy fluxes of ecosystems, strongly influencing vegetation structure and composition, predation dynamics, seed dispersal and nutrient cycling, widely affecting biological

communities also indirectly through cascading effects (Lacher et al., 2019). Large grazers maintain and create shrubland and grassland habitats by slowing or halting the vegetation succession towards closed forests, increasing landscape heterogeneity, and providing habitats for grass or shrub dependent birds and reptiles (Pringle et al., 2008). In temperate forests browser ungulates affect the understory density and species richness, successively influencing birds, lepidopterans, and spiders (Ramirez et al., 2018). The density and spatio-temporal habitat use of herbivores is impacted by the presence of mammalian apex predators, which therefore indirectly influences vegetation dynamics. Parallelly, large carnivores can either negatively affect mesocarnivores, indirectly favouring smaller prey targeted by these species (Ripple et al., 2014) or facilitate them through increased opportunities for scavenging (Ferretti et al., 2021). Meso-carnivores regulate populations of small mammals and compete with similar sized species in complex ways, with larger species usually dominating smaller competitors within the meso-carnivorous guild, and have been reported to even modify vegetation communities and nutrient cycling and acting as apex predators in numerous ecosystems of the world where large carnivores have been extirpated (Roemer et al., 2009). Many large and especially medium sized mammalian carnivores are facultative scavengers that opportunistically feed on carrion, carrying out a crucial ecological function, particularly so where obligatory scavengers as vultures have gone locally extinct (Molèon et al., 2014; Cirovic et al., 2016; Inagaki et al., 2022). Within forest ecosystems, seed-caching small mammals store seeds below the ground, thereby dispersing tree propagules and enhancing plant establishment, guaranteeing up to 95% of total germination for some tree species (Vander Wall, 2008). Specialised granivorous rodents are not the only mammals involved in zoochory, since also many species of medium sized carnivores, with broad and generalist diets, disperse seeds, usually at longer distances than rodents and granivorous birds, after fruit ingestion (Jordano et al., 2007; Nakashima et al., 2022). Many mammalian species are ecosystem engineers that construct complex underground denning systems and burrows, which modify soil properties increasing habitat heterogeneity (Yoshihara et al., 2009; Kurek et al., 2014; Clark et al., 2016; Beca et al., 2022) and providing refuge and denning possibilities for a wide range of other species (Mori et al., 2015). Both short and long-distance migrations are a common adaptations of large mammalian herbivores to seasonal changes in resource availability and have been shown to be a crucial force of nutrient movements and cycling, enriching nutrient-poor systems with elements collected at nutrient-rich ones by traversing different habitats (Wolf et al., 2013; Kauffman et al., 2021).

Though mammalian communities provide these and other ecological functions and ecosystem services to humanity, and the scientific evidence on the subject is vast, a quarter of terrestrial mammal species, and a larger fraction of their populations, is threatened of extinction (Schipper et al., 2008; Hoffman et al., 2011). The relentless decline of mammals is hampering many vital ecological and socio-economic services that these species provide, transforming and impoverishing ecosystems (Ripple et al., 2016). Moreover, this continuous loss of mammalian diversity worldwide is not only worrying on a utilitarian basis, given that human societies and economies ultimately depend on ecosystem functions, but also on an ethical basis. Ethical considerations indeed cover a fundamental role in a mission-driven discipline like conservation biology (Meine et al., 2006), and populations and species extinctions are increasingly being acknowledged as 'interspecific genocides' (Cafaro, 2015).

While human population growth and the more than 2000 % increase in the global human economy in the last century (Maddison project Database, 2020) are likely to be the ultimate causes for wild mammals decline (McKee et al., 2013), several proximate, more specific, drivers have been identified. Habitat loss is widely recognized as the most important current threat to mammals (Brodie et al., 2021), with urbanisation as primary land cover change at global scale (Mousivand et al., 2019; Gerard et al., 2010): urban population is growing steadily, urban sprawl is devouring surrounding natural habitats at a fast pace, and cities are projected to triple in extent before 2050 (Laurance et al., 2022; Simkin et al.,2022). Deforestation for agriculture expansion and mining is reducing biodiversity-rich tropical rainforests and is pushing the Amazon towards a possible regime shift in structure from humid forest to sparse shrubland (Ritchie et al., 2021; Brienen et al., 2015). Mammalian movements and migrations are increasingly being limited by proliferating networks of human infrastructures that currently fragment the terrestrial surface into 600,000 patches (Tucker et al., 2018; Ibish et al., 2016). In low-income countries of the world's south poaching is resulting in extensive defaunation, with animal biomass decreasing even in relatively intact forests due to overharvesting (Benítez-López A, 2019). In contrast to public opinion perception, climate change is currently not a major driver of mammalian decline, but will certainly become a more severe threat in the future (Caro et al., 2022). Other less studied anthropogenic impacts on biological communities are emerging threats such as free-ranging livestock rearing, and human disturbance linked to outdoor recreational activities (Schulze et al., 2018). These two surging pressures on ecosystems are the research topics of this thesis, addressed respectively in Part 1 and Part 2.

The demand for meat, wool and other animal products is on the rise at global level, due to increasing consumptions and changing lifestyles (Machovina et al., 2009; Berger et al., 2013). The expanding livestock sector impacts the environment in many ways, from overgrazing and land-degradation, to nitrogen pollution, greenhouse gases emission, and competition with wild animals (Herrero et al., 2009; Krausman et al., 2009). In those primary grasslands that have not been transformed into cropland (often used for fodder crops), domestic herbivores are now several orders of magnitude more abundant than wild ones, and the biomass reduction of wild prey has cascading effects on carnivores, and various impacts on small mammals (Krausman et al., 2009; Davidson et al., 2012). In part 1 I focus on how the increasing demand of animal products, and particularly of cashmere wool, due to globalised markets and heightened consumptions is indirectly affecting the communities of wild mammals in Mongolia, by incrementing the number and size of livestock herds (Berger et al., 2013). The case of Mongolia, and Central Asia more in general, is particularly interesting, since human population in this areas is among the lowest recorded worldwide, yet human-related threats to wild animal populations and ecosystems are far than being absent: a mixture of overgrazing by increasingly numerous herds of domestic animals, climate change, big infrastructure development projects, poaching and wildlife trade is affecting biological communities of these relatively understudied dry grasslands (Snow Leopard Network, 2014), that still host an impressive variety of mammalian species. Pastoralism has always been practised in these prairies, and herders have coexisted with wild animals for millennia, yet the recent changes in the global market could be upsetting this equilibrium. Negative effects of free-ranging livestock rearing in this area have already been observed, like competition for grazing areas with wild herbivores. High density of domestic animals also seem to be detrimental for large carnivores (Ekernas et al., 2017; Sharma et al., 2015).

The research included in part 2 have instead taken place in Italian mountains, where the socio-ecological patterns and tendencies are strongly dissimilar to Central Asia: the human population densities are in the opposite extreme of the range, but the population drift towards industrial and urban areas has led to rural abandonment in more mountainous, steep, and unproductive terrain. Like many other European countries, Italy has reached during the second half of the XX century the forest transition point, given that socio-economic transformations have decreased the amount of land and labour devoted to agriculture (Rudel et al., 2005) and freed land for natural re-expansion of forests. This factor, combined with legal protection of species, hunting regulations, PAs creation, population reintroductions, has allowed the

recovery of many medium and large mammals that were rare or absent only one century ago, and that find in forests either their natural habitats, or refuge from human disturbance, or both. At the same time however, this increasingly urban human population is searching for opportunities to hike, cycle or simply reconnect with nature by recreating outdoors, and pours into hills and mountains during vacation or spare time, with the potential of disturbing and negatively affecting mammals. Mammals can respond to human frequentation of their habitat by increasing vigilance levels, shift towards nocturnal activity, seek refuge within dense vegetation, reduce their movements in disturbed areas or avoid people both in space and time (Gaynor et al., 2018; Tucker et al., 2018; Richard et al., 2016). Human disturbance can however increase levels of stress and decrease foraging and reproduction efficiency, with potential negative consequences on whole communities and even ecosystem functionality (Carbillet et al., 2020; Li et al., 2022).

In a global effort to halt the biodiversity crisis, governments have created protected areas (PAs) to safeguard ecosystems and limit human harmful activities, and the proportion of protected land surface has steadily increased in the last decades. Evidence shows that animal communities are indeed faring better within PAs than in non-protected land (Gray et al., 2016), yet PAs suffer from a long list of pitfalls that may hinder their capacity to conserve nature in the long-term. Low funding, lack of law enforcement, absence of ecological connectedness between PAs, exposure to urban and infrastructure development are all well-known vulnerabilities of PAs that can jeopardise the aim to conserve biodiversity and ecosystem integrity (Geldmann et al., 2019; Wittemyer et al., 2008) and result in species decline even within PAs (Western et al., 2009; Craige et al., 2010). Beyond these well-known pressures on PAs, recreational activities have recently been identified as the most reported threat in PAs of Eurasia, and among the top three in the other regions of the globe, while widespread presence of free-ranging livestock and overgrazing are particularly influential in PAs across Central Asia (Schulze et al., 2018), making research on these topics pivotal also within PAs.

Rather than focusing on single species, the research included in this thesis is directed towards communities (or assemblages) of mammals. To understand the complex repercussions that human activities have on the environment, biological communities are indeed a better study object than single species, given that they represent a wider part of the complex interrelations between organisms that characterise an ecosystem, and can be more cost-effective than single species approaches to conservation (Olden, 2003). Among the recent technological advances in biodiversity monitoring, camera-trapping has the inherent

advantage of simultaneously detecting multiple species inhabiting an area, therefore it is naturally suited for community ecology studies (Ahumada et al., 2013). In contrast to radio-tracking, which utilises a Lagrangian approach reconstructing trajectories to study animal movements, systematic camera-trapping can be considered a Eulerian approach, inferring animal behaviour dynamics from single point detectors (Franklin et al., 2022; Cagnacci et al., 2010). This Eulerian approach with camera-trapping presents both advantages and disadvantages. A non-exhaustive list of strengths include: the potential to monitor multiple species and large areas; the capacity to collect data in continuum, regardless of time of day, temperature, or weather conditions; the low disturbance (virtually zero) on sampled individual animals; the high amount of data collected; a relatively low cost; the possibility to estimate density for species with marked or distinguishable individuals; the potential to estimate spatial and temporal overlap among species within communities (Rovero et al., 2016). For these reasons systematic camera-trapping has surged as one of the most popular techniques for monitoring and studying mammals worldwide (Rowcliffe and Carbone, 2008). Weaknesses are however emerging from the ecological literature, and in general revolve around the difficulty to relate camera-trapping data to the two fundamental processes that underlie detections: animal movements (including home range formation) and population density. The metric of occupancy, namely the probability that a species is present at a sampling site, was initially developed for discrete habitat patches, but has been widely applied to camera-trapping data in continuous habitats, in which case it depends upon camera-spacing, animal densities and movement rates (Efford and Dawson, 2012; Kays et al., 2021). Due to its asymptotic nature, that quickly reaches 100% occurrence probability after few detections, occupancy cannot represent gradients of population densities, that are rather better approximated by the number of detections (Parsons et al., 2017; Rovero and Marshall 2009). However, the number of detections (i.e., trap rate, or relative abundance index) does not correct for imperfect detectability and is thus prone to underestimations (Rowcliffe and Carbone, 2008). Nonetheless, new analytical tools are emerging, and the versatility of camera-trap data for ecological inferences is improving. New advances include multi-species co-occurrence models (Rota et al., 2016; Tobler et al., 2019), density estimation for unmarked animals (Palencia et al., 2021), spatio-temporal modelling (Ait Kaci Azzou et al., 2021). In part1 of this thesis I applied recently developed, multi-species analytical approaches to infer networks of spatial co-occurrence in mammalian communities and integrated them with temporal modelling to gain a broad perspective on the potential inter-specific interactions under anthropogenic impacts.

Occurrence and co-occurrence probabilities were estimated in the framework of hierarchical modelling, by which "presence" data can be corrected for imperfect detectability. I exploited the potential of hierarchical modelling also in part 2: in chapter 3 I inferred multi-year trends of occurrence for a community of wild mammals targeted by a long-term monitoring project, and in chapter 4 I assessed responses to human disturbance in four areas through a multi-area, multi-species occupancy model. However, I did not limit my analyses to hierarchical modelling, but integrated them also with other approaches to assess spatial and temporal responses of mammalian habitat use to anthropogenic variables. In particular, I used the number of detection events as a proxy of intensity of use, also differentiating them in different time-slots, thereby connecting the spatial dimension of habitat use with the temporal one. Systematic camera-trapping, coupled with different statistical tools, proved to be a powerful method to study mammalian communities and collect robust spatial and temporal information on their behaviour and ecology under various anthropogenic pressures, pivotal to inform conservation practice under the current biodiversity crisis.

Part 1. Effects of livestock rearing on communities of wild mammals

Chapter 1. Co-occurrence of snow leopard, wolf and Siberian ibex under livestock encroachment into protected areas in the Mongolian Altai

Marco Salvatori, Simone Tenan, Valentina Oberosler, Claudio Augugliaro, Philippe Christe, Claudio Groff, Miha Krofel, Fridolin Zimmermann and Francesco Rovero

Abstract

In countries such as Mongolia, where globalisation of the cashmere market has spurred herders to massively increase their livestock numbers, an important conservation concern is the effect of livestock encroachment on wildlife. This is especially important inside protected areas (PAs), which often represent the last refugia for threatened large mammals. We used camera-traps to

sample four areas with different protection status across the Mongolian Altai Mountains, and targeted a predator-prey system composed of livestock, one large herbivore, the Siberian ibex, and two large carnivores, the snow leopard and the wolf. To determine the effect of livestock on habitat use by the wild species and their spatio-temporal co-occurrence we applied an occupancy framework explicitly developed for modelling interacting species. We recorded a widespread presence of domestic animals in the PAs, and observed avoidance of sites used by livestock by snow leopard and ibex, while wolves tended to co-occur with it. Snow leopard and ibex showed clear mutual co-occurrence, indicating a tight predator-prey relationship. Results provide evidence that, at the scale of sites sampled primarily to maximise snow leopard detections, grazing livestock interferes with wild species by inducing avoidance in snow leopards, and attraction in wolves. We suggest that (1) PAs management should enforce real grazing limitations on the ground, especially in the core areas of the parks; (2) new policies incorporating wildlife conservation into government subsidies to pastoralists should be envisaged, to prevent increasing displacement of snow leopards and ibex; (3) as wolves co-occurred with livestock, with the potential for human-wildlife conflicts, we encourage the use of a set of prevention techniques to mitigate livestock depredation.

Introduction

Demand for livestock products has more than doubled in the last forty years globally (FAO, 2009), and as a result 30% of the terrestrial surface is currently used for pastures and fodder crops, making the livestock industry the largest land-use sector on the planet (Herrero et al., 2013). As the biomass of domestic animals has concomitantly increased (currently estimated at 60% of the total global mammalian biomass; Bar-On et al., 2018), there is growing concern for the impact that animal farming exerts on wildlife and ecosystems (Reid et al., 2009; Machovina et al., 2015; Ripple et al., 2015). In this context, an important conservation issue is the encroachment of free-ranging livestock inside protected areas (PAs), where livestock can outcompete wild mammals for space and resources and trigger human-wildlife conflicts (e.g., Mishra et al., 2004; Gandiwa et al., 2011). Yet, PAs often represent the last refugia for many threatened and rare species of mammals around the globe (Pacifici et al., 2020).

Across central Asia, highlands and mountains host a unique grassland ecosystem that has been used as rangeland for centuries. However, in recent decades livestock numbers have strongly increased, mainly because of the rapid growth of the global cashmere trade market

(Berger et al., 2013). As a result, the biomass of wild ungulates in many regions of central Asia is currently between one and two orders of magnitude lower than that of domestic animals (Berger et al., 2013; Tumursukh et al., 2016), and free-ranging livestock often encroaches into PAs (e.g., Rovero et al. 2020). Several studies have shown the negative effects of high livestock densities on wild ungulate populations, mainly attributed to competitive exclusion due to the similar diets (Bagchi and Mishra, 2006; Sharma et al., 2015; Siraj-ud-Din et al., 2016). Pastoralism also threatens large carnivores in the region, through a complex, but still poorly documented cascade of effects (Ekernas et al., 2017), with reduction of wild prey and predation of livestock, triggering human-carnivore conflicts and retaliatory killings, being considered the main processes involved (Snow Leopard Network, 2014; Mishra et al, 2016; Ali et al, 2016). However, and in spite of the plausible link between prey reduction and livestock predation by carnivores, it remains poorly understood how the pervasive presence of livestock influences the occurrence of the whole large carnivore-wild herbivore system (Gordon, 2018). This question is of both ecological and conservation relevance especially within PAs, because knowledge on how mutually interacting wild species respond spatially and temporally to livestock encroachment informs on the vulnerability of these wild species. It can also give insights on strategies to increase the efficiency of PAs and harmonise their protection with pastoralism, hence mitigating human-wildlife conflicts. Here, we aim to provide a contribution to address this question using data from the Mongolian Altai Mountains.

In Mongolia more than one third of the land is devoted to pastures and 40% of the gross domestic product comes from livestock farming (Mijiddorj et al., 2018). The country has become the world's second exporter of cashmere after China (Lecraw, 2005), with total livestock numbers estimated at 71 million in 2019 (National Statistics Office of Mongolia, 2019), of which 29 million were goats. We focused on four areas in the Altai Mountains in the western part of the country, where snow leopard (*Panthera uncia*) and wolf (*Canis lupus*) are the top predators, and both are known to prey on domestic animals (Mijiddorj et al., 2018). However, there are key relevant differences between these two predators: the snow leopard is a strict mountain-dweller felid considered as Vulnerable by the IUCN and has a fragmented distribution and declining global population. Habitat degradation, decline of wild prey and retaliatory killing are considered to be the major threats faced by the snow leopard globally (McCarthy et al., 2017). However, knowledge on the effects of livestock on snow leopard remains scant. Evidence from the Indian Himalaya indicates increased intensity in snow leopard site use with increasing livestock numbers, and a decrease beyond a threshold of

livestock densities (Sharma et al., 2015). The wolf, on the contrary, is relatively widespread across Mongolia, typically preying on plains-dwelling wild ungulates but reported to frequently raid livestock (Chetri et al., 2017). Wolves were reported to prey on livestock more often than snow leopards (Shresta et al., 2019) and a recent study in our study region found that predation by wolves accounts annually for 4.1% of the total livestock holdings, while predation by snow leopards accounts for 0.2% (Augugliaro et al., 2020). A similar study in the Tost Mountains in Southern Mongolia reports higher proportions of livestock depredation attributed to wolves than snow leopards (Mijiddorj et al., 2018). Among wild prey, the Siberian ibex (*Capra sibirica*; hereafter, ibex) is the only mountain and cliff-adapted ungulate that we consistently recorded across the study areas and it is also the main prey for snow leopards in the region (Shehzad et al., 2012). Similar to snow leopard, mountainous PAs protect optimal habitat for the ibex, yet data from one of the four PAs we targeted showed that encroaching livestock may displace ibex (Rovero et al., 2020).

We used camera-trapping data from systematic sampling at 216 sites in four areas across the Mongolian Altai, representing a gradient from a Strictly Protected Area where livestock grazing is not allowed and two National Parks (NPs) where livestock grazing is allowed with limitations, to an area that was not protected at the time of our survey. We analysed the data using multi-species, co-occurrence occupancy models (Rota et al., 2016), and aimed to assess how livestock encroaching into PAs influences the spatio-temporal occurrence of snow leopard, wolf and ibex, and their spatial interactions. We analysed species occurrences at the scale of camera trap sites that we selected primarily within habitat deemed suitable to snow leopards, hence we framed our hypotheses and interpretation of results based on such spatial scale. Relative to a previous study based on data from the first of the four areas here considered (Rovero et al., 2020), our study provides for a novel assessment of the targeted ecological system, in view of the wider area and gradient of protection sampled, the inclusion of the wolf, and the use of an unconditional relationship between species. Specifically, by relaxing the dominant-subordinate assumption and focusing on a wider pool of species over a wider area we aimed to address the following questions: (1) does the presence of livestock herds decrease ibex habitat use spatially and/or temporally? We expected a decrease in ibex occurrence probability in the presence of livestock, but no major segregation in diel activity pattern given the diurnal/crepuscular habits of ibex (Xu et al., 2012). (2) Do wolves and snow leopards avoid or co-occur with livestock in space and time? Main hypotheses were that (i) both predators occur with lower probabilities at sites where livestock is also present, and their diel

activity peaks at times of lower livestock activity. Alternatively, (ii) we hypothesised that wolf shows more neutral or even positive co-occurrence with livestock than snow leopard given the evidence of greater livestock depredation by the former. (3) Is there a co-occurrence pattern between snow leopard and ibex? We hypothesised a positive co-occurrence probability given the marked dependence of snow leopard on wild prey (McCarthy et al., 2016). (4) Is there a spatial segregation of the two carnivores as a result of competition? Our main hypothesis was that their co-occurrence is neutral given that they have different focal wild prey, and assuming that their propensity to predate on livestock, which may drive their use of space, is also different (Mijiddorj et al., 2018; Augugliaro et al., 2020). 5) Is there a co-occurrence pattern between wolves and ibex? We expected a neutral pattern, given the low suitability of ibex as a wolf prey (Chetri et al., 2017).

Material and Methods

Study areas

The Altai Mountains of Mongolia stretch over 900 kilometres from the north-western part of the country to the south, through the provinces of Bayan Olgii and Hovd. The area has cold semi-arid continental climate with long cold winters and short summers during which most precipitation falls, and supports alpine meadows and tundra. High plateaus extend for hundreds of square kilometres with desert-steppe vegetation, lichens and mosses being the principal ground cover, while peaks host a rugged, rocky and steep environment; valley bottoms are sparsely covered by coniferous forest and shrubs.

During 2015 and 2017-2019 we surveyed one area per year in the spring (March-June). Study sites (Figure 1.1) include: (1) Siilkhem-B National Park (49°49'N; 89°44'E) in north-western Mongolia bordering Russia, with highest elevation up to 3,900 m a.s.l. The park is characterised by steep, rocky and dry habitat, with grassland as main vegetation cover and scattered larches *Larix sibirica* along valley bottoms. (2) Tavan Bogd National Park (48°33′N; 88°37′E), in western Mongolia bordering Russia and China; this is the largest PA in Mongolia, reaching the highest elevation in the country (4,374 m a.s.l.). The northern part that we surveyed presents large portions of alpine and glacial habitat, with lower elevation covered with grasslands. (3) Khork Serkhe Strictly Protected Area (47°93′N; 90°99′E) located in western Mongolia and reaching 4,127 m a.s.l. It is mainly represented by steep grasslands and valleys. (4) Sutai massif (46°37′ N; 93°35′ E) was surveyed in 2019, when it had no legal protection, but was declared a Natural Reserve shortly after the end of our study. Sutai holds

the highest mountain of the Gobi-Altai chain, with elevations reaching 4,220 m a.s.l. at the main peak, which is permanently covered by the southernmost glacier of the region. Overall, the four study areas present very similar environmental characteristics relevant to our analysis, with mountainous grassland as the dominant vegetation type and broadly consistent elevation range. Details on sampling areas and efforts are provided in Appendix S1.1.

Pastoralism is the main livelihood in all four study areas. The herders inhabiting the Bayan Olgii province (where Siilkhem-B, Tavan Bogd and Korkh Serkhe are located) belong to the ethnic group of the Kazakhs, professing Islam, while in the Sutai massif they belong to the ethnic group of the Mongols, which profess Buddhism. In the Bayan Olgii province alone, 2.2 million livestock were reported in 2018, of which 1.9 million were sheep and goats (National Statistics Office of Mongolia, 2019). Herder families move seasonally to change the grazing areas. Goats and sheep are guarded by herders and dogs during the day and held in corrals at night, except in summer (July-August), when often no corral is used, while horses, camels, cattle and yaks are mostly free ranging (Augugliaro et al., 2020). According to the Mongolian law, the NPs are subdivided into three zones: special zone, travel and tourism zone, and limited use zone. Traditional pastoralism is only allowed in the latter, whereas it is not allowed in the Strictly Protected Areas.

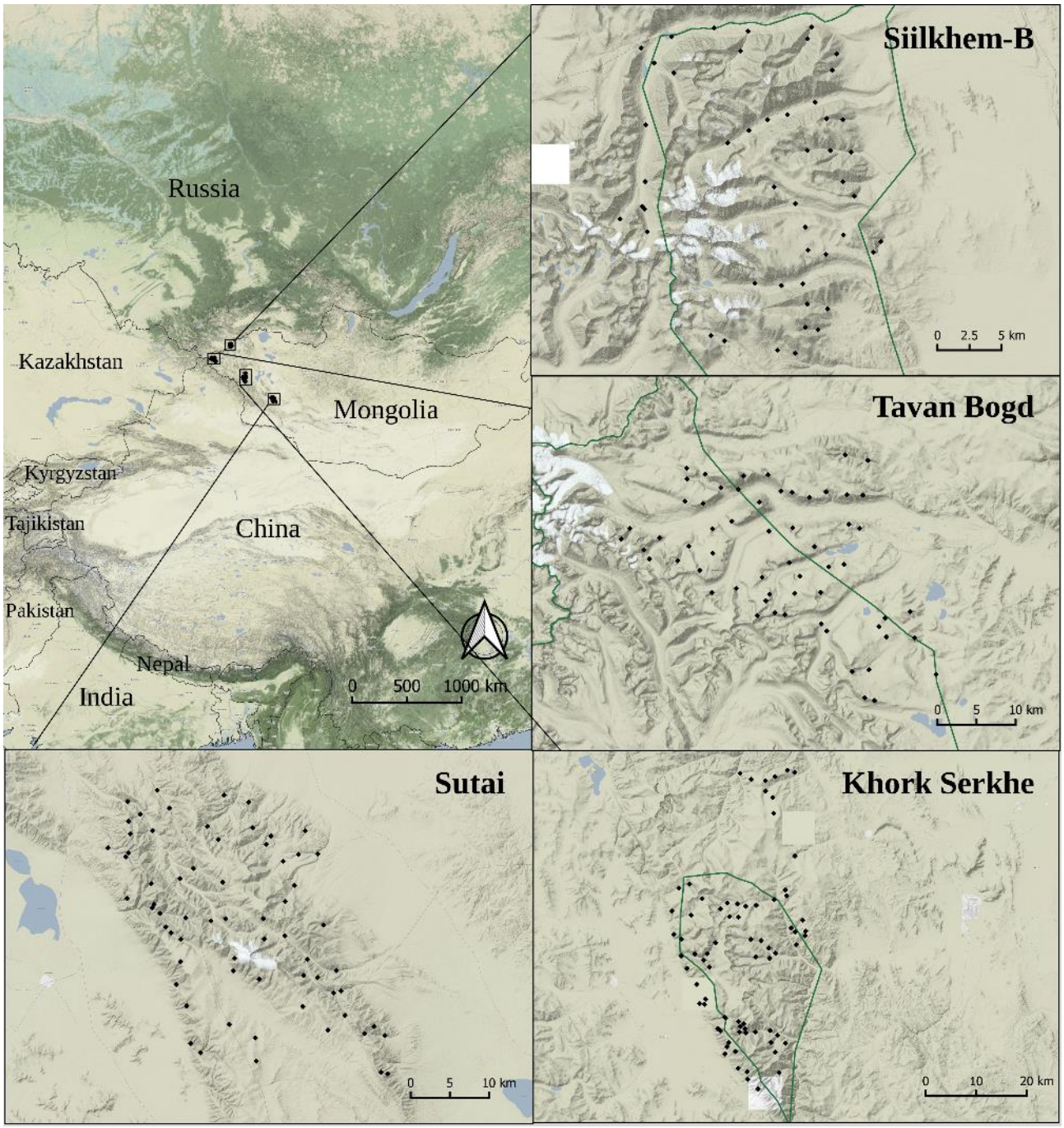

Figure 1.1. Map of the four study areas across the Altai range, western Mongolia. From upper right to bottom left: Siilkhem-B National Park, Tavan Bogd National Park, Khork Serkhe Strictly Protected Area and Sutai Massif. The locations of camera-trap sites within each area are indicated by black dots and the borders of protected areas are shown with green lines (not shown for Sutai, since this area was not protected at the time of the survey).

Data collection

For each area, our sampling design was based on a regular grid with cells of 4 km^2 that aimed to cover at least the minimum extent of 500 km^2 recommended for snow leopard population estimate studies (Jackson et al., 2005). Within each cell we located in the field one camera-trap site. The number and locations of sites sampled were constrained by accessibility (conditioned mainly by terrain morphology and snow cover) and the number of camera-traps available for sampling (see Table A.1). Thus, in the two PAs that were too large for complete coverage, we selected portions that we considered optimal snow leopard habitat according to the literature and local knowledge. Specifically, in Siilkhem-B we did not sample the southern end of the PA as this is lower elevation and least suitable habitat, and in Tavan Bogd we targeted the north-eastern portion of the PA. In Khork Serkhe we sampled the whole PA and surrounding suitable areas, and in Sutai we sampled the whole mountain massif. Overall, the area sampled ranged in size from 513 to 1110 km^2 (Table A.1). At the selected sampling locations, we fitted camera-traps on small rock piles c. 50 cm above the ground at approx. 2-4 m from the target trail, and set them to record photos in continuous mode, with no delay between consecutive triggers. We maintained a minimum distance between contiguous sites of approximately 1.5 km. We did not use baits or lures. Camera-trap models were of 3 different manufacturers, characterised by high (Reconyx) and medium (Cuddeback and Bushnell) trigger speed. Camera-traps ran on average for 65 days (SD = 20.7; see Table A.1). Camera-trapping sites were mainly set on narrow passing trails, ridges and valley bottoms, to maximise detections of the rarest and most elusive species, the snow leopard. While we are aware that such design may under-sample the other focal species (such as livestock or ibex), our preliminary study (Rovero et al. 2020) and the results of this study indicate that the selected sites were also widely used by the other species (in 79.2 % of sites in which snow leopard was detected we also detected at least one of the other three focal species). However, we acknowledge that inference from our findings should be interpreted as co-occurrence patterns within expected snow leopard habitat. Environmental covariates included camera-trap site elevation, terrain slope and distance from the closest herders' settlement, and were derived from a Digital Elevation Model and satellite maps through the software Quantum Gis (QGis, 2018). The chosen covariates were not correlated according to Spearman's correlation test (rho < 0.5).

Spatial analyses

Given our aim of assessing the overall effects of livestock on selected wild species, and that herds of grazing livestock most often grouped multiple domestic species, we merged detections of all domestic animals and humans (which were all of herders or other local community members) into a single entity, henceforth referred to as 'livestock'. For snow leopard, wolf, ibex and livestock, we then arranged detections into matrices of sites *i* by sampling occasions *j*, using five days as the resolution, as such interval outperformed occasions of 1 or 2 days in terms of model convergence and precision of estimates.

We modelled detection/non-detection data of the $S = 4$ species (including the category livestock) collected in the four areas using the multi-species co-occurrence model developed by Rota et al. (2016), which is a generalization for two or more interacting species of the single-species occupancy model by MacKenzie et al. (2002). The modelling framework includes a latent occupancy state (Z_i) for each of the $s = 1, \ldots, S$ species at site $i = 1, \ldots, I$, where Z_i is represented by a sequence of 0/1 values indicating whether each species is present (1) or absent (0) at site *i*. The latent state is modelled using a multivariate Bernoulli distribution, $Z_i \sim \text{MVB}(\boldsymbol{\psi}_i)$, where $\boldsymbol{\psi}_i$ is a vector of length $2^S = 16$ probabilities for each possible absence/presence combination of S = 4 species, with $\Sigma_k \psi_{ik} = 1$. These probabilities are modelled on the logit scale, as log odds of occupancy, also referred to as natural parameters (f). The vector of natural parameters for each site ($\boldsymbol{f}_i$) can have maximum length 2^S-1, depending on the number of species and the nature of the interactions included in the model. In our case, we used a model with four interacting species, and considered only pairwise interactions between species (i.e., we did not consider three-species and four-species interactions), resulting in ten natural parameters being modelled. Four natural parameters *f* represented the log odds a single species individually occurs at a site, and the other six natural parameters were the log odds of the probabilities that two species occur together: $\boldsymbol{f}_i = \{f_{1,i}, f_{2,i}, f_{3,i}, f_{4,i}, f_{12,i}, f_{13,i}, f_{14,i}, f_{23,i}, f_{24,i}, f_{34,i}\}$, with numbers from 1 to 4 denoting species identity. The single-species natural parameters $f_{1,i}$, $f_{2,i}$, $f_{3,i}$ and $f_{4,i}$ were modelled as a linear function of covariates while co-occurrence parameters $f_{12,i}$, $f_{13,i}$, $f_{14,i}$, $f_{23,i}$, $f_{24,i}$ and $f_{34,i}$ were kept constant across sites, since we did not expect inter-specific interactions to vary along covariates gradients. The observation model relates the true underlying occupancy states (z_{si}) to the observed detection data (y_{sij}) for species *s*, at site *i*, and sampling occasion $j = 1, \ldots, J_i$: $y_{sij} \sim \text{Bernoulli}(z_{si}\ p_{sij})$, with detection probability p_{sij} independent for each species.

Given the complexity of the multi-species co-occurrence model, that allows to express both single-species occurrence and co-occurrence parameters *f* as a function of covariates, we

used a two-step approach following Twining et al. (2020). In the first step we selected the most supported covariates for each species using single-species occupancy models, on the basis of the Akaike Information Criterion (AIC, Burnham and Anderson, 2002). For each species, we formulated specific hypotheses for the effects of covariates on occupancy and detection probability (Table S1.2.1). We first tested the distance to the closest herders' settlement and the camera performance (high trigger speed for Reconyx models *versus* medium trigger speed for Cuddeback and Bushnell models) as covariates on detection probability while modelling occupancy with all relevant covariates (i.e., a full model for occupancy, following MacKenzie et al., 2017), resulting in four models being compared. We then tested the distance to the closest settlement, terrain slope, elevation, and the sampling area as categorical variable, on occurrence probability while keeping the best encounter structure previously selected, resulting in 16 models being compared. In the second step, the most supported covariates from single-species occupancy models were included as predictors of occurrence and detectability of single species in the multi-species model. The multi-species model included six co-occurrence parameters *f*, one for each species pair. These six co-occurrence parameters represented our six specific hypotheses on co-occurrence of species pairs described in the Introduction (see also Table A.3), and we judged their significance according to the 95% confidence intervals. We implemented the models using the R (R Development Core Team, 2019) package 'unmarked' (Fiske and Chandler, 2011). In view of the large home ranges of the studied species and the fact that co-occurrence dynamics may vary with the spatial scale sampled, we acknowledge that our occupancy estimates should be interpreted as metrics of site use rather than occupancy sensu stricto.

Temporal analyses

In addition to modelling co-occurrence, we investigated the diel activity pattern for the three wild species and livestock. We subsampled the detection data considering consecutive detections within a 30 min interval as a single event and created temporal activity curves (Zimmermann et al., 2016). Then we performed pairwise comparisons of activity patterns between all the three wild species and livestock by estimating the overlap coefficient Δ (ranging from 0, no overlap, to 1, complete overlap) and its confidence interval using the package 'overlap' (Meredith and Ridout, 2016).

Results

Overall, livestock was detected at 110 out of 216 sites, resulting in a naïve occupancy of 0.51, snow leopard was detected at 81 sites (0.37), wolf at 49 (0.23), ibex at 54 (0.25; Table S1.2.1.). Livestock encroachment occurred in all the four areas, with livestock detected at 30 % of sites in Tavan Bogd, 44 % in Siilkhem-B, 60 % in Khork Serkhe and 62% in Sutai (see also Appendix S1.2). Livestock site use was negatively associated with elevation (β = -0.56 ± 0.20 SE, Figure 1.2) and distance to the closest settlement (β = -0.67 ± 0.21). This latter variable was also negatively related to livestock detection probability (β = -0.51 ± 0.08), together with camera-trap sensitivity (β = -0.49 ± 0.13, Figure S1.4.1). Snow leopard site use was significantly different among study areas, with the highest estimated site use probability in Sutai (β = 2.63 ± 0.55) and the lowest in Tavan Bogd (β = -2.07 ± 0.85). Its detection probability was positively correlated with camera-trap sensitivity (β = 1.46 ± 0.35). The best model for wolves did not include any covariates for detection probability (p = 0.08 ± 0.12), while site use probability increased with increasing distance from settlements (β = 0.51 ± 0.22) and decreased with increasing elevation (β =-0.11± 0.22). Finally, ibex site use was positively related to terrain slope (β = 0.39 ± 0.17) and site elevation (β =0.20 ±0.21). It was lower in Siilkhem-B compared to the other areas (β = -1.41 ± 0.66), and its detectability was lower at sites with camera-traps with higher sensitivity (β = -0.85 ± 0.29; see also Table S1.3.1 for single-species model selection and S1.3.2 for the multi-species model output on covariate coefficients).

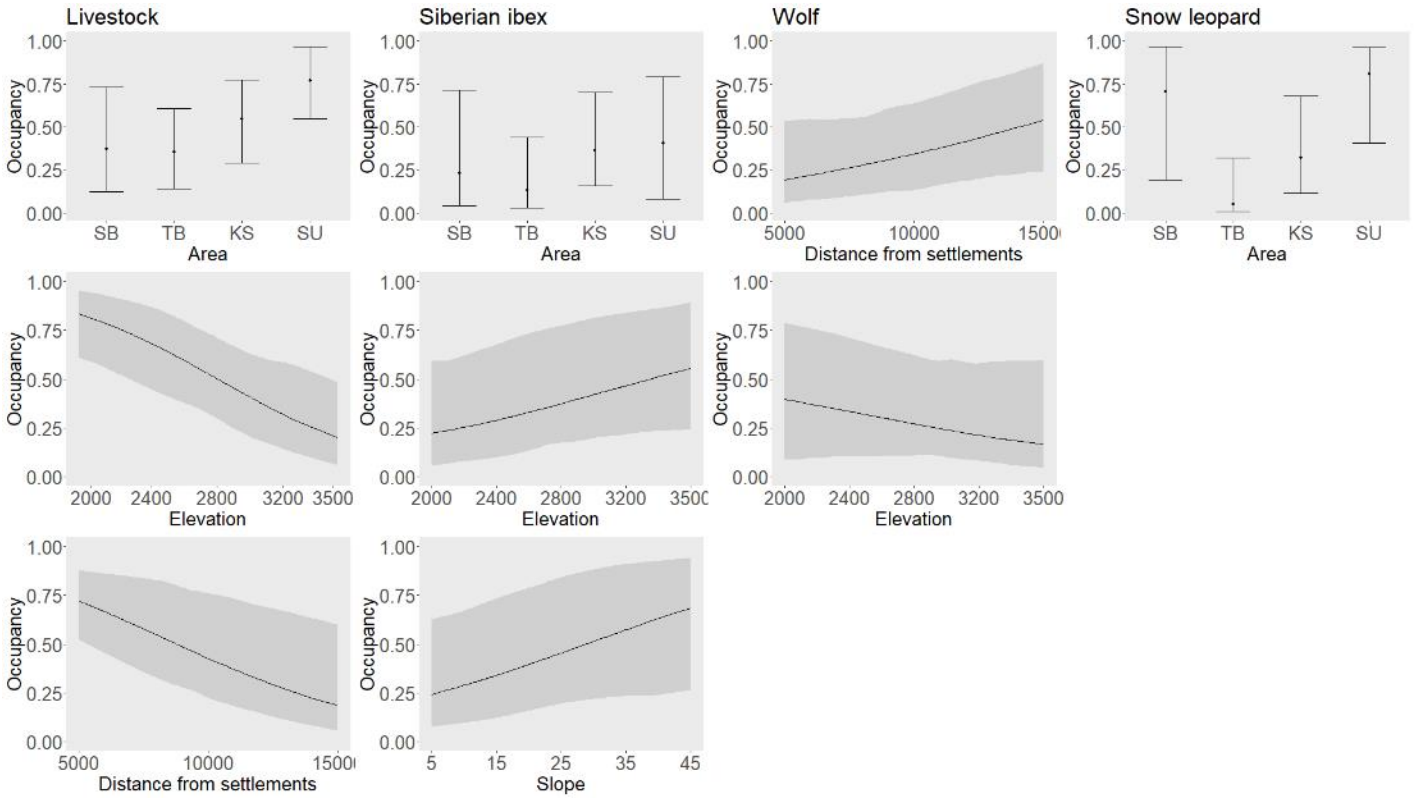

Figure 1.2. Bivariate plots of the relationships between each species occurrence probability, extracted from the multi species co-occurrence model, and the selected covariates from camera-trapping surveys in four areas of western Mongolia. SB stands for Siilkhem-B NP, TB for Tavan Bogd NP, KS for Khork Serkhe SPA, and SU for Sutai Massif. The error bars and bands represent 95% confidence intervals. To extract predicted probability of occurrence for one covariate all other covariates were set to their mean (i.e. zero). Bivariate plots for the effects on detectability are reported in Appendix S1.3.

The co-occurrence parameter for the species pair livestock – ibex was estimated as α = -0.30±0.4 (Figure 1.3b and Table S1.3.2). The co-occurrence estimate for livestock and snow leopard was α = -0.94±0.54. Livestock and wolf co-occurrence had an estimated parameter of α = 0.98±0.49. The species pair with the highest co-occurrence parameter was snow leopard – ibex, with an estimate of α = 1.70±0.61. The two predators showed an estimated co-occurrence of α = 1.02±0.51. Lastly, the pair wolf – ibex had a parameter estimate of α = -0.98±0.54. The predictions of each species site-use probability conditional on the presence or absence of the interacting species, derived from the multi-species co-occurrence model, are shown in Figure 1.4.

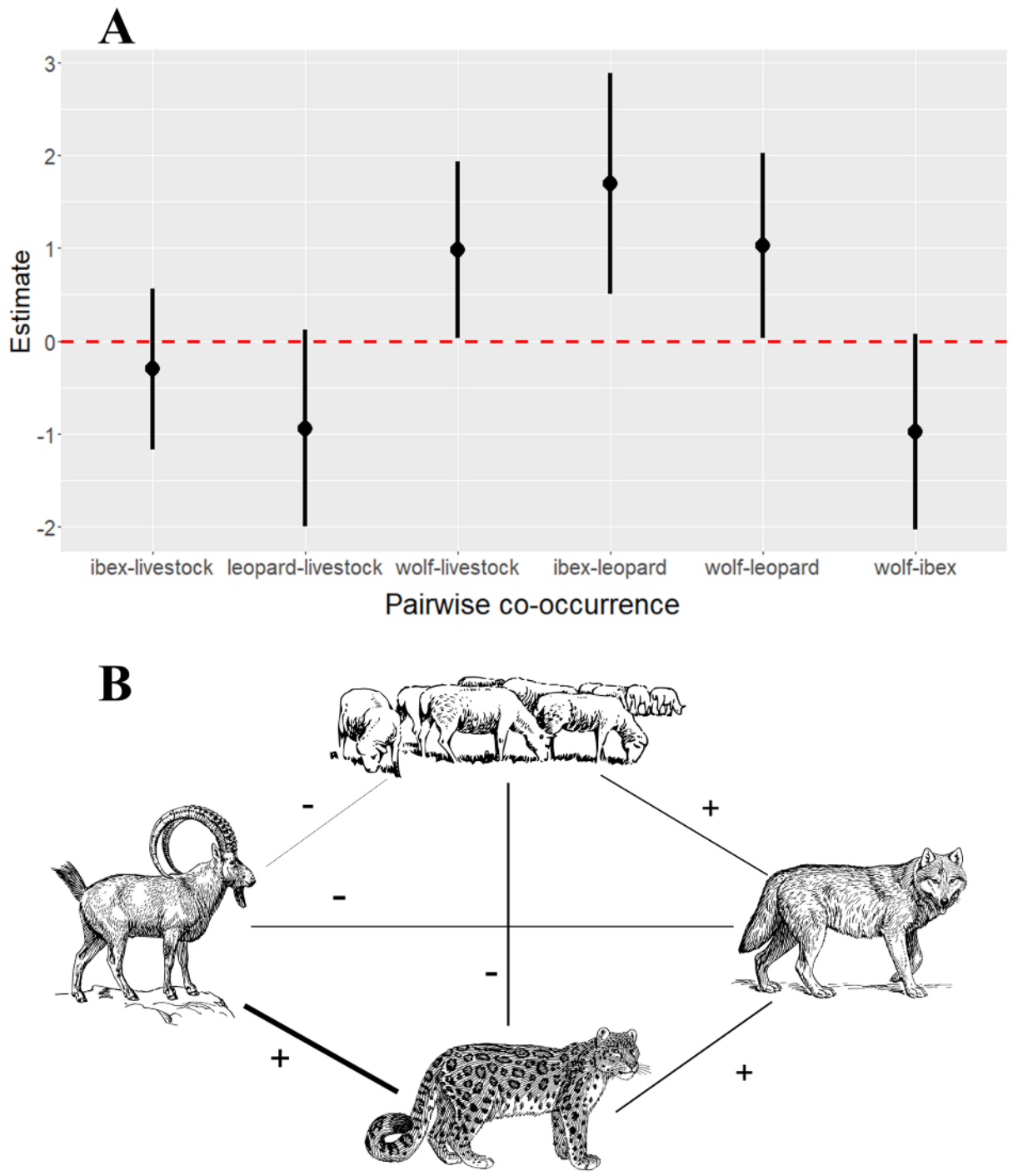

Figure 1.3. (A) Mean co-occurrence parameter estimates from the multi species co-occurrence model. Bars show 95% confidence intervals. The red dotted line stands for a co-occurrence parameter estimate equal to zero. Values above the line indicate positive co-occurrence, while values below indicate negative co-occurrence. (B) Schematic representation of the sign of co-occurrence relationships between species pairs. The line width is proportional to the magnitude of the co-occurrence estimate.

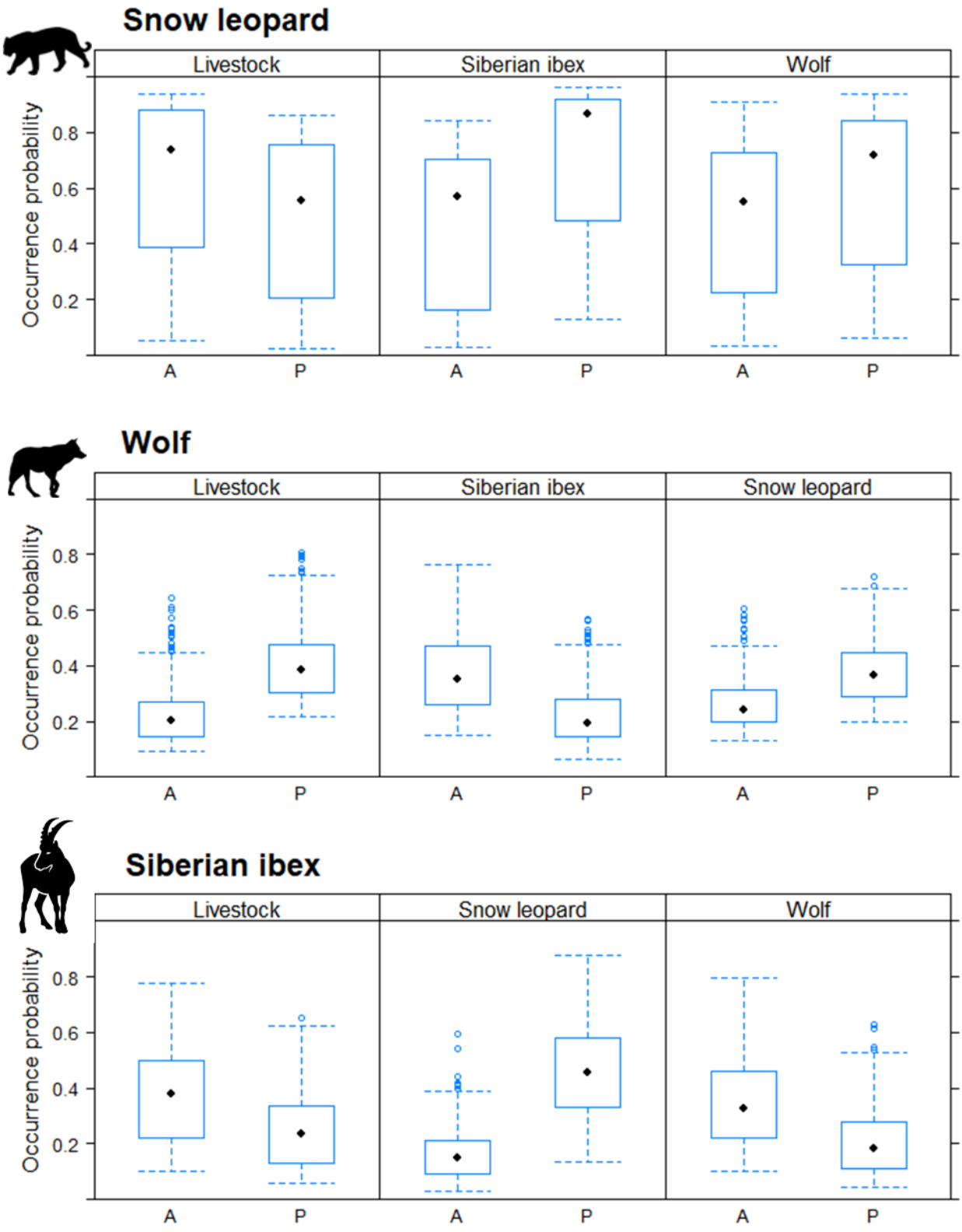

Figure 1.4. Predicted occurrence probabilities from the multi species co-occurrence model, developed on camera-trapping data from four areas of western Mongolia. Each species occupancy (y axis) is predicted conditional on the presence (P) or absence (A) of another (x axis), reported in each box title. Black dots and lines indicate median and mean value

respectively, the light blue boxes show first and third quartiles and the horizontal dashed lines indicate minimum and maximum values. Predictions were extracted at the real covariate values for our 216 sampling sites.

Domestic animals and humans showed a markedly diurnal activity pattern, with activity peak around midday. Ibex were also mainly active during daylight, with two peaks in the early morning and in the late afternoon. The pattern of the two carnivores differed: snow leopards showed a crepuscular and nocturnal activity pattern with two peaks at dusk and dawn and a higher activity level during night than day, while wolves had a more constant activity pattern with no marked difference between daylight and night hours (Figure 1.5). The maximum coefficient of overlap between activity patterns was between ibex and livestock (Δ= 0.80; 95% CI: 0.74 – 0.87), followed by snow leopard and wolf (Δ= 0.79; 0.70 – 0.88). An intermediate level of overlap was shown by wolf and ibex (Δ= 0.69; 0.59 – 0.79) and wolf and livestock (Δ= 0.62; 0.53 – 0.71). The lowest values were recorded for the pairs snow leopard - ibex (Δ= 0.51; 0.43 – 0.58) and snow leopard - livestock (Δ= 0.44; 0.39 – 0.49).

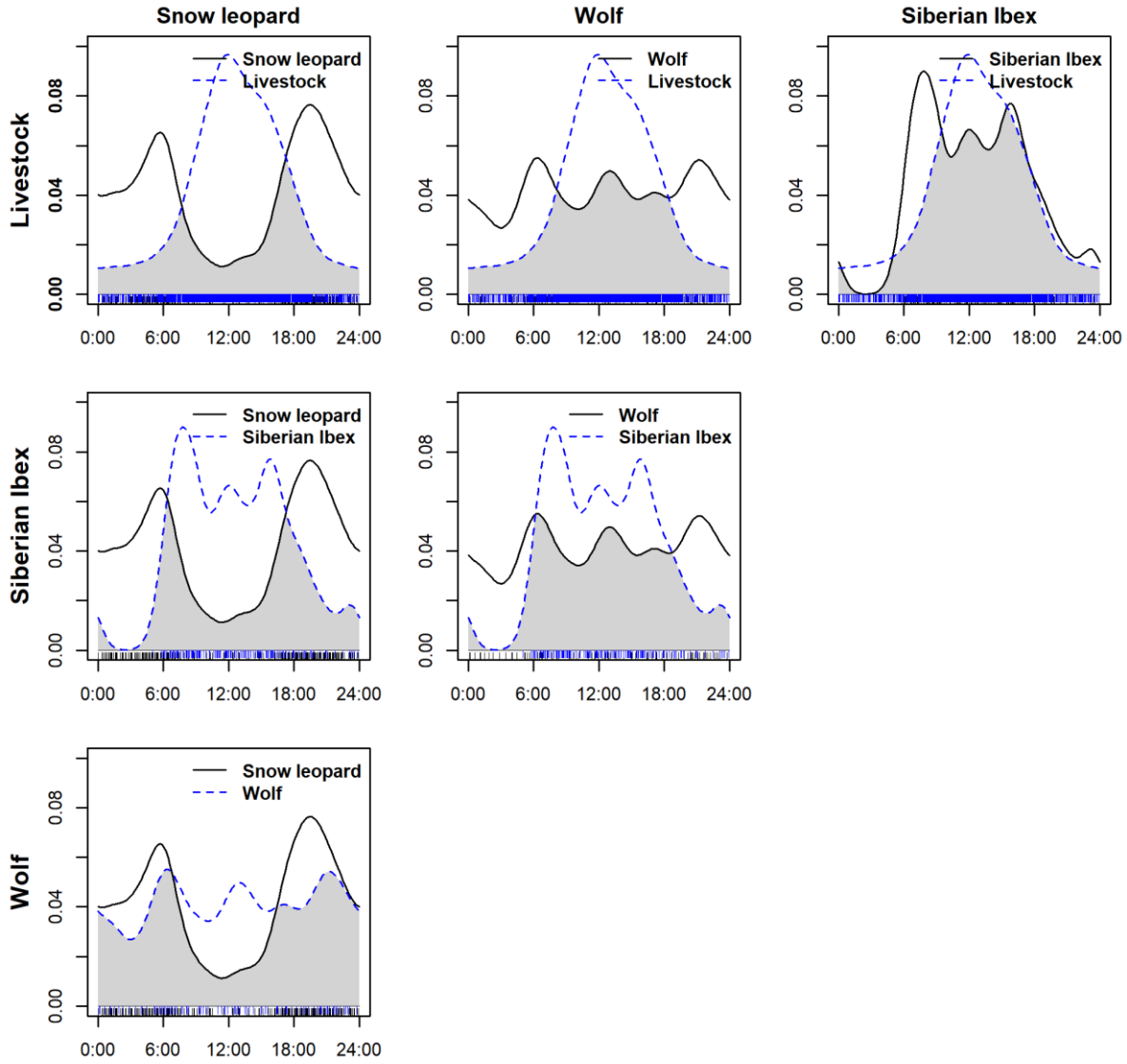

Figure 1.5. Curves of the activity pattern for each species and their temporal overlap with the other species from camera-trapping detections in four areas of western Mongolia. The overlap in activity between species is highlighted in grey. The y axis shows the density in activity and the x axis indicates the hour. Different species in each pair are denoted with a solid black line and a blue dotted line.

Discussion

By modelling the co-occurrence of snow leopard, wolf, Siberian ibex and livestock in the Mongolian Altai, at the scale of sites selected to maximise snow leopard detections, we provided a contribution to understand how livestock encroaching into PAs affects wildlife. We recorded the presence of livestock in large portions of all the areas sampled, with an estimated average occurrence of 0.52. This diffused presence of livestock clearly points to a lack of protection

effectiveness of target PAs, as according to the Mongolian law grazing is not allowed within Strictly Protected Areas and only allowed in "limited use zones" within NPs. Surprisingly, despite a high occurrence of livestock in Sutai, we also found the highest occurrence of the three wild species in this area that had no legal protection when surveyed. Reasons for these differences among areas are not readily apparent, however we qualitatively observed skins and traps in the herders' houses in all areas except Sutai (F.R., unpublished data), suggesting that wildlife poaching might be more practised by the Kazakhs than Mongols, as their different religious beliefs are reported to influence the attitude of local communities towards wildlife (Bhatia et al., 2016). Besides these general observations, our modelling results reveal a number of patterns on spatial occurrence of target species within the areas sampled, that generally point to a potentially negative effect of livestock on snow leopard presence, while to a positive effect on wolf, possibly mediated by the hunting prohibition in PAs and its persecution outside PAs.

The positive co-occurrence of snow leopard and ibex support the hypotheses of a predator-prey relationship that apparently holds regardless of livestock presence. Given that no environmental covariates had significant effects on snow leopard site use, this result suggests that the abundance of wild prey might be a key driver of snow leopard habitat use (Suryawanshi et al., 2017). Moreover, we found a potential indication of a negative effect of livestock on snow leopard as revealed by the negative spatial co-occurrence parameter, that yet had a 95% confidence interval that slightly overlapped zero. Moreover, snow leopard temporal activity was markedly nocturnal, meaning that the co-occurrence of this predator with livestock was low both spatially and temporally, given the distinctly diurnal pattern of domestic animals. This is a valuable result, as knowledge on whether livestock represents an additional food resource and hence 'attracts' snow leopards or displace them through direct disturbance remains limited, yet Sharma et al. (2015) found evidence of negative effects of high livestock density on snow leopard's habitat use in the Indian Himalayas. The higher site use probability of snow leopard in absence of livestock might also derive from a relatively low livestock depredation rate by the snow leopard in the target areas, as suggested by other studies in Mongolia (Mijidorji et al., 2018; Augugliaro et al., 2020). However, data on snow leopard diet and prey selection will be necessary to assess the validity of this interpretation (e.g., Johansson et al. 2015; Hacker et al., 2021).

Our hypothesis on the negative effect of livestock presence on ibex was not supported, since the 95% confidence interval of the co-occurrence parameter largely overlapped zero.

However, the sign of the species co-occurrence was negative, indicating that either a negative effect was present but weak or that our sample size was not sufficient to resolve the nature of this potential inter-specific interaction. The dietary niche composition of ibex and domestic goats and sheep largely overlaps, and previous studies have generally found detrimental effects of livestock on wild mountain ungulates in central Asia and Himalaya (e.g. Bagchi and Mishra, 2006; Sharma et al., 2015; Siraj-ud-Din et al., 2016). Opposite to the spatial interaction patterns observed in the snow leopards, wolves positively co-occurred with livestock while there was an indication of a possible negative co-occurrence with ibex. The negative, though non-significant, co-occurrence of wolf and ibex agrees with our hypothesis on the low suitability of this cliff-adapted ungulate as wolf prey, as well as findings from previous studies in Central Asia (e.g. Chetri et al., 2017). That wolf site-use probability was higher in the presence of livestock bears potential implications in view of the human-wildlife conflicts documented in the study areas. Indeed, results from Augugliaro et al. (2020) show that wolf predation of livestock increases in PAs, as wolf hunting is not allowed and hence wolves' numbers within PAs might be higher compared to non-protected areas where they are persecuted. Thus, even though the interior portion of PAs may not represent optimal wolf habitat, PAs seemingly provide both protection from poaching (Clark et al., 2006) and livestock as a food source for this carnivore. The fact that wolves were active throughout the day, with no evidence of temporal avoidance of livestock and humans, further corroborates this hypothesis, and points to its lower sensitivity to disturbance than snow leopard. However, the site-use probability of the wolf significantly increased at greater distances from human settlements, an opposite pattern compared to livestock. The higher site-use probability of wolves far from herders' houses and where livestock is also present matches evidence that most predations take place when herds are not supervised (Mijidorj et al., 2018). The positive co-occurrence we found between wolf and snow leopard might reflect a lack of direct competition through interference. However, this is also likely contributed by the sampling design, whereby sites chosen to maximise snow leopard detection may also have been suitable to wolf. The opposite spatio-temporal overlap of snow leopard and wolf with ibex and livestock might also indirectly reflect the environmental preferences and hunting strategies of these two species: wolves are gregarious and cursorial predators that favour milder slopes while snow leopards are solitary ambush predators that target steep and rugged terrain in high altitudes, where livestock are less present, and ibex are typically found.

Conclusions and conservation recommendations

This study shows that recently developed co-occurrence modelling that relaxes the dominant-subordinate assumption is a useful approach to determine the effects of grazing livestock on multiple wild species. It allowed us to assess both the effects on single species and on their spatial interactions while accounting for preferences in habitat use, which provides for a more comprehensive understanding of how the interacting prey-predator system responds to anthropogenic influence. Within PAs, our sampling design targeted the presumed optimal snow leopard habitat, and therefore the inference on spatio-temporal interactions between species should be primarily related to such areas within the wider landscape. Our findings bear several conservation implications: (1) the diffuse presence of livestock inside PAs, even within core wildlife habitats, calls for more effective protection and the establishment of sustainable grazing regimes. We found no evidence on the ground of the existence of the supposed "special zone" in the two NPs, and our data on livestock occurrence do not seem compatible with such limitations. (2) The possible avoidance of livestock by snow leopard could mirror the sensitivity of this threatened species to grazing herds. This is particularly worrying when considering that the number of goats in the region has more than tripled in the last 30 years (National Statistics Office Mongolia, 2018) and that most herders in our study areas seemingly aim for increasing the size of their herds (Augugliaro et al., 2020). Currently the Mongolian government is encouraging pastoralists to increase livestock numbers (Endicott, 2012), and this policy does not seem compatible with the conservation of the snow leopard – Siberian ibex predator-prey system in the Altai Mountains. We advise for including wildlife conservation into government support schemes, enhancing compatibility between livestock rearing and biodiversity. (3) The positive co-occurrence of wolf with livestock draws attention on the potential for human-wildlife conflicts. Indeed, Augugliaro et al. (2020) found that wolves were responsible for most livestock depredations taking place in western Mongolia. Since wolf predation occurs mostly when herds are left unattended, limiting wolf-human conflicts may require a more constant guarding of herds (Mijidorji et al., 2018). Corrals are generally not used in summer, and this might increment the amount of free-ranging livestock within PAs in this season and increase the risk of nocturnal depredation by predators. We therefore advise for promoting the use of predator-proof corrals year-round.

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Chapter 2. Effects of free-ranging livestock on occurrence and inter-specific interactions of a mammalian community

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Abstract

Mammalian communities inhabiting temperate grasslands are of conservation concern globally, and especially in Central Asia, where livestock numbers have dramatically increased in recent decades, leading to overgrazing and land-use change. Yet, how this pervasive presence of livestock herds affects the community of wild mammals remains largely unstudied. We used systematic camera trapping at 216 sites across remote, mountainous areas of the Mongolian Altai to assess the spatial and temporal patterns of occurrence and the inter-specific relationships within a mammalian community that includes different categories of livestock. By adopting a recently proposed multi-species occupancy model that incorporates inter-specific

correlation in occupancy, we found several statistically strong correlations in occupancy among species pairs, with the majority that involved livestock. The sign of such associations was markedly species-dependent, with larger wild species of conservation concern, namely snow leopard and Siberian ibex, avoiding livestock presence. As predicted, we found evidence of a positive correlation in occupancy between predators and their respective main prey. Contrary to our expectations, a number of intra-guild species pairs also showed positive co-occurrence, with no evidence of spatio-temporal niche partitioning. Overall, our study suggests that livestock encroaching into protected areas influences the whole local community of wild mammals. Though pastoralism has co-existed with wildlife for millennia in central Asian grasslands, our findings suggest that policies and practices to decrease the pressure of livestock husbandry on wildlife are needed, with special attention on large-sized species such as the snow leopard and its wild prey, which seem to be particularly sensitive to this pervasive livestock presence.

Introduction

Species are not distributed at random across space, but form communities whose structure and composition are moulded by biotic interactions (Davis et al., 2018; Wisz et al., 2013). With the dramatic increase of the human footprint on the planet (Venter et al., 2016), however, anthropogenic disturbance, particularly land use change, has become a prominent factor altering interspecific interactions, and even community composition (e.g., Kiffner et al., 2014; Rovero et al., 2020; Suraci et al., 2021). Human activities such as hunting can for example affect mammalian communities through apex predator removal, causing the increase of large herbivore density and in turn a change in vegetation (Hebblewhite et al., 2005). Top-down perturbations can also lead to mesopredator release with higher pressure on small prey and other alterations of ecosystem functioning (Brook et al., 2012; Newsome et al., 2017). Another relevant anthropogenic activity is livestock grazing, as in some regions like central Asia it has increased steadily over the last decades, raising concern over the effects it may exert on communities of wild mammals (e.g., Berger et al., 2013). However, how grazing livestock affects the spatio-temporal occurrence and inter-specific interactions of whole communities of mammals remains largely unstudied.

Mammalian communities inhabiting temperate grasslands are indeed of particular conservation concern globally, as these constitute one of the most endangered and

understudied biomes worldwide, threatened by land use change, overgrazing by livestock, and climate change (Hoekstra et al., 2005; Ritcher & Osborne, 2014; Nunez et al., 2020). Palearctic prairies are characterised by strong seasonal variations in precipitation and temperature, hence in grass greenness and palatability, driving herbivores' use of space (Mueller et al., 2008). On the other hand, pastures are influenced by herbivore grazing: for example, in central Asia pikas (*Ochotona* spp.) and Brandt's voles (*Lasiopodomys brandtii*) impact vegetation community structure and composition through burrowing (Bagchi et al., 2006; Sawamukai et al., 2012). The presence and density of herbivores in turn influence the distribution and abundance of carnivores (Ross et al., 2010a; Chetri et al., 2017). In these grasslands, livestock grazing is a major factor at play, especially in Central Asia where the number of domestic animals has dramatically increased in recent decades following the globalisation in the cashmere wool market (Berger et al., 2013). Detrimental effects of livestock encroachment and competition on mammals have been documented, particularly on wild ungulates (Mishra et al., 2004; Ekernas et al., 2017) and large carnivores (Sharma et al., 2015). However, the overall effect on the whole community of medium and large-sized mammals is poorly understood, and evidence shows that livestock may also alter the interactions among wild species (e.g. Rottstock et al. 2020; Feng et al. 2021).

In this study, we aimed to assess the spatial and temporal patterns of occurrence and the inter-specific relationships within a mammalian community in central Asia that includes livestock. We sampled four areas in remote and rugged environments within the Mongolian Altai mountains through systematic camera trapping on a total of 216 sampling sites. We took advantage of the ability of camera traps to detect multiple species, including domestic ones, simultaneously and at the same spatial scale. We analysed data with a recently proposed multi-species occupancy model that accounts for imperfect detection and incorporates inter-specific correlation in occupancy (Tobler et al., 2019). This analytical approach allowed us to study the effects of both environmental and anthropogenic factors on occupancy at community- and species-level while quantifying the strength of potential interactions among species, as inferred from patterns of species co-occurrence (Richmond et al., 2010).

Our main research questions and predictions were: (1) Is there strong evidence for spatio-temporal interactions between wildlife and livestock? We predicted a generally negative co-occurrence of wild species with livestock. (2) If associations between livestock and wild species exist, are these related to species' body size? We predicted that larger species would display more negative associations with livestock. (3) Do predators and prey in the community

co-occur in space and time? We expected a positive co-occurrence of predators and their respective prey. (4) Is there evidence of intra-guild competition through spatial and/or temporal avoidance? We predicted a negative co-occurrence in space and/or time of species of the same guild as a result of niche partitioning.

Methods

Study areas

This study was conducted in the Mongolian Altai mountains, in the western provinces of Bayan Olgii and Hovd, that are characterised by a mosaic of high plateaus and mountain ranges. The climate is semi-arid, with short summers and long, cold and dry winters. The dominant vegetation cover is steppe grassland, with sparse conifers and shrubs along valley bottoms and lower elevation slopes. We surveyed one area per year during spring (March-June) from 2015 to 2019, except 2016. Study areas (Figure 2.1) included: (1) Siilkhem-B National Park (49°49'N; 89°44'E) in north-western Mongolia bordering Russia, with highest elevation up to 3,900 m a.s.l. This protected area (PA) includes grassland habitat along rocky slopes and sparse larches *Larix sibirica* along valley floors. (2) Tavan Bogd National Park (48°33′N; 88°37′E), in western Mongolia bordering Russia and China; this is the largest PA in Mongolia and hosts the highest mountain of the country (4,374 m a.s.l.). The portion that we surveyed is characterised by alpine and glacial habitat at the highest elevations and grasslands at lower altitudes. (3) Khork Serkhe Strictly Protected Area (47°93′N; 90°99′E), located in Western Mongolia and reaching 4,127 m a.s.l. Its mountainous landscape is shaped by an alternation of slopes and valleys. (4) Sutai massif (46°37′ N; 93°35′ E), which had no legal protection when surveyed in 2019 but was declared a Natural Reserve in 2020. Sutai reaches 4,220 m a.s.l. at the highest peak, covered by the southernmost glacier of the region. More details on sampling areas and efforts are provided in Appendix S2.1.

In the four study areas most inhabitants are nomadic herders. The pastoralists in the Sutai massif belong to the ethnic group of the Mongols, and profess Buddhism, while in the other areas they mainly belong to the ethnic group of the Kazakhs, professing Islam. In the sole Bayan Olgii province, where the first three surveyed areas occur, 2.2 million livestock were reported in 2018, 1.9 million of which were sheep and goats (National Statistics Office of Mongolia, 2019). Large-sized livestock, represented by horses, camels, cattle and yaks, are mostly free ranging, while sheep and goats are guarded by herders and dogs during the day and

held in corrals at night, except in summer (July-August), when usually no fence is used (Augugliaro et al., 2020). Mongolian National Parks are subdivided into three zones with different regulations: special zone, travel/tourism zone, and limited use zone. Traditional pastoralism is only allowed in the limited use zone, whereas it is not allowed at all in the Strictly Protected Areas.

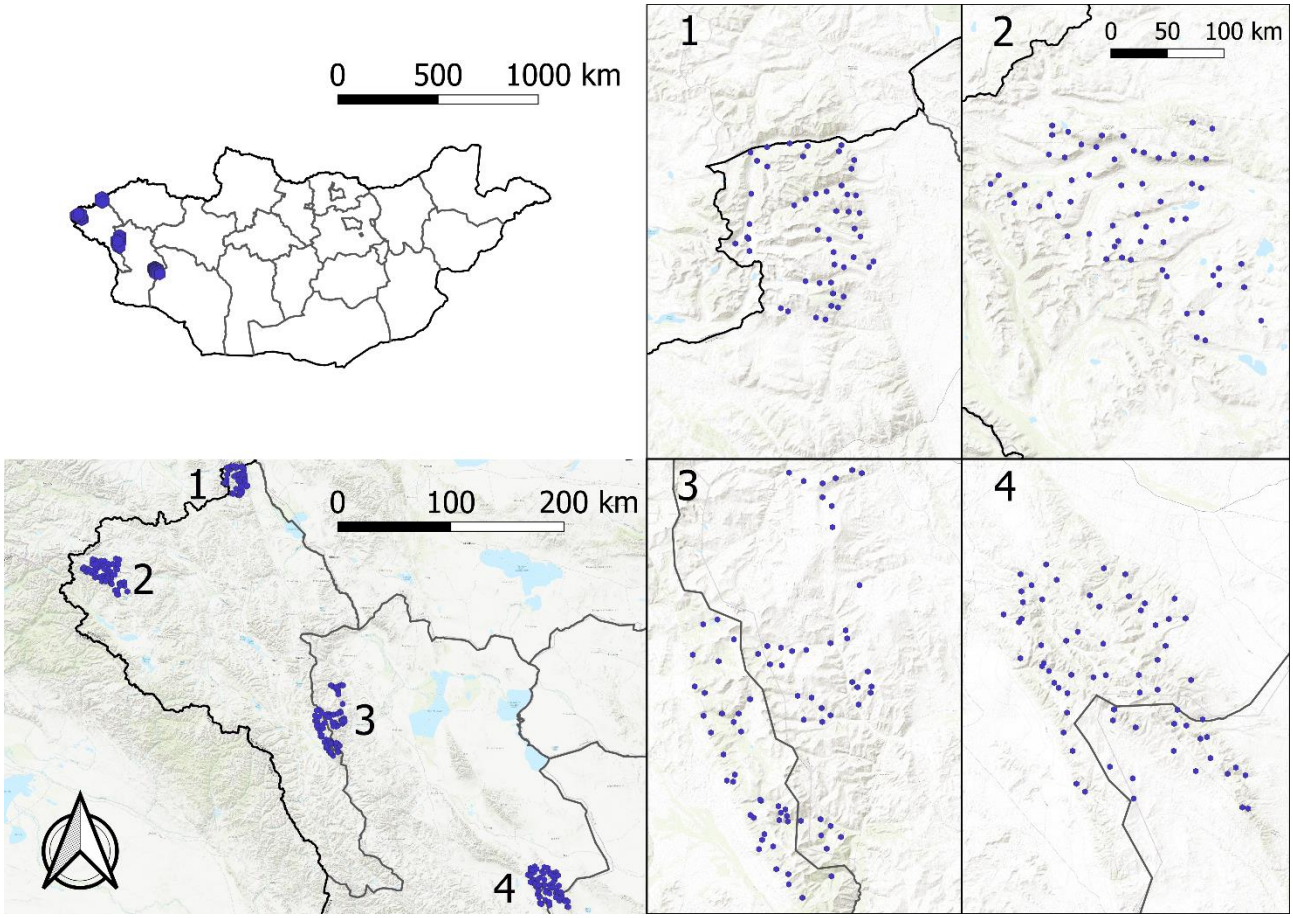

Figure 2.1. Map of the four study areas in the Altai Mountains of western Mongolia where wild and domestic mammals were detected by camera traps at 216 sites (shown as blue dots): (1) Siilkhem-B National Park, (2) Tavan Bogd National Park, (3) Khork Serkhe Strictly Protected Area and (4) Sutai massif. Black lines represent national (thick) and provincial (thin) borders.

Data collection: camera trapping and covariates

For each area we first created in GIS a regular grid with cells of 4 km^2 that aimed to cover at least the minimum extent of 500 km^2 recommended for snow leopard (*Panthera uncia*) population estimate studies (Jackson et al., 2005). Within each cell we located in the field one camera-trap site. The number and locations of chosen sites were constrained by terrain morphology, snow depth and the number of camera-traps available for sampling (see Appendix

S2.1: Table S2.1.1). Two of the PAs were too large to monitor their entirety, thus we selected a portion that we considered optimal habitat for the snow leopard according to previous research and local knowledge. Specifically, in Siilkhem-B we did not sample the southern end of the PA, that includes low elevation and less suitable habitat, and in Tavan Bogd we focused on the north-eastern part of the PA, since the southern part hosts mainly coniferous forests. In Khork Serkhe we sampled the whole PA and surrounding suitable areas, and in Sutai we sampled the entire mountain massif. Overall, the area sampled ranged in size from 513 to 1110 km^2 (Appendix S2.1: Table S2.1.1). As a result, we sampled with camera traps a total of 216 sites (48, 44, 63 and 61 for the four areas, respectively) that ran on average for 65 days each (SD = 20.7). The minimum distance between contiguous sites was 1.5 km. We placed camera traps on small rock piles c. 50 cm above the ground at a distance of approximately 2-4 m from a target trail, setting no delay between consecutive triggers. Sites were usually located on passes, ridges, narrow passages or valley bottoms and were chosen to maximise the detection of snow leopards, which we considered to be the most elusive species. However, our data show that these sites were used by several medium to large sized mammals and by livestock. We did not use any baits or lures. Camera-trap models were of three different manufacturers, characterised by high (Reconyx) and medium (Cuddeback and Bushnell) trigger speed. We annotated camera-trap images using the software Wild.ID (Fegraus & MacCarthy, 2016), and screened the data to derive for each area the checklist of species and their total number of detections. We set the temporal resolution of detections to 1 day, thus repeated detections of the same species on the same day were counted as a single detection event, as is common practice in occupancy modelling.

Using a Digital Elevation Model and a satellite map in the software Quantum GIS (QGIS, 2018) we derived three environmental covariates for each camera trap site: elevation, terrain slope and distance from the closest herders' settlement (consisting of gers, houses, villages or mining camps), whose geographic localization was acquired in the field with a GPS device.

Data analyses

Out of all species detected (Appendix S2.1: Table S2) we excluded those found at only one or two areas, which generally yielded <5 detections (namely *Ursus arctos*, *Lynx lynx*, *Ovis ammon*, *Mustela erminea* and *Sciurus vulgaris*), and focused on the following 12 species of medium to large sized mammals detected across at least three areas: one large herbivore (*Capra sibirica*), 3 large carnivores (*Canis lupus, Panthera uncia, Gulo gulo*), 4 medium carnivores (*Martes foina,*

Mustela eversmanni, Otocolobus manul, Vulpes vulpes) and 4 medium to small herbivores (*Lepus* spp.*, Marmota* spp.*, Ochotona* spp.*, Spermophilus* spp.). The last four were either represented by more than one species of the same genus occurring in different areas (i.e., *Marmota sibirica* was found in all areas except for Tavan Bogd NP where *M. baibacina* occurs, and *Lepus timidus* was found in the first two areas whereas *L. tolai* in the latter two) or occurring in the same area but indistinguishable from one another in camera-trap photographs. Hence, given the similar ecology of these congeneric species we merged them at the genus level. Moreover, we merged the detections of horses, yaks, camels and cattle into the category 'Large-sized livestock' and those of sheep and goats into 'Small-sized livestock'. The subdivision of domestic animals in these two classes is justified by previous research, which found that large and small-sized livestock are managed differently by herders and may therefore affect wild species' spatio-temporal patterns differently (Augugliaro et al., 2020).

We arranged the number of daily detections per species at camera-trap sites into a matrix of n = 216 sites by S = 14 species. We modelled these detections/non-detections using the joint species distribution model with species correlation and imperfect detection developed by Tobler et al. (2019). This framework is an extension of the multispecies occupancy model (Dorazio & Royle, 2005) that explicitly models the residual correlation in species' occupancy probability (c), corrected for imperfect detection. Our modelling approach is detailed in Appendix S2.2.

We tested the effect of study area, elevation, terrain slope and distance from herder settlements on occupancy, and of camera-trap sensitivity and distance from herder settlements on detection probability, both at community and species level. The chosen covariates were not correlated according to Spearman's correlation test ($|rho| < 0.5$). We then calculated the matrix of residual inter-specific correlations in occupancy with their corresponding BCI (Bayesian credible intervals). We implemented the model in a Bayesian framework using JAGS (Plummer, 2003) via R (version 3.6.2; R Development Core Team, 2019) with the package 'R2jags' (version 0.5.7–7; Su et al., 2015). We specified vague prior probabilities for occupancy and detection community hyper-means through normal distributions centred on zero, through uniform priors in the interval from 0 to 10 for the variance of species-specific random effects, and through uniform distributions in the interval -1 to 1 for the latent variables' regression coefficients (except for the mathematical constraints required for parameter identifiability, see Tobler et al., 2019). The regression coefficients of large- and small-sized livestock were not extracted from the community hyper-means, but were instead treated separately, since their

inclusion could have biassed the estimation of the response of the wildlife community to covariates. Community hyper-means are therefore to be interpreted as mean effects for the assemblage of wild species only. We generated three parallel chains of 200,000 iterations with a burn-in of 20,000 iterations and thinning by 10 to derive summaries of parameter posterior distribution. We checked for convergence of the Markov chains based on the Gelman-Rubin statistic (Gelman et al., 1992) and with visual examination of the chains.

To explore the potential relationship between species-specific body mass and the correlation in occupancy with livestock, we regressed the estimated correlation coefficient of each wild species with the two livestock classes against the log of the species' body mass, which we sourced in Smith et al. (2003) and Hayssen (2008).

We also analysed the temporal activity pattern of each species using a non-parametric Kernel Density Estimation function implemented with the package 'overlap' (Ridout & Linkie, 2009) in R. We first extracted independent events by aggregating detections separated by less than 30 minutes, and then created the activity distribution curve of each species. To evaluate potential patterns of temporal avoidance or coexistence between the species in the target community we computed the coefficient of overlap for each pair of species. The coefficient of overlap Δ ranges from 0 (no overlap) to 1 (complete overlap) and is obtained performing pairwise comparisons of diel activity patterns.

Results

Out of the 91 estimated pairwise residual correlation coefficients in occupancy (*c*), 24 had a 90% BCI that did not overlap zero (Figure 2.2). Of the correlations in occupancy between wildlife and livestock of both classes, 12 had a 90% BCI that did not overlap zero (see Figure 2.2 and Figure 2.3), of which 7 were positive (with wolf, red fox, marmot, ground squirrel and hare) and five were negative (with snow leopard, Siberian ibex and beech marten). Snow leopard, Siberian ibex and beech marten occupancies were all positively and mutually correlated (snow leopard – Siberian ibex: c = 0.34 [90 % BCI: 0.11, 0.52]; snow leopard – beech marten: c = 0.44 [0.21, 0.63]; Siberian ibex – beech marten: c = 0.28 [0.09, 0.45]). Pallas's cat occupancy was positively correlated with marmot (c = 0.22 [0.22, 0.61]) and pika occupancies (c = 0.31 [0.05, 0.54]). Pika occupancy was instead negatively related with red fox (c = -0.34 [-0.12, -0.53]), wolverine (c = -0.37 [-0.04, -0.64]) and snow leopard (c = -0.28 [0.05, 0.54]). Red

fox was positively correlated with marmot (c = 0.27 [0.08, 0.46]) and wolf (c = 0.29 [0.07, 0.49]). Finally, ground squirrel and marmot were positively correlated (c = 0.40 [0.13, 0.63]).

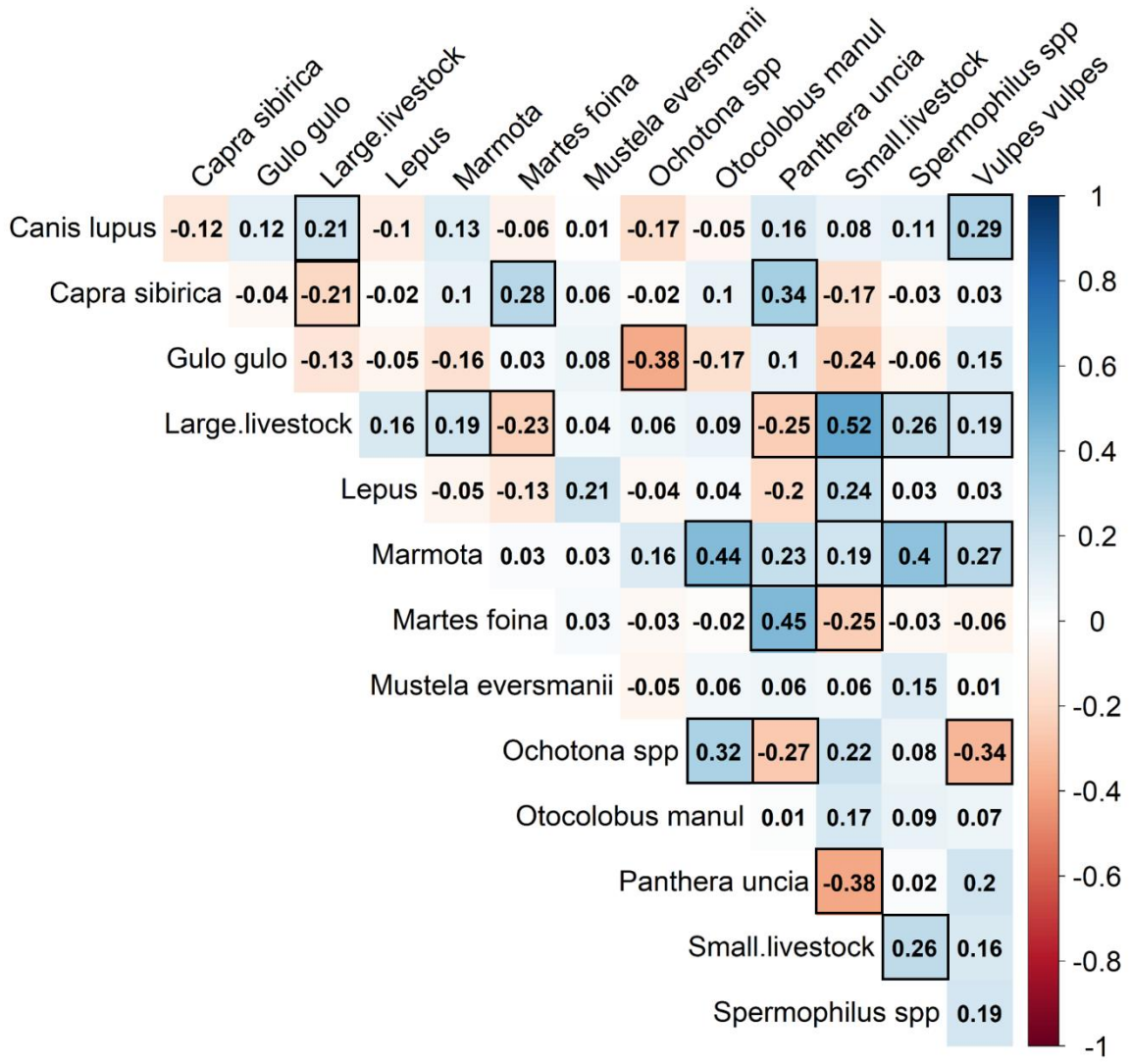

Figure 2.2. Matrix of all inter-specific correlation coefficients (c) in occupancy for wild and domestic mammals detected by camera traps at 216 sites in the Mongolian Altai mountains. Positive correlations are highlighted in blue, negative correlations in red. Species are listed in alphabetical order. Values with a black border are correlation coefficients whose 90% CI did not overlap zero.

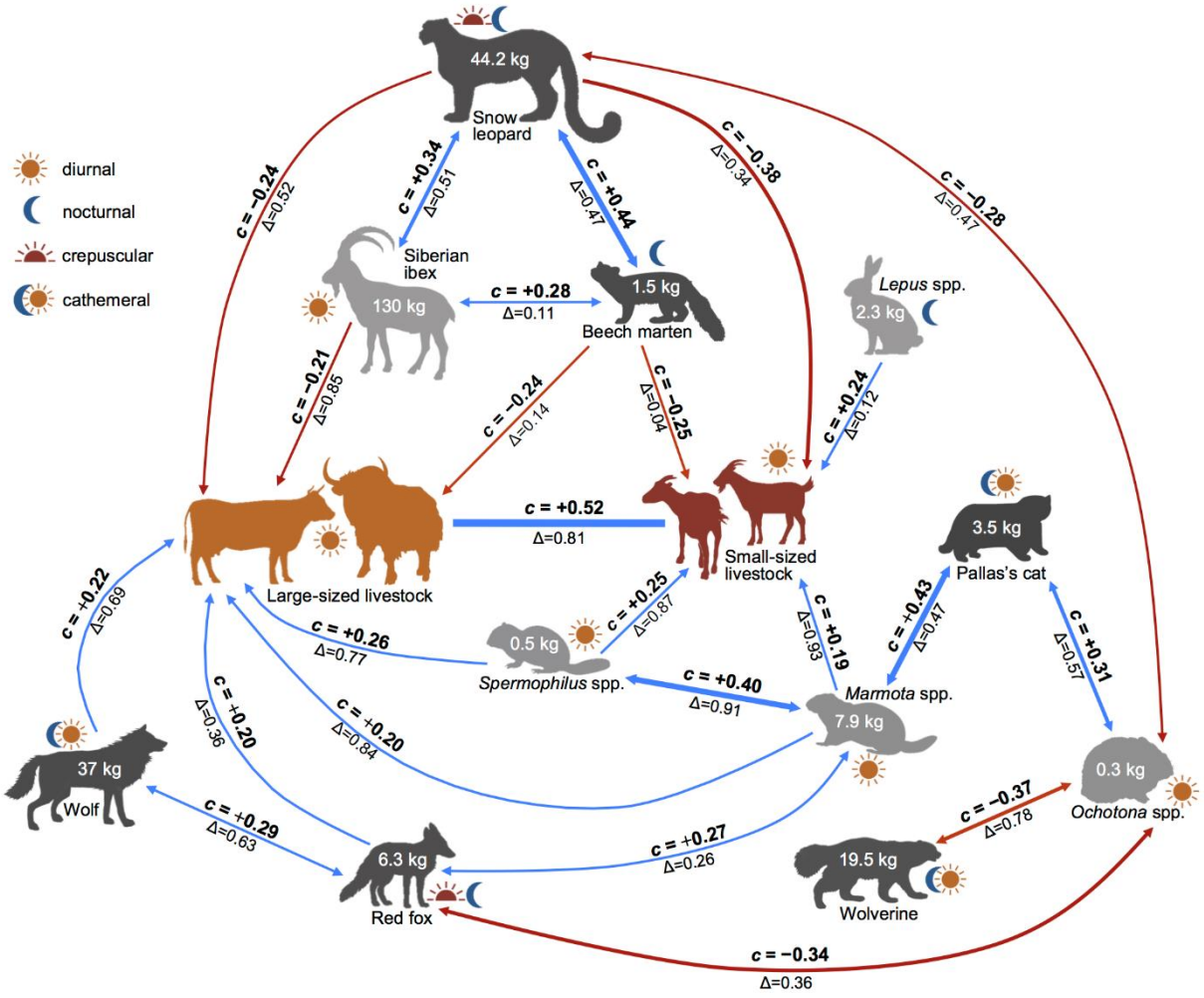

Figure 2.3. Diagram of statistically strong pairwise spatial and temporal interactions among 11 members of the medium-to-large mammal community and 2 livestock categories (large- and small-sized in orange and red, respectively) detected by camera traps in western Mongolia. For each pair of species, the value above the arrow shows the correlation in occupancy (*c*), while the one below is the coefficient of overlap (Δ) in activity patterns (see Data analyses). Arrows are blue for positive spatial interactions and red for negative ones. The average body mass for each species is also reported, along with the main diel activity pattern (see legend). Carnivores and herbivores are in dark and light grey, respectively.

The correlation in occupancy between wild species and livestock appeared negatively related to species body mass, a pattern that was more marked when considering small-sized livestock, as illustrated in Figure 2.4. Hence, larger wild species tended to have a more negative correlation in occupancy with large- and especially small-sized livestock.

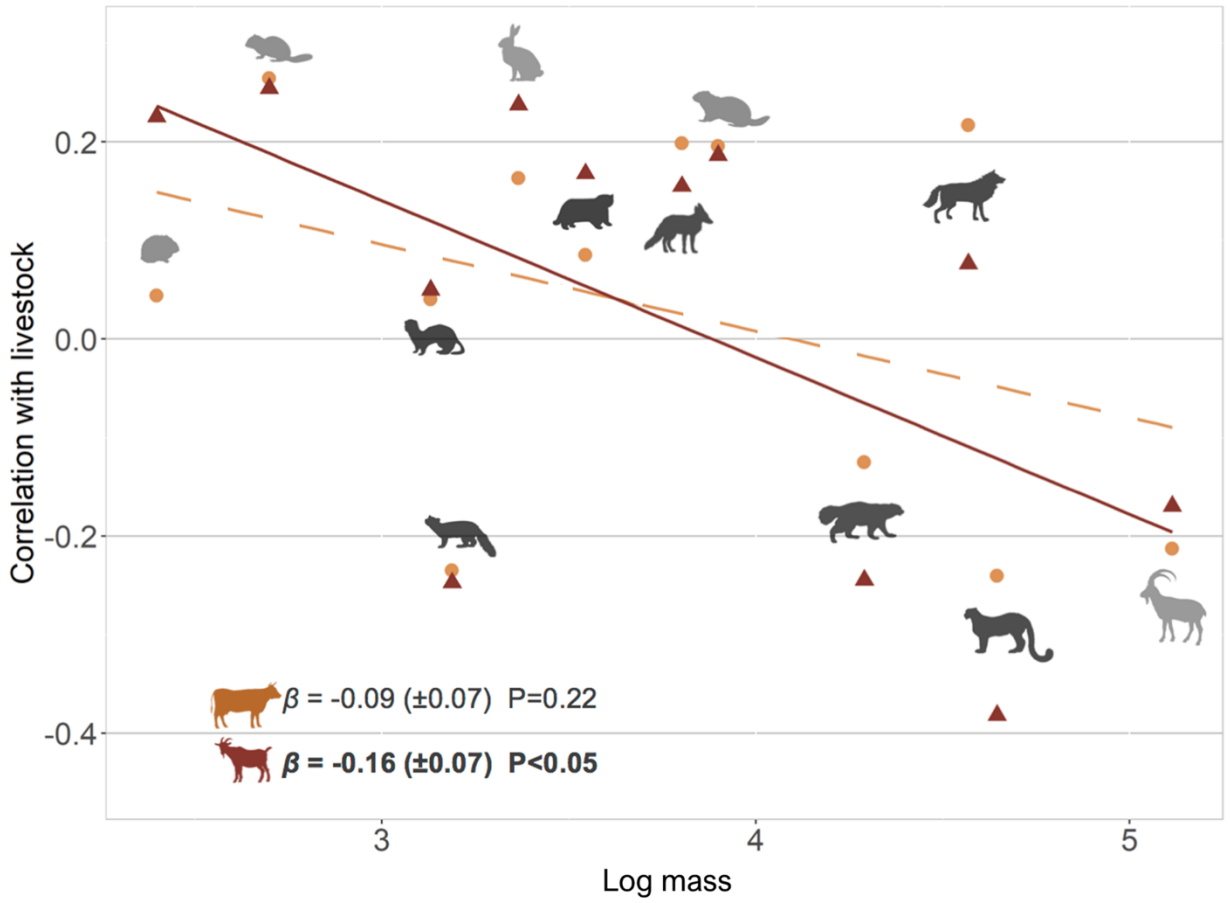

Figure 2.4. Coefficients of correlation in occupancy (*c*) between wild species and livestock detected by camera traps in western Mongolia, in relation to the log mass of each species. Orange circles and red triangles indicate the coefficients of correlation with large and small-sized livestock, respectively. Lines show the regressions for large- (orange dashed line) and small- sized livestock (red full line). See Figure 2.3 for names of the species depicted.

The analyses of diel activity indicated a clear diurnal pattern for both livestock classes. Among wild species patterns were highly variable: from clearly nocturnal (*Martes foina, Mustela eversmanni, Vulpes vulpes*) to fully diurnal (*Marmota* spp., *Ochotona* spp., *Spermophilus* spp.), and more crepuscular species (*Panthera uncia*) or cathemeral species with irregular activity throughout the day (*Canis lupus, Otocolobus manul*). All curves are presented in Figure 2.5. The temporal overlap in activity between livestock and wildlife was low for nocturnal and crepuscular species (in particular *Martes foina, Mustela eversmanni, Lepus* spp., *Panthera uncia*) while it was high for diurnal species (such as *Capra sibirica, Marmota* spp., *Ochotona* spp., *Spermophilus* spp.). The small and medium-sized rodents and lagomorphs that presented a high

degree of temporal overlap with livestock also had a high correlation in occupancy with it. Temporal overlap tended to be intermediate between predators and prey (e.g. *Panthera uncia* – *Capra sibirica* Δ = 0.51), while it tended to be more pronounced for species in the same trophic guild (e.g. *Marmota* spp. – *Spermophilus* spp. Δ = 0.91; see Appendix S2.4: Figs. S1).

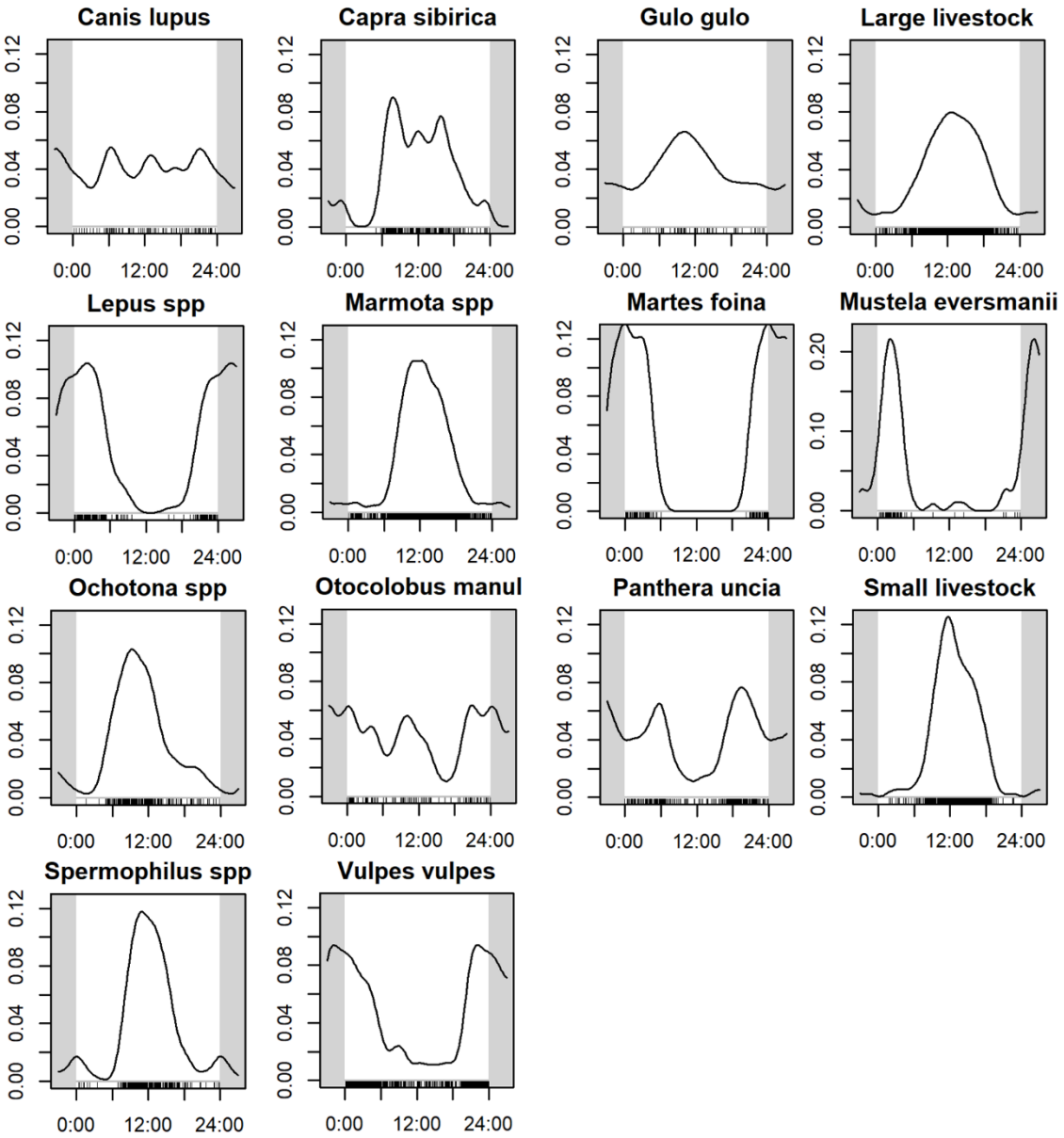

Figure 2.5. Diel activity patterns of wild and domestic mammals detected by camera traps in western Mongolia. Species are listed alphabetically, with Latin names shown above the subplots. The white box indicates the 24-hour diel cycle, with time of day on the x axis, and kernel density estimate of activity on the y axis.

The mean occupancy estimates for the wildlife community in the four areas were very similar, ranging from 0.35 (0.27 – 0.43) in Tavan Bogd to 0.38 (0.24 – 0.53) in Sutai. The regression coefficient for elevation (β_{elev}) on community occupancy was weakly positive, with 90% BCI that overlapped zero (0.06 [-0.03, 0.16]) and species-specific estimates that varied from -0.09 [-0.27, 0.07] for the red fox to 0.18 [-0.01, 0.42] for the wolverine *Gulo gulo* (see Appendix S2.3); as predictable, domestic animals and humans were negatively related to elevation (-0.33 [-0.51, -0.16] and -0.51 [-0.71, -0.32], for large and small-sized livestock, respectively). Community occupancy was also lightly related to terrain slope (β_{slope}= 0.07 [-0.01, 0.14]), with relatively consistent species coefficients. In particular, the effects were positive for both *Capra sibirica* and *Otocolobus manul* with BCI that did not overlap zero (0.12 [0.01, 0.26] and 0.12 [0.01, 0.28], respectively). The coefficients for large and small-sized livestock overlapped zero. The community coefficient for distance from settlements (β_{dis}) on occupancy was positive (0.10 [0.02, 0.18]) but again with interspecific variability, with lowest values for *Otocolobus manul*, *Martes foina* and *Ochotona* spp. (β_{dis} = 0.08) and highest for *Spermophilus* spp. (0.13 [0.03, 0.27]; Appendix S2.3). As predictable, the association was negative for domestic animals, both large- (-0.43 [-0.61, -0.25]) and small-sized (-0.53 [-0.75, -0.32]). Finally, community detection probabilities for medium and high sensitivity camera-trap models were largely overlapping (medium sensitivity: β_{medium} = -3.6 [-4.45, -2.83]; high sensitivity: β_{high} = -3.11 [-3.53, -2.69]). Distance from herders' settlements was negatively related to community detectability (β_{dist} = -0.15 [-0.32, 0.01]; see Appendix S2.3).

Discussion

By using camera-trapping data, activity pattern analysis and a multi-species occupancy model that incorporates inter-specific correlation in occupancy and imperfect detection, we studied the spatio-temporal patterns of occurrence and inter-specific relationships within a mammalian community in the Mongolian Altai.

Each of the 14 species and livestock categories considered showed strong statistical evidence for spatial co-occurrence (i.e., 90% BCI of *c* that did not overlap zero) with at least another species, with the only exception of the steppe polecat (*Mustela eversmanni*). Remarkably, of the 13 interactions that each species can display with any other, the largest number of statistically supported ones involved one of the livestock categories (8 and 6 for

large- and small-sized livestock, respectively), while the highest number of interactions involving wild species was five, for both snow leopard and marmot. Considering such scores as a simple measure of the magnitude of spatial co-occurrence among species regardless of their signs, the results support our choice of including livestock in the analysed community, given their widespread presence in the region and the potential influence on wildlife (e.g., Berger et al., 2013; Soofi et al., 2018).

Large areas of Mongolia have been subject to semi-nomadic pastoralism for centuries, but the recent increase in livestock numbers has raised concerns about possible degradation effects (Wesche et al., 2010). While the numbers of cattle and camels remained relatively constant across the country, a steep increase in sheep and goat populations has been recorded since the early 1990s, with the latter likely to represent a greater impact to wildlife than large-sized livestock given their much larger herd size (Hilker et al., 2014). Indeed, we found that the relationship between residual correlation in occupancy of wild and domestic species and wildlife body mass was negative, with a more pronounced effect for the small-sized livestock. This pattern points to a higher sensitivity of larger species to livestock encroachment into protected areas, which is of particular concern for the snow leopard and the Siberian ibex, and more generally mirrors known patterns of size-dependent vulnerability across mammals (Cardillo et al., 2005; Ripple et al., 2019).

We also found that the probability of site use for the community of wild species increased with increasing distance from permanent sources of human disturbance, mainly herder houses/settlements, which adds evidence to the general influence of livestock herding on co-occurrence patterns. Notably, such effect was higher than those of other environmental covariates we considered (elevation and slope). On the one hand, this may be the result of contrasting environmental effects at species level compensating each other in the mean effect values, or as species effects are themselves generally weak it may also reflect the relatively uniform habitat that characterises the target landscapes. On the other hand, inter-specific interactions and anthropogenic disturbance might be more important drivers of species distributions than abiotic variables.

While, as predictable, the correlation in occupancy between large- and small-sized livestock was the highest estimated ($c = 0.52$), it also highlighted differences in site use between the two size classes that support our choice of considering them separately, matching the documented differences in herding practices in the same region, and hence potential impacts on wildlife (Augugliaro et al., 2020). Notably, the snow leopard showed strong evidence for

negative correlation in occupancy with both livestock categories, with the stronger being with small-sized livestock. At the same time, temporal overlap in diel activity patterns was higher with large-sized livestock, consistent with them being generally free ranging, while sheep and goats are held in corrals at night (Augugliaro et al., 2020). The negative correlation in occupancy between Siberian ibex and large-sized livestock (c = -0.21) may indicate a detrimental effect of pastoralism on ibex as a consequence of direct competition for grazing (Mishra et al., 2004; Ripple et al., 2014). Additionally, spatial patterns of interaction among large-sized domestic species and this wild ungulate are possibly sharpened by the high degree of overlap in daily activity patterns (Δ=0.85). Ibex correlation with small-sized livestock was also negative, though statistically weak, while the positive effect of terrain slope on its site use supports the preference of ibex for rugged habitat (Han et al., 2021).

The positive correlation in occupancy between wolf and large-sized livestock (c =0.22) suggests a role of this carnivore in livestock depredations in the region, especially if considering that such spatial association is not compensated by temporal avoidance (Δ=0.69). This is in accordance with an earlier study in the same area that carried out a focal investigation on predator and prey co-occurrence (Salvatori et al., 2021). We acknowledge that a high degree of spatio-temporal overlap does not necessarily indicate prey preference, but it suggests potential for high encounter rates between carnivores and their prey, which is a key component of prey preference (Fortin et al., 2015; Allen et al., 2021). Conversely, no statistically strong spatial correlation in occupancy was detected for the wolf with herds of small-sized livestock. Overall, results are consistent with Augugliaro et al. (2020), who found wolves to hunt preferably large- rather than small-sized livestock based on interviews to herders.

Marmots and ground squirrels showed positive correlations with both livestock categories, consistent with previous research reporting that these species have likely benefited from the recent increase of livestock in Mongolia (Gankhuyag et al., 2021). However, this apparent tolerance of burrowing mammals towards livestock is at odds with the documented severe decline of Siberian marmots (*Marmota sibirica*) in Mongolia in the last decades, possibly related to poaching for the fur market (Batbold, 2002; Kolesnikov et al., 2009) and thus requires further investigation.

As for predator-prey interactions, our results indicated a positive spatial correlation of the snow leopard with its primary wild prey in the region, the Siberian ibex (McCarthy et al., 2016). Similarly, snow leopard site use was positively, although weakly, correlated with that of marmots, which also represent a significant part of its diet (Hacker et al., 2021; Lukarevskiy et

al., 2019). Overall, our results are of relevance for this IUCN-Vulnerable top predator for at least three reasons: (1) they provide an indication of spatial displacement of snow leopards by livestock, especially small-sized, which is concerning given the growth of the cashmere market (Berger et al., 2013; e.g. Tumursukh et al., 2016). (2) Siberian ibex appears as a key driver of occurrence for this carnivore, while there was no strong evidence of an effect of any abiotic covariates on its site use. (3) Snow leopards in western Mongolia may prey primarily on wild prey and kill livestock opportunistically, even where the abundance of domestic animals is at least one order of magnitude higher (Augugliaro et al., 2020; Sharma et al., 2015; Johansson et al., 2015; Hacker et al., 2021). These dynamics markedly differ from what was found in other parts of this predator range (Bagchi & Mishra, 2005; Aryal et al., 2014), supporting the notion that the magnitude of human-snow leopard conflicts is highly context-specific (Snow Leopard Network, 2014). No association emerged instead between wolf and ibex, possibly matching the typical preference of these cursorial predators for structurally less rugged habitat than the one selected by ibex (Suryawanshi et al., 2013). The strong evidence of a positive correlation in occupancy between foxes and marmots (c =0.27) could mirror both direct predation by the fox on marmots and the use of marmots' galleries as refuges/resting sites by foxes (Murdoch et al., 2016). Similarly, Pallas's cat displayed a remarkably high spatial association with marmots (c =0.43), whose cavities the cats depend on as denning and resting sites (Ross et al., 2010b), and also a positive association with pikas (c =0.31), considered the small felid's preferred prey (Ross et al., 2010a).

Concerning intraguild interactions, spatio-temporal overlap between red fox and wolf (c =0.29, Δ=0.63) has been documented in other ecological contexts, where wolves attract foxes through increased opportunities to scavenge (Ferretti et al., 2021), a facilitation also observed in relation to other carnivores such as the Eurasian lynx and the snow leopard (Krofel et al., 2019, 2021). As a complementary result supporting co-occurrence, both canids showed similar environmental and anthropogenic covariate effects on site use. On the contrary, no spatial association or avoidance was observed between the two felids, the snow leopard and the Pallas's cat, probably reflecting low dietary niche overlap and infrequent interactions among them. The clear spatio-temporal association between ground squirrels and marmots (c =0.40, Δ=0.91) is not surprising given that they belong to the ecosystem engineering group of colonial-living burrowing animals in grasslands, and they likely present very similar habitat preferences.

As general limitations of our study we acknowledge that: (1) the sampling design was aimed at maximising snow leopard detections, potentially biassing detections of other species and limiting the spatial extent of our inference to the sites sampled; (2) we interpreted occupancy as the probability of site use by the species, given the marked differences among species in home range and movement patterns relative to our sampling design (Neilson et al., 2018), and considering that 'true' occupancy estimates in continuous habitat depend upon the product between the density of the target species and its home range area (Efford & Dawson, 2012); (3) Given the generally high sensitivity of the camera traps we used, the probability of detecting a species was likely largely dictated by its availability for detection (Kéry & Schmidt, 2008), namely by how often a species passed through the camera's detection zone, given that the camera was located within the home range of one or more individuals of that species; (4) the residual correlations in occupancy we estimated may not entirely reflect actual interactions, as they could also be caused by unaccounted differences in habitat use due to missing environmental covariates (Tobler et al., 2019). While limitation 1 is unlikely to affect our inference, given that the sites chosen were used by multiple species of the target community, limitation 2 should be taken into account when interpreting our results. Our sampling design potentially led to overestimate the proportion of area used by species with large home ranges and high mobility (for example snow leopard, wolf and livestock), while underestimating the proportion of area used by species with small home ranges and short distance movements (such as rodents and lagomorphs; Neilson et al., 2018; Efford & Dawson, 2012). This in turn may inflate the positive co-occurrence between species with large home ranges, since they have a higher probability of being detected at the same sampling sites though the home range overlap might, in reality, be limited. Limitation 3 may bear minimal effects on our results, since the duration of our surveys likely allowed to gain a good representation of the asymptotic proportion of area used by each species, i.e., individuals had enough time to cover a consistent proportion of their home range. Regarding limitation 4, we cannot rule out that the inclusion of other abiotic covariates in our model might have changed the output for the biotic relationships. However, the target ecosystem is characterised by low vegetation diversity and most environmental variability derives from topography, which we accounted for by including elevation and terrain slope in our model.

In conclusion, systematic camera trapping proved a valuable tool to study the interspecific relationships within a community of wild and domestic mammals inhabiting remote and hardly accessible mountain landscapes. In line with our predictions, livestock

encroaching into protected areas influenced the whole community of wild mammals, with their average probability of occurrence increasing away from herders' settlements, and a predominant number of potential spatial interactions involving livestock. The sign of the co-occurrence of livestock and wildlife was species-dependent, with larger-sized species that generally showed a tendency to avoid livestock (with the remarkable exception of the wolf that often prey on it), while rodents and lagomorphs tended to positively co-occur with it. As predicted, predators and their focal prey generally had positive correlation in occupancy, while, contrary to our expectations, a number of intra-guild species pairs also showed positive co-occurrence, with no evidence of spatial or temporal niche partitioning, and further, focal investigations are needed to clarify if this pattern is caused by the use of similar resources by species of the same guild. Though pastoralism has co-existed with wildlife for millennia in central Asian grasslands, our findings suggest that the recent dramatic increase in livestock numbers calls for new policies and strategies to decrease the pressure of livestock husbandry on wildlife communities, with special attention on large-sized wild mammals, namely snow leopard and Siberian ibex, which seem to be potentially more sensitive than smaller mammals to the pervasive presence of domestic animals.

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Part 2. Effects of human outdoor recreation on communities of wild mammals

Chapter 3. Crowded mountains: long-term effects of human outdoor recreation on a community of wild mammals monitored with systematic camera-trapping

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Abstract

Outdoor recreation in natural areas has become an increasingly popular activity globally, yet the long-term effects on wildlife are poorly known. Reconciling human access to nature and wildlife conservation requires sound evaluations of how outdoor activities affect biodiversity in space and time. We aimed to contribute to this topic by asking whether tourism in the world-renown Dolomites, Italy, affected wild mammals in the long term, and if it elicited spatial or temporal avoidance. We detected mammals by systematic camera-trapping over seven consecutive summers at 60, consistently sampled, sites and estimated trends in occurrence at community and species levels through a dynamic community occupancy model, combined with

site use intensity and an index of nocturnality. Overall, 70% of the 520,000 images obtained depicted humans, whose presence intensified over the 7-years period. Nonetheless, both community and most species-level occurrences increased. However, human activities caused a strong temporal avoidance in the whole community, especially in most disturbed sites, while spatial avoidance was observed only for bigger-sized species.

Introduction

Natural areas have become popular destinations for outdoor recreation across the globe (Bell et al., 2007). By reconnecting people with the natural world, recreation in natural areas plays a crucial role in an increasingly urban society, bringing well-known benefits to human mental health (Coventry et al., 2021). Nature tourism is also a conspicuous source of revenue for local economies (Kuenzi et al., 2008), and attracting outdoor tourists has increasingly become a key aim of protected areas, alongside nature conservation (Eagles, 2014). However, as demand for nature tourism continues to rise globally, there is growing concern on the possible side effects on wildlife (Winter et al., 2019). Humans not only exert direct impacts on ecological communities by structurally modifying the landscape through infrastructure building and soil sealing but also through their widespread presence in natural areas, and these two types of pressures might have distinct effects (Nickel et al., 2020). Indeed, in areas where human-induced mortality of wildlife occurs, people are generally perceived by wild animals as super-predators (Clinchy et al., 2016; Smith et al., 2017) and generate a landscape-of-human-fear that shapes wildlife behaviour and habitat use, and ultimately ecosystem processes (Mendes et al., 2020). In particular, by altering animal spatial behaviour and activity rhythm, humans can disrupt feeding and reproductive activities and lead to reduced fitness and decreased abundance (Larson et al., 2016; Lott et al., 1995).

While natural areas are increasingly crowded by recreationists in many parts of the world, a parallel trend in spontaneous afforestation is taking place especially in Eurasia: here forested areas have steadily increased since the 1970s (FAO, 2022), with potential advantages for forest mammals. Particularly in Europe, the decline in mountain agriculture and the concentration of human settlements in densely populated urban areas has allowed the ecological succession to evolve towards more mature stages in the abandoned areas (Falcucci et al., 2007). Forests have thus reclaimed the lands that rural communities anciently cleared to obtain pastures and crops (Camarretta et al., 2018). This phenomenon has concomitantly

allowed the re-expansion of many forest-dependent animal species, and in general of wildlife seeking shelter from human disturbance (Regos et al., 2016). Many mammal species have benefitted from the growth in tree cover in Europe, and are currently re-gaining parts of their formerly wide and continuous distribution across the old continent (Chapron et al., 2013), through a rewilding process (Helmer et al, 2015). Two different tendencies are thus affecting forest mammals in Eurasia: on one side they are benefitting from an expansion of their potential habitat, but on the other this habitat is being increasingly visited by humans engaged in outdoor leisure activities, with potential negative impacts. The net result of these two conflicting drivers on wild mammals largely depends on the magnitude and spread of disturbance, both in space and time, and on the ability of wild species to adjust their behaviour to cope with human presence (Blanc et al., 2006).

Wildlife can respond to human recreational activities within natural areas through three main, non-mutually exclusive, strategies: spatial avoidance, by modifying their movement patterns eluding areas more intensely visited by people; temporal avoidance, by shifting their activity to the days or time of day when humans are less active; behavioural avoidance, e.g. increasing their vigilance rate when closer to human activities. At the spatial level, the presence of humans in the landscape often influences individual movement patterns through a downsizing of the home range to exclude the surroundings of disturbance sources, which ultimately can lead to a large-scale cumulative habitat loss for the whole population (Plante et al., 2018; Richard et al., 2016). At the temporal level, wild mammals are increasing their level of nocturnality to cope with a pervasive presence of humans during daylight (Gaynor et al., 2018). In addition, several studies reported a decrease of animal activity during weekends, when the flow of people involved in outdoor recreation peaks (e.g., Pelletier, 2006). The proximity to sources of human disturbance influences also the level of vigilance and consequently physiological stress: for example, the levels of the stress hormone cortisol in roe deer was found to be negatively related to the distance from human settlements and infrastructures when human activity is higher (Carbillet et al., 2020). Red deer vigilance rate is more strongly related to the vicinity to human activities than to natural predators, resulting in a decrease of the time spent feeding when closer to human disturbance (Ciuti et al., 2012). Mammals often combine these avoidance strategies, for example exploiting areas rich in forage but more exposed to humans during the night and taking shelter in wooded areas during daylight (Salvatori et al., 2022). Though the responses to human presence have been widely studied at the level of single species and for short time span, knowledge on the long-term effects

at the level of biological community is still scarce (Ahumada et al., 2013). Indeed, a systematic review (Marion et al., 2020) found that studies on the effect of human disturbance on animals are mostly focused on a single species, and have seldomly exceeded a duration of two years.

In this study, we used systematic camera-trapping in 7 consecutive summers, from 2015 to 2021, to study the long-term effects of human outdoor recreation on a community of 8 medium to large sized mammals in a highly touristic area of the central Alps, aiming to test whether the community of species was affected by the amount of human outdoor activities resulting in a long-term decrease in the proportion of area occupied (occupancy; Hypothesis A1). Alternatively, despite the intense and diffused human presence in the area, the strategies adopted by the mammal species may result in a stable community occupancy in the long term (Hypothesis A2). Moreover, we aimed to evaluate if the mammalian community responded to the pervasive presence of humans mainly by spatially avoiding sites more heavily visited by recreationists (Hypothesis B1), or by adjusting their temporal activity to avoid the overlap with human activities, diminishing the probabilities of encountering people (Hypothesis B2). The strategies of spatial and temporal avoidance might also be applied simultaneously, by avoiding humans both in space and time (Hypothesis B3).

Materials and methods

Data collection

We conducted the camera trap surveys during seven consecutive summers, from 2015 to 2021, each year between the first week of June and the last of August. The study area covers about 220 km^2 and is located in Trento Province, NE Italy (centred on 46◦ 06 45”N and 10◦ 55 50”E), partially including the regional park “Parco Naturale Adamello Brenta” (PNAB), and coincides with the core area of the brown bear population of the central Alps, that was reintroduced here in the early 2000s (Tosi et al., 2015). This area is a major touristic destination for hiking, mountain biking and outdoor recreation in general, with around one million visitors each year and 100,000 vehicle passages in the main valleys (ISPAT, 2021). The study area has a dominant mountainous terrain (300–2800 m a.s.l.) with a vegetation composition that ranges from mixed broad-leaved and coniferous forest, dominated by common beech (*Fagus sylvatica*), European larch (*Larix decidua*) and pine (*Pinus* spp.), to subalpine forest communities dominated by pine, spruce (*Picea excelsa*) and silver fir (*Abies alba*). At about 1800 m the vegetation becomes

dominated by mountain pine (*Pinus mugo*) and open habitats comprised of alpine herbaceous species. The climate varies from continental to alpine, in relation to altitude.

The sampling design derived from the Tropical Ecology Assessment and Monitoring Network (TEAM Network, 2011; Jansen et al., 2014), a pan-tropical biodiversity monitoring program (Rovero and Ahumada, 2017). In the first year of the study, we designed a regular grid with 4 km^2 cell size in which we placed 60 camera-trap stations, one per cell, evenly spaced and positioned to cover an altitudinal gradient from 500 to 1900 m a. s. l. We randomly selected one forestry road or trail within each cell and placed a random point on it. These points were then adjusted in the field based on accessibility. We placed 30 sites on trails and 30 on forestry roads, and positioned camera traps on trees at about 60 cm above the ground and a distance of 3-5 metres from the target trail or road. The 60 sampling sites chosen in the first year of the study were kept unvaried for the following years. For more details on the study area and sampling design see Oberosler et al. (2017). In all years we deployed the same camera-trap model Reconyx HC 500 (Reconyx Inc., Holmen, WI, USA) with a 0.20 s trigger delay, except for the first year, in which we also deployed UOVision UV572 IR+ (UOVision Technology, Shenzhen, China) with 1 s trigger delay in half of the sampling sites. The possible effects on detection performance were accounted for by including a camera model covariate in the observation component of our occupancy model. The pictures collected were annotated at the species level by the authors through the software Wild.ID (Rovero and Zimmermann, 2016). Our results are therefore limited to the spatio-temporal use of trails and roads by wild mammals and humans, and not of the whole study area. Indeed, Tanwar et al. (2021) found that camera-traps placed on trails gave different estimates of relative abundance and activity patterns compared to randomly placed cameras. However, they also concluded that study designs that exploit trails are more cost effective and efficient, especially at detecting carnivores, which are seldomly detected by randomly placed cameras, and that they can provide robust assessments of temporal trends. In addition, the choice of sampling trails and roads was functional to our aim of simultaneously monitoring wildlife and human site use to assess the potential effect of human disturbance on wildlife.

We defined our mammal community as composed of eight species of body mass greater than 500 g, that were also the species regularly captured by our camera-trap array. Since beech marten *Martes martes* and stone marten *Martes foina* cannot be distinguished with certainty from camera-trap pictures and the two species are sympatric in the Italian Alps (Fonda et al., 2021), we merged these two species at the genus level. This resulted in the following species

being modelled: *Martes* spp., *Lepus europaeus, Vulpes vulpes, Meles meles, Capreolus capreolus, Rupicapra rupicapra, Cervus elaphus* and *Ursus arctos.* The grey wolf *Canis lupus*, that is currently naturally recolonizing the study area, was detected in 5 total events during the 7 years of the study, therefore we could not include this species in the analysis due to the low number of detections.

We calculated the average number of independent events in the monitoring period for each species (including humans and domestic animals, this latter category being composed by dogs, cows, sheep, goats, horses, donkeys, llamas, and domestic cats), defining events as photographic sequences separated by at least 15 minutes (Rovero and Zimmermann, 2016). The number of events was then converted into a Relative Abundance Index (RAI) dividing it by the number of sampling days and multiplying by 100. In this manner, RAIs summarise the average number of independent events every 100 days of sampling, for each species. We calculated RAIs for humans in each sampling year, to qualitatively consider possible trends, and assessed whether the presence of humans was different inside and outside the PNAB protected area through a Wilcoxon sum rank test on the RAI values. To explore the relative abundance of the species composing our target community we calculated yearly RAI values and their mean across the seven years with both independent events separated by a 15-minute interval and daily detection events.

Spatial analysis

To assess whether the use of camera-trapping sites by the mammalian community was influenced by the amount of human activity and by the vicinity to human settlements we used two methods: first, we applied a community dynamic occupancy model (Dorazio et al. 2010) in a Bayesian framework; second, we applied General Linear Models (GLMs) to the site-level cumulative number of independent photographic events of each species. We used these two methods to gain a complete picture of mammals' space use: occupancy modelling utilises binary 'presence-absence' data (0 for a non-detection and 1 for a detection) to estimate species and community level occurrence and its trend over time, corrected for imperfect detection, but does not differentiate much between intensely used sites and sites visited only seldomly, which both represent a 'presence' and therefore are usually assigned high occupancy probability. Since animals can respond to human presence not only through complete spatial segregation but also by modulating their site use in response to that of humans, we also modelled the number of photographic events to evaluate the intensity of site use by mammals and which anthropogenic and topographic variables affect it. This latter method does not account for imperfect detection.

The dynamic occupancy model has a hierarchical formulation, that accounts for variation in detection probability to estimate a corrected occurrence probability for the first year of the study, and estimates the yearly probability of persistence and colonisation at each site from the second year. All species-level parameters were modelled as random effects from a common distribution for the biological community under study, so to obtain both species and community level estimates. In the ecological process model the presence/absence of a species k at a camera-trap point i in the first year is an unobserved latent variable Z_{ik1} resulting from a Bernoulli process with expected probability Ψ_{ik1}: $Z_{ik1} \sim \text{Bernoulli}(\Psi_{ik1})$. For the first year of observations, occupancy (Ψ_{ik1}) was modelled as a function of covariates using a logistic link: $\text{logit}(\Psi_{ik1}) = \beta X_{ik}$ where X_{ik} is a matrix of covariates, and β is a vector of regression parameters to be estimated. In the following t years, a site remains occupied by the species with probability Φ_{ikt}, or becomes unoccupied with probability 1- Φ_{ikt}, where Φ_{ikt} is the persistence probability of species k in site i from year t-1 to year t, and 1- Φ_{ikt} is the probability of site i becoming unoccupied by species k in year t. If site i was not occupied by species k in year t-1 ($Z_{ik(t-1)} = 0$), the species can colonise this site by the following year t with probability γ_{ikt}. The temporal dynamics in occurrence probability of species k in site i can be described as:

$$\Psi_{ikt} = Z_{ik(t-1)}\, \Phi_{ikt} + (1 - Z_{ik(t-1)})\, \gamma_{ikt}$$

The persistence probability Φ and the colonisation probability γ were modelled as a function of site-specific, year-specific, and site-year specific covariates using a logistic link as described above. The observation sub-model assumes the observations for each species k at each sampling point i and year t, Y_{ikt}, as realisations of a Binomial process with mean $Z_{ikt}\, p_{ikt}$ where p_{ikt} is the detection probability of species k at site i in year t: $Y_{ikt} \sim \text{Binomial}(Z_{ikt}\, p_{ikt}, e_{it})$, with e_{it} being the sampling effort in terms of number of days in which the camera was active at site i in year t. This formulation accounts for imperfect detection at the sampling site (i.e., false negatives), allowing to model detection probability p as a function of site-specific covariates and therefore providing a corrected estimate of occupancy. Thus, we were able to estimate a probability of occurrence for each species and each year, and to summarise the community occurrence dynamics through the Wildlife Picture Index (WPI, O'Brien et al. 2010). The WPI is a biodiversity indicator based on the geometric mean of relative occupancy estimates derived from camera-trap sampling at a landscape scale. Each species occupancy in a time series is scaled with reference to the first year of the study and is then averaged across the species composing the community through a geometric mean. The WPI can thus indicate whether the community occupancy is decreasing, increasing or is stable during a precise time range. We also

estimated, for each species, the rate of change in occupancy between years ($\lambda_{k,t}=\psi_{k,t}/\psi_{k,t-1}$), which is analogous to the growth rate of a population (MacKenzie et al. 2018). We then averaged these values for each species across the 7-year period to obtain an average growth rate of species-specific occupancy probability with relative confidence intervals.

We used as site covariates distance from the closest town, elevation and terrain slope, that were extracted from thematic maps and Digital Elevation Model (DEM) raster from the Autonomous Province of Trento Geoportal (http://www.territorio.provincia.tn.it) and elaborated through the software QGis (QGis Development Team, 2021). We also used the Relative Abundance Index (RAI) of humans and vehicles (number of independent events divided by sampling days and multiplied by 100), as a site-year covariate on first year occupancy and on persistence and colonisation probability. All covariates were included both at community and species level, linked through random effects. For the detection probability we included distance from towns, track type (trail or forestry road) and camera model (Reconyx or Uovision). All numeric covariates were standardised by subtracting their mean and dividing by their standard deviation, to facilitate the comparisons in coefficient estimates among them.

We ran the model in jags through the R package R2jags (Su and Yajima, 2015) with 3 chains and 100,000 iterations with a burn-in of 20,000 and a number of thinning equal to 5. We checked for chain convergence visually and through the r-hat values (considering a parameter as correctly converged if its r-hat was less than 1.02, Gelman and Rubin, 2003).

To estimate the intensity of site use by each species and which factors affect it, we used Negative Binomial GLMs to regress the total number of photographic events at each site (dependent variable) against sampling effort (expressed as total number of camera-trap days and treated as an offset term), number of human photographic events, distance from human settlements, elevation and terrain slope. We chose negative binomial regression because an exploratory analysis with Poisson GLMs revealed that residuals were overdispersed. For each of the eight mammalian species, we performed a model selection procedure based on Akaike Information Criterion (AIC, Burnham and Anderson, 2002) comparing models with all possible additive combinations of the explanatory variables. When multiple models were within 2 units relative to the one with the lowest AIC value, we performed model averaging to weigh covariate coefficients. The null model was considered the one with sampling effort as the only covariate.

Temporal activity analysis

To assess whether the community of medium to large wild mammals and humans were temporally segregated we modified the approach developed by Patten and Burger (2018). For each sampling site, we merged detections of all the 8 selected species across all years and subsequently categorised them into 4 daily time windows: the first window from 0 to 6 AM, the second from 6 to 12 AM, the third from 0 to 6 PM, and the fourth from 6 to 12 PM. The total number of time windows was therefore equal to the days of sampling at site *i* times 4. To test the null hypothesis of no temporal segregation we calculated a probability of occurrence of mammals M_i by summing all the time windows in which at least one of the eight mammalian species was detected at site *i* and dividing by the total number of time windows in which the camera was active at site *i* (tw_i). In the same way we calculated the probability of occurrence of humans and vehicles H_i. By multiplying the two probabilities we obtained an expected probability of joint occurrence at each site under the null hypothesis of independence of mammals' and humans' detections: $J_i = M_i H_i$. Indeed, If the occurrences of mammals were independent of those of humans, we would expect that the probability of joint occurrence of mammals and humans was simply the product of their separate occurrence probability. Following Patten and Burger (2018), we used a simulation procedure to obtain 1000 simulated joint occurrences of mammals and humans for each site. For each simulation run we obtained a value of expected joint occurrences Exp_i at site *i* through a Binomial distribution with probability J_i and sample size tw_i equal to the total number of time windows for that site: $Exp_i \sim \text{Binomial}(J_i, tw_i)$. Thus, for each site *i* we simulated 1000 values of expected joint occurrence Exp_i. The final site-specific P for the test was taken to be the number of times a simulated Exp_i was less than or equal to the observed number of joint occurrences of mammals and humans Obs_i, divided by 1000, i.e., the total number of simulation replicates. We could thus assess whether at each site the observed number of joint occurrences of mammals and humans was significantly smaller than expected under the null hypothesis of independence. We repeated this approach also considering each wild species separately, to check whether the overall pattern was driven by some species in particular or not (See Appendix S3.2).

To explicitly test whether the rate of nocturnal activity of the mammalian community was influenced by the amount of human frequentation we calculated an index of nocturnality as follows: we divided the number of nocturnal events summing those of the eight wild species at each site in each year by their total number of events in that site and year. A nocturnality index of 0.7 for site *i* in year *t*, for example, would mean that 70% of the events of the mammalian community in site *i* in year *t* were recorded during the night, defined as the time

between sunset and sunrise calculated through the R package *suncalc* (Thieurmel and Elmarhraoui, 2019). We then regressed this index against the site and year-specific RAI of humans and the distance from the closest human settlement, expressing the year as a random effect, to avoid pseudoreplication. We used the beta distribution as probability density function for the mixed model, since this distribution is well suited to model proportional dependent variables (i.e., variables bounded between 0 and 1). We ranked the four possible models (the constant model, the model with human RAI, the model with distance from settlements and the model with both variables) according to the AIC score, and applied model averaging for models within 2 unit of AIC.

Finally, we calculated the cumulative activity pattern of humans and mammals taking the timestamp of independent events, defined as detections separated by at least 15 minutes, through a kernel density estimation with the R package 'circular' (Agostinelli and Lund, 2017) for each year. We estimated the temporal curves separating sites with low human frequentation (below or equal to the 50^{th} percentile of human RAI) and sites with high human frequentation (above the 50^{th} percentile of human RAI). We then estimated the overlap coefficient Δ between the activity patterns of humans and wild mammals at both high and low human passage with the R package 'overlap' (Ridout and Linkie, 2009). To test whether the activity pattern of the mammalian community changed with the rate of human passage, we also calculated the overlap coefficient between the curves of mammals at sites with low and high human passage. In all cases, the estimated overlap coefficient was the Δ_4 since our sample size was larger than 100 events (Ridout and Linkie, 2009).

Results

We collected in total 522,564 pictures of humans and mammals, for an average of 74,652 per year. Net of pictures of camera-trap set-up and blank images, 69.75% were pictures of humans or vehicles, and 21.08% were of mammals (Appendix S3.1). In the 7 years, the average number of independent events of humans (vehicles included) was 7 times larger than that of the most detected wild species, the red fox, and 71 times larger than that of the least detected wild species, the brown bear (Figure 3.1). The number of events relative to humans fluctuated but increased overall in the 7-year time span, from 137 events every 100 days of sampling in 2015 to 212 in 2021 (Figure S3.1.2), and we found no significant difference between the numbers

recorded inside and outside the PNAB protected area (Wilcoxon sum rank test: W = 463, p = 0.25; number of sites inside PNAB = 20, number of sites outside PNAB = 40).

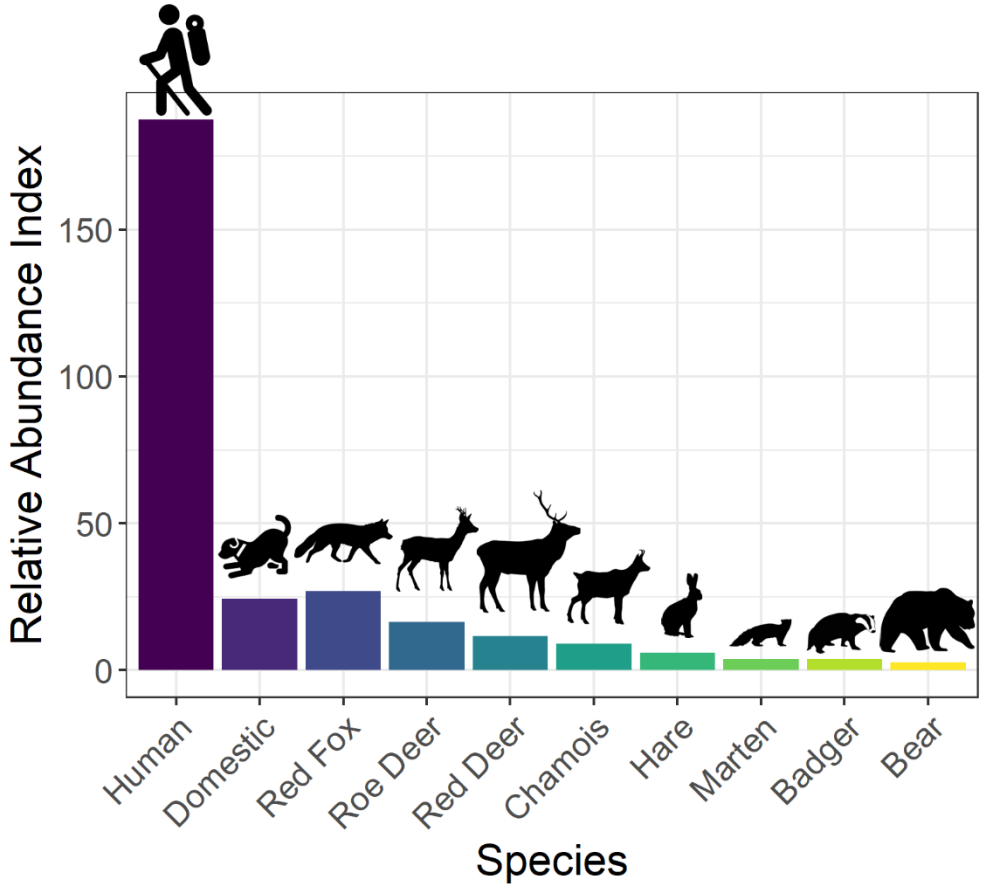

Figure 3.1. The barplot illustrates the average RAI (events normalised by sampling effort) of the 8 wild mammals, domestic animals, and humans (including vehicles) in the 7 years of systematic camera-trapping in the central Alps. Each species/category is indicated by its silhouette and a colour of the scale.

Spatial analysis

All parameters of the dynamic community occupancy model reached convergence, and the R-hat values were <1.01. At the community level, detection probability was not different between trails and forestry roads, was higher for the camera model Uovision IR+, and was not affected by the distance from the closest town. Distance from towns did not have any effect also on community occupancy at first year, nor persistence or colonization. Similarly, at the community level human activity did not affect occupancy at first year, persistence or colonization (Appendix S3.3). At the species level, human disturbance was positively related to first year occupancy for the hare and negatively for the red deer. It had a negative effect on the

persistence of chamois and red deer and a positive one on the colonization of the hare. Distance from towns was negatively related to the colonization probability of hare and red deer. Colonization probability of chamois and hare was positively related to elevation, while that of red deer, roe deer and red fox was negatively related to terrain slope, which was instead positively related to the colonization probability of *Martes* spp. (Appendix S3.3). The WPI had a positive trend, with the estimate for the last year 13% larger than the first one (WPI_{2021} = 1.13; 90% BCI: 1.00, 1.27; Figure 3.2), confirming hypothesis A2 (favorable trend) and rejecting A1 (declining trend). The annual growth rate, averaged across years, and hence the trend in occupancy, was positive for *Martes* spp. (λ = 1.11; 1.04, 1.21; Figure 3.2), brown bear (λ = 1.06; 1.00, 1.14) and red deer (λ = 1.03; 1.00, 1.07), it was also positive, but with 90% credible interval overlapping 0, for hare (λ = 1.04; 0.97, 1.12), badger (λ = 1.04; 0.98, 1.10) and chamois (λ = 1.01; 0.96, 1.07), it was neutral for red fox (λ = 1.00; 0.98, 1.04) and negative, but with 90% credible interval overlapping 0, for roe deer (λ = 0.99; 0.97, 1.02).

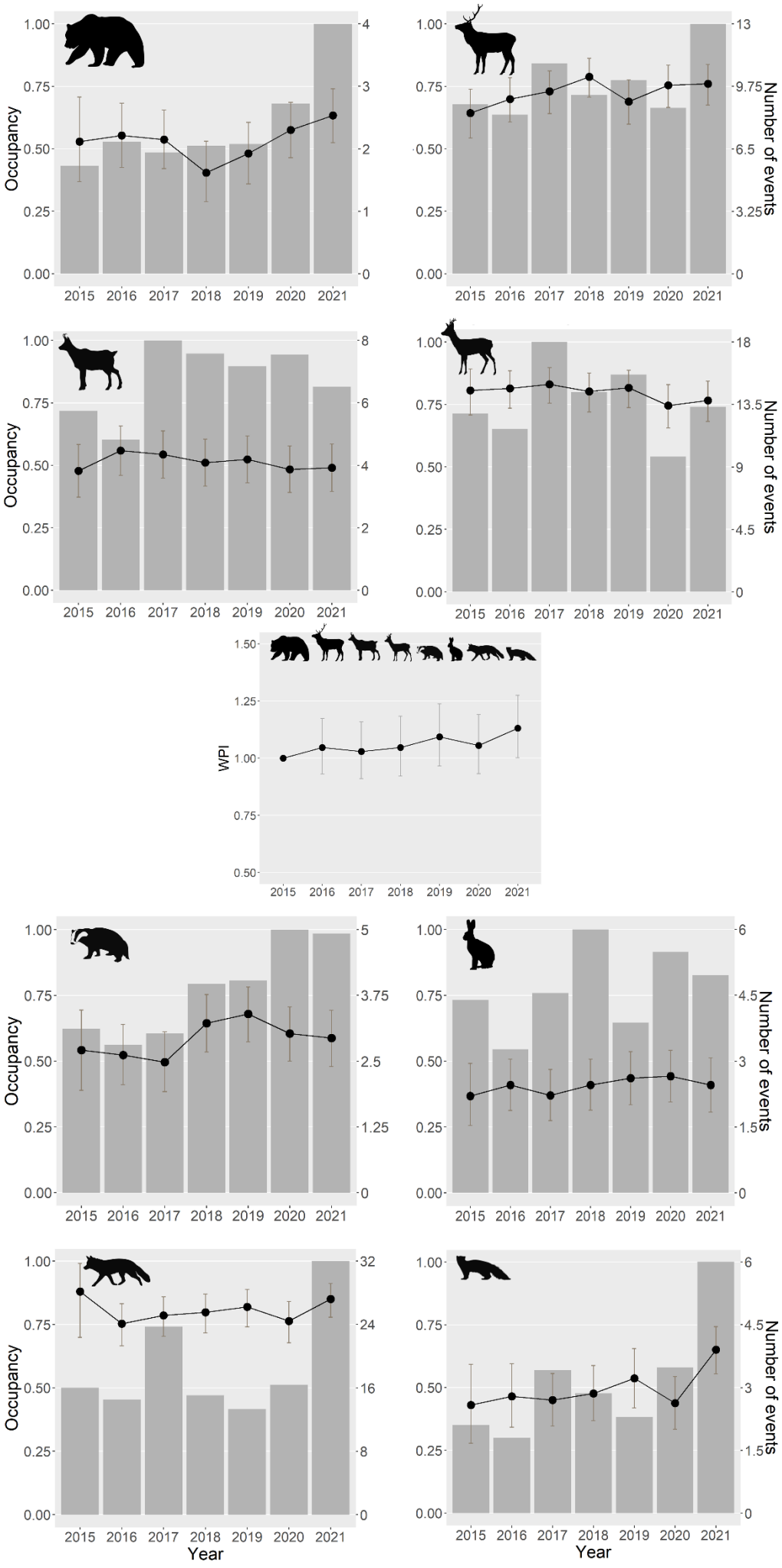
Occupancy
Number of events
WPI
Year
2015
2016
2017
2018
2019
2020
2021

Figure 3.2. Yearly occupancy estimates (black dots) with 90% confidence intervals (grey segments) for the eight mammal species, indicated by their silhouette, monitored by camera-trapping in the central Alps from 2015 to 2021. The background barplots show the number of daily detection events normalised over 100 days, for each year (right y axis). The central panel reports the estimated Wildlife Picture Index (WPI) for the whole mammalian community in each year. The species are ordered by body mass from top left to bottom right.

The GLMs on the number of photographic events showed that human events negatively affected brown bear, red deer and chamois, while it positively affected hare and red fox. Roe deer events were negatively related to those of humans, oppositely to those of *Martes* spp., but in both cases the confidence interval overlapped 0. Human presence did not seem to affect badger events, since the coefficient estimate was 0. The number of events of bear, red deer and chamois tended to increase at increasing distance from human settlements, whereas it tended to decrease for badger, hare, red fox and *Martes* spp., but the relationship was significant only for badger, hare and red fox. Bear and chamois used more intensely sites at higher elevation and with steeper terrain, oppositely to roe deer. The hare had a negative relationship with terrain slope but a positive one with elevation. Red fox was negatively influenced by elevation and *Martes* spp. was positively related with terrain slope (Figure 3.3; Appendix S3.4).

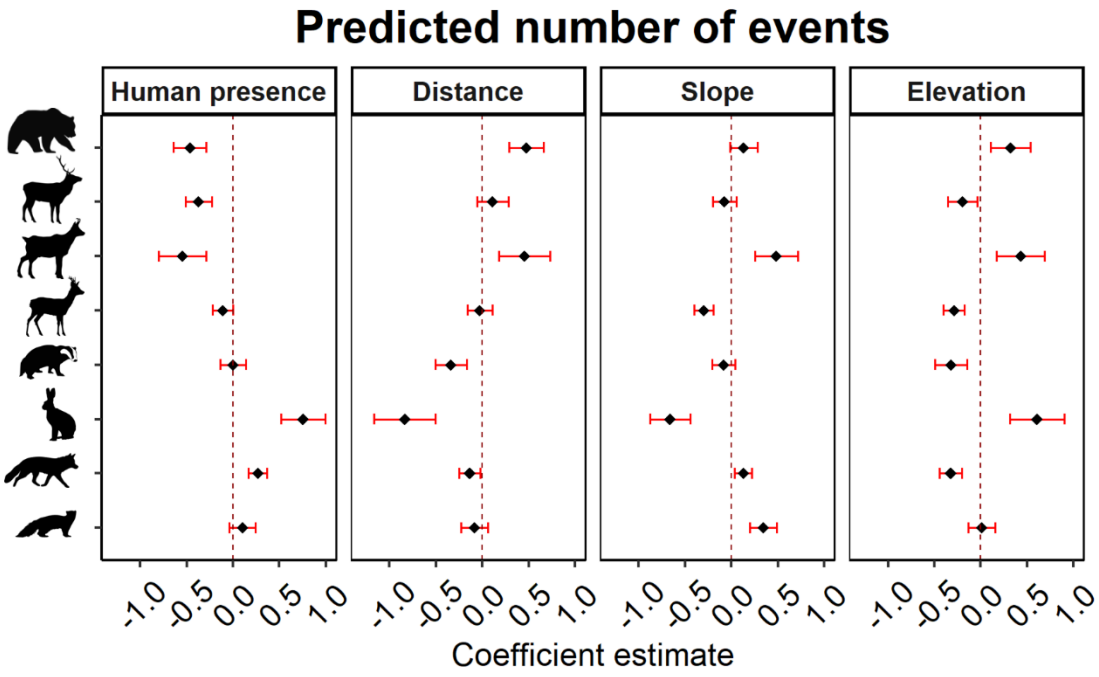

Figure 3.3. The graph illustrates the estimates of the regression coefficients of human presence, distance from settlements, terrain slope and elevation on the independent photographic events of 8 mammalian species, indicated by their silhouette on the y axis. In each variable box, the vertical dotted line corresponds to zero, mean estimates are shown by black diamond and the standard errors by red intervals. Data derive from 7 years of systematic camera-trapping in the central Alps. The species are ordered by body mass from top to bottom.

Temporal activity analysis

In 50 out of 60 sites (83.3%) the number of observed occurrences of both mammals and humans Obs_i in the same time windows was lower than expected under the null hypothesis of independence. In 35 sites (58.3 %) the observed value was statistically lower than the expected value Exp_i simulated through the simulation test (Figure S3.2.1). This pattern was not driven by a few particular species, but was concordant for all species, since all showed on average an observed number of time windows with co-occurrence with humans Obs_i smaller than the expected number Exp_i under the null hypothesis of independence Exp_i (Appendix S3.2).

The index of nocturnality of the mammalian community was negatively related to the rate of human passage (RAI of humans; β_{humans} = 0.24 ± SE 0.06; Figure 3.4) and positively to

the distance to the closest town (β_{towns} = -0.04 ± SE 0.05), with low variance between years (random intercept variance = 0.02).

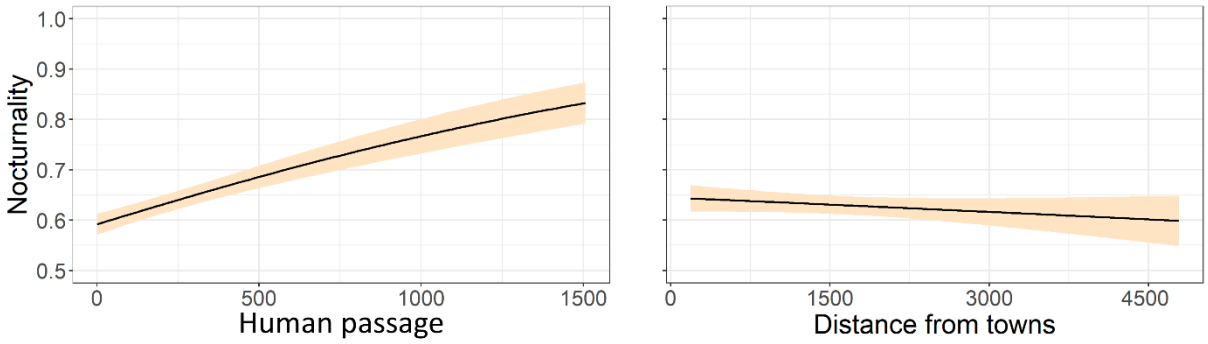

Figure 3.4. Model predictions on the index of nocturnality of the mammalian community in relation to the rate of human passage (RAI of humans; left hand panel), and the distance from the closest town (in metres, right hand panel). A site-specific index of nocturnality of 0.7 means that 70% of the mammalian detections at that site were recorded during the night. The shaded band represents the standard error of the estimate.

The cumulative activity pattern of mammals showed in each year a markedly lower activity level in the middle of the day, in correspondence with the peak of human activity, especially at sites with high human passage and an increase during crepuscular and particularly nocturnal hours. Human activity peaked in the late morning and early afternoon and decreased to almost zero in the core hours of the night (Figure 3.5). The overlap in temporal activity between mammals and humans decreased by more than half where human passage was higher, with Δ = 0.42 (95%CI 0.39-0.43) at low human passage, while Δ = 0.17 (0.16 – 0.19) at high human passage. The temporal curves of mammals at low and high human passage were also significantly different according to a Wald test, confirming that their temporal activity changed in relation to the level of disturbance (W = 13.82, P < 0.001). Hypothesis B2 (temporal avoidance) was therefore confirmed.

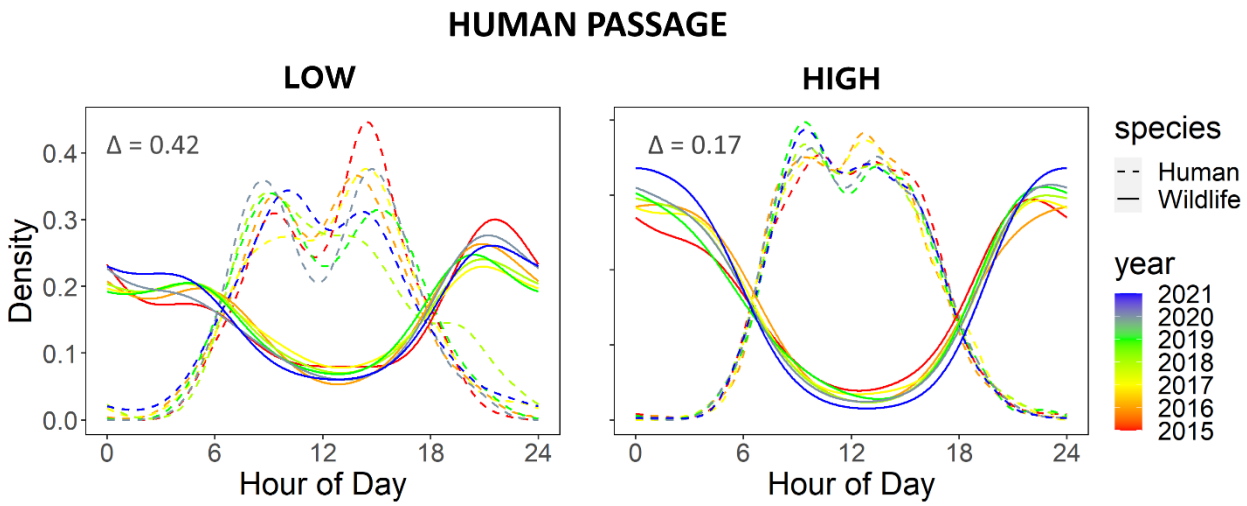

Figure 3.5. Temporal activity curve for humans (vehicles included, dotted lines) and mammals (solid lines) at sites with low (left hand panel) and high (right hand panel) human passage (RAI of humans), obtained by seven years of systematic camera-trapping in the central Alps. The years are indicated by the spectral colour scale: from 2015, red, to 2021, blue. The temporal overlap coefficient Δ between wild mammals and humans is reported in the top left angle of each panel for both levels of human passage.

Discussion

We provided long-term evidence that a community of wild mammals exposed to intense and diffused human presence can increase its occurrence in the long term by temporally avoiding people, confirming hypotheses A2 and B2. A remarkable 70% of the 520,000 camera-trap photographs were of humans engaged in hiking, biking or driving vehicles, with an increase in the number of independent photographic events in the 7 years, which on average were 7 to 70 times larger than those of wild mammals (Figure 3.1 and Appendix S3.1). These data are in line with the increasing trend in outdoor recreational activities in natural areas across the globe (Winter et al., 2019) and indicate a strong potential pressure on wildlife. Yet, that the target community did not show signs of decline emerged clearly: indeed, the Wildlife Picture Index indicated a positive trend. Also, the average growth rates of the single species were mainly positive or neutral, pointing at increasing or stable trends in the use of trails and roads during the seven years. Marten's increase in occupancy was particularly marked in 2021, and this might derive from a peak of small mammals' abundance, and hence prey availability, following

the mast year of beech of the previous year (Pucek et al., 1993). Brown bear positive trend is instead attributable to the ongoing demographic growth following the reintroduction project of the early 2000s and suggests that this species seemingly has not yet reached carrying capacity in the study area, which overlaps with the core area of this population (Tosi et al., 2015; De Barba et al., 2010). The growth in red deer site use is concordant with a more general tendency of range expansion and increasing abundances in Europe (Milner et al., 2006). All other species showed signs of slightly positive or stable trends, except for the roe deer, whose trend in occupancy in the 7 years was slightly negative (though with confidence interval overlapping 0). Though this result cannot rule out a stable trend in the long term, the potential decrease could be attributed to the lower amount of ecotonal habitats derived from the trend of natural regeneration of forest in abandoned agricultural patches (Chirichella et al., 2017), and/or to competition with the bigger sized red deer (Richard et al., 2010).

The relationship of our target species with human outdoor activities seemed to follow a pattern related to body size: bigger-sized species tended to show a negative spatial response, while smaller-sized species presented a neutral or positive one. Brown bear's, red deer's and chamois' site use intensity decreased at sites with higher human activity, while on the opposite extreme hare's and red fox's site use was positively related to human activity, with the intermediate-sized roe deer and badger presenting also intermediate behaviours. Also regarding distance from the closest settlement, the size-dependent pattern seemed to hold: the brown bear and the two bigger ungulates visited more intensely sites at greater distances from towns, while badger, hare and red fox used more often sites at closer proximity to settlements. The preference of chamois for sites at higher elevation and steeper slope, that are instead avoided by the two cervids, matches the known ecological requirements of these ungulates. On the contrary, the predilection of bears for sites at higher altitude and slope might indirectly derive from a strategy to avoid humans, since this species does not possess specific adaptation for high elevation habitats, and occurs also in lowlands where human presence is scarce (Penteriani and Melletti, 2020). The fact that the hare visited more often sites at higher elevation but milder slope might derive from its propensity to exploit open habitats, that in alpine landscapes are usually located in valley bottoms (that we did not monitor) and at higher elevations in mountain pastures. These patterns were in general more evident from the analysis of events than from occupancy modelling, and this suggests that in areas were human recreational activities are widespread, mammals might tune their site use intensity, more than their presence or absence, relative to the rate of human activity.

The impact of human recreation on the temporal activity of the mammalian community was unambiguous, with the number of events of temporal co-occurrence of mammals and humans being lower than expected under the null hypothesis of no temporal segregation. Interestingly, the proportion of nocturnal events of the mammalian community increased with increasing rate of human passage and closer proximity to towns. The curves of activity pattern confirmed this result, showing that the mammalian community reduced by more than half the overlap in activity with humans in most disturbed sites. This strategy is adopted globally by mammals facing intense human activity, resulting in a general shift towards nocturnality (Gaynor et al., 2018). While on one side this behavioural adjustment can ease human-wildlife coexistence by reducing encounter probability, on the other side it may result in deep alterations of natural patterns of activity, with noxious consequences for fitness and population persistence (Griffin et al., 2017; Suraci et al., 2019). Species physiologically adapted to daylight or twilight when active at night can suffer from a reduced foraging efficiency, lower movement and orientation ability, perturbed social interactions (Shamoon et al., 2018; Frey et al., 2020; Ordiz et al., 2013) and suboptimal thermoregulation. In the study area mammals are forced to shift their activity to night hours given that hiking trails and forestry roads are saturated with recreationists during daylight, especially where human outdoor activity is more intense (Figure 3.4 and 3.5).

Therefore, while the temporal segregation with humans seems to be the general strategy adopted by the whole mammalian community, only more sensitive species, as brown bear and the three ungulate species, appear to combine this strategy with a spatial avoidance of people, diminishing their passage at most disturbed sites. Mesocarnivores and the hare instead showed a preference for sites closer to human settlement and a higher tolerance to human passage. These results demonstrate that while smaller-sized generalists, that are able to exploit anthropogenic food sources and to acclimate to human modified habitats, can prosper even in the presence of intense human use of their habitats, bigger-sized species select for more secluded areas to avoid the presence of people. These findings match global patterns of size-dependent vulnerability of mammalian species to past and current anthropogenic pressures (Suraci et al., 2021; Davidson et al., 2009), and point to a higher potential susceptibility of larger species to human recreational activities in natural areas.

The general positive trend in occurrence of the mammalian community despite the exposure to human recreational activities is reassuring for their conservation in the long term. However, we observed similar rates of human disturbance outside and inside the protected

area, suggesting that protected areas in densely populated regions of the world such as western Europe face the risk of becoming "paper parks" under the increasing popularity of outdoor recreation, if human access is not accurately managed (Leung et al., 2018; Ngoprasert et al., 2017). Wauchope et al. (2022) found that globally how a protected area is managed is key in determining its effectiveness in conserving animal populations, and restricting human access can be an important component of the overall management when protected areas are also popular touristic destinations. Indeed, protected areas can attract recreationists from nearby and far away areas, reaching the paradoxical result of increasing human presence, hence potential human disturbance for wildlife, compared to non-protected areas (Fredman et al., 2007; Reed et al., 2008). Though imposing strict regulations on human access can deteriorate local public support for conservation (Michel et al., 2021), management measures to partially restrict outdoor recreation in natural and protected areas have been successfully applied in numerous parts of the world. These include a range of options, from complete closure to the public (Reed et al., 2008), to spatial zoning into areas with different levels of restriction of human and domestic animal access (Stigner et al., 2016; Pineiro et al., 2012), or periodical closure allowing access only during specific time windows (Whittington et al., 2019; Patten and Burger, 2018; Penteriani et al., 2017).

In conclusion, systematic camera-trapping proved a powerful detection tool to study the long-term effects of human outdoor recreation on a community of medium and large-sized mammals in a highly touristic Alpine area. Though exposed to high levels of human presence, the mammalian community increased its occupancy in the 7-year time span, responding by temporally segregating their activities with those of humans, especially in most disturbed sites, showing that mammalian species can exhibit stable and even increasing trends even if exposed to intense human activity. We also found evidence that the bigger-sized species decreased their passage at sites closer to settlements and more intensely visited by people, while mesocarnivores and the hare tended to increase their presence closer to settlements and showed a higher tolerance to human presence. However, it remains to be assessed whether the pressure for increased nocturnality alters feeding and reproductive strategies and inter-specific interactions, with the need for *ad hoc* investigations and possibly the comparison with areas with low human presence. The intensity and spread of human outdoor activities exhort to implement specific management strategies to decrease the impact on wildlife, both at the spatial and temporal level, to avoid impairing the protected areas' mission of conserving biodiversity and functional ecological communities. Finally, our results highlight the

importance of long-term standardised studies to assess changes in species distribution and the effects of human activities on wildlife.

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Chapter 4. The night as a refuge from humans: standardised camera trapping reveals the effects of human presence on mammalian communities across Italian protected areas

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Abstract

Protected areas (PAs) networks are a pivotal tool to conserve nature under the current biodiversity crisis, yet they often suffer a wide range of anthropogenic impacts that can hinder their efficacy in providing safe habitats for wildlife. One emerging and often overlooked threat is outdoor human recreation and nature tourism that can disturb wild animals and prompt

behavioural modifications or range shifts with the potential to affect population dynamics and modify important ecological processes, like trophic cascades and nutrient cycling. We deployed a systematic camera trapping protocol at over 200 sites to sample the community of medium and large mammals in four PAs of the European Natura 2000 network in central and northern Italy to address spatio-temporal responses of wild mammals to human frequentation and proximity to settlements. We detected a total of 18 mammalian species as well as a presence of humans, engaged in recreational activities, in the range of one to two orders of magnitude higher than of wild mammals. By applying multi-area and multi-species models on the number of diurnal, crepuscular and nocturnal detections and on occurrence probability we estimated both species-specific and meta-community level effects, finding that increased nocturnality appears the main strategy that mammals use to cope with human disturbance, thereby diminishing the probability to encounter humans. We also found differences in behavioural responses according to species' body size: larger species tended to avoid humans in space as well as in time, and became more diurnal further away from urban areas. Our results show the effectiveness of standardised field sampling and provide relevant insights for planning the expansion of PAs as foreseen by the Kunming-Montreal Global biodiversity framework. In particular, regulating human access to PAs might be necessary to assure a safe environment for wild mammals and preserve ecological processes.

Introduction

The progressive artificialisation of the planet is eroding and modifying natural habitats through structural alterations of the environment such as deforestation, reclamation, and urbanisation, ultimately resulting in wildlife population declines (Elhacham et al., 2020; Living Planet Report 2022). At the same time humans can influence animal physiological and cognitive processes also through mortality risk perception, noise emission, artificial light and chemical pollution (non-structural alterations). These anthropogenic impacts often co-occur and interact, merging into a complex and multimodal sensory pollution (Halfwerk et al., 2015), impacting wild animals' perception and leading to human-induced behavioural changes, with potentially noxious consequences on foraging and reproductive efficacy, and therefore survival (Wilson et al., 2020; Challéat et al., 2021). Among the top-down effects of humans on animal behaviour, the spatial and temporal modification of perceived risk caused by human presence in the environment can provoke fear responses that often surpass those caused by natural predators

both in magnitude and extent (Ciuti et al., 2012). As super-predators, humans shape a landscape of fear that affects not only herbivore or meso-carnivore behaviour and movement, but also that of apex predators, de facto limiting their ecosystem role as top consumers and disrupting trophic cascades (Wilmers et al., 2021; Wooster et al., 2022; Londber-Holm et al., 2019). Behavioural modifications elicited by fear of humans include increased vigilance and elusiveness (Jayakodi et al., 2008; McBlain et al., 2020), home range contraction (Plante et al., 2018), spatial shifts towards less accessible areas (Richard et al., 2016) and increased nocturnality (Diao et al., 2021). Some biological traits seem to correlate with the sensitivity of mammals to human disturbance and landscape anthropization, particularly large body size, slow maturation, and wide home ranges, due to high energetic and spatial requirements of larger species and a demographic recruitment too slow to counterbalance anthropogenic mortality (Suraci et al., 2021).

The landscape of human fear is not restricted to densely settled areas, but penetrates also into natural and protected areas (PAs), for example when humans visit them for outdoor recreation and nature tourism. PAs are one of the most important instruments in the conservation biology toolbox, and are considered pivotal for the long term conservation of ecosystems under the current biodiversity crisis (Hoffman et al., 2018). However, despite evidence shows that biological communities are faring better within PAs compared to unprotected landscapes (Geldmann et al. 2013; Gray et al. 2016), many PAs suffer from insufficient funding, lack of protection enforcement, ineffective management, urban and infrastructure development (Coad et al., 2019). For these reasons, though legally protected land has increased in the last decades, reaching 15.8% of terrestrial surface (as of November 2022, https://www.protectedplanet.net), this might not directly translate into real improvement in species conservation status if protection remains mainly on paper (Visconti et al., 2019).

One of the most overlooked threats that PAs are currently facing is represented by human disturbance linked to outdoor recreational activities. This pressure is among the most widespread within PAs globally, and is the most frequently reported threat in high-income countries (Schulze et al., 2018). Even if the emphasis on nature protection has progressively shifted towards a multi-functional role of PAs that includes social, recreational, and economic contributions to local human communities (Schmitz et al., 2012; Gavin et al., 2015), recreational and economic activities should be managed not to impair the primary goal of biodiversity conservation (Eagles et al., 2002). Unfortunately, quantitative assessments of the effects of human disturbance on biological communities are often lacking, hindering the implementation

of science-based management strategies to mitigate potential impacts (Marion et al., 2020). In Europe, the Natura 2000 network is the backbone of the EU's Biodiversity Strategy for 2030 (European Commission, 2021), but efficient monitoring and research projects across network sites are generally hampered by a lack of consistency in data collection methods, spatial scales and analytical approaches (McKenna et al., 2014). Yet, drawing generalised conclusions about the effectiveness of the Natura 2000 network and the threats insisting on PAs clearly requires standardised and systematic approaches, whereby the same methodology is applied at the same spatial scale to multiple sites of the ecological network (Lindenmayer et al., 2013).

In this study we aimed to contribute to fill this gap, and sampled mammalian communities within and around four PAs in northern and central Italy through systematic camera trapping carried out during 2020 on a total of 204 sites. We took advantage of the ability of camera traps to detect both wild mammals and human outdoor activities simultaneously, and aimed to evaluate wildlife responses to human presence. Specifically, we addressed the following research questions: 1) Do recreational activities and the proximity to human settlements decrease the probability of site use of mammals? 2) Do mammals adjust their diurnality in relation to human activities and the proximity to settlements? 3) If spatio-temporal avoidance of anthropogenic disturbance occurs, does it depend on species body size? We predicted that increasing rates of human outdoor activities would decrease mammal site use (prediction P1A) and force mammals towards more crepuscular and nocturnal activity (prediction P1B). We also predicted that mammals' use of sites would increase at increasing distance from human settlements (prediction P2A) as would their tendency to diurnality (prediction P2B). Finally, we predict that species with larger body size would display a more evident spatio-temporal displacement by humans (prediction P3A) and avoidance of human settlements (P3B). By rolling out a first network of PAs that implement standardised mammal assessment, we also aimed to evaluate the potential of our protocol and approach to scale-up at national and European level.

Material and Methods

Study areas

In 2020 we surveyed one national park and three regional protected areas in northern and central Italy. The study areas (Figure 4.1) include: (1) Parco Naturale Adamello Brenta (Area 1;

46° 6' N, 10° 56' E), a regional protected area in the central Italian Alps, with highest elevation of 3558 m a. s. l., was surveyed between the first day of June and the last of August. One third of Area 1 is covered by forest, dominated by broadleaved species at lower elevation, which are gradually replaced by conifers from 1000 to 2000 m a. s. l. Above the tree line the landscape is characterised by extensive grasslands and pastures, which precede steep slopes and cliffs of dolomite rocks. (2) Parco Naturale Paneveggio Pale di San Martino (Area 2; 46° 12' N, 11° 48' E), a regional protected area in the eastern Italian Alps, with the highest peak at 3192 m a.s.l, was surveyed between early September and late November. This area is characterised by a vast coniferous forest, bordering a high and rocky dolomitic massif. (3) Parco Regionale Naturale delle Alpi Apuane (Area 3; 44° 4' N, 10° 15' E), located in the northern part of Apennini mountain range, central Italy, with the highest elevation of 1946 m a.s.l., and surveyed from June to November. This mountainous area is detached from the main Apennines ridge and neighbours the Ligurian Sea coast. Area 3 has a typical alpine-like environment, with widespread cliffs and peaks composed of limestone and white marble rocks, whose extraction involves many quarries intercluded and around the protected area. Vegetation is mainly represented by broadleaved woods followed by grasslands above the tree line. (4) Parco Nazionale Foreste Casentinesi (Area 4; 44° 4' N, 10° 15' E), a National Park of 368 km^2 located in the centre-northern Apennines and gazetted in 1993, with the highest peak reaching 1658 m a.s.l. The park was surveyed between early September and late November. The area is characterised by dense forests, in particular ancient fir forests, beech woods, and mixed forests, as well as a sub-montane vegetation area dominated by oak forests and chestnut groves, and pastures at higher elevations. In the core of the park, Area 4 includes Sasso Fratino Integral Nature Reserve, which is a strictly protected biogenetic area and part of the UNESCO World Heritage.

All four areas are popular tourist destinations for outdoor recreation and have an extensive network of forestry roads, hiking and biking trails, and numerous touristic facilities.

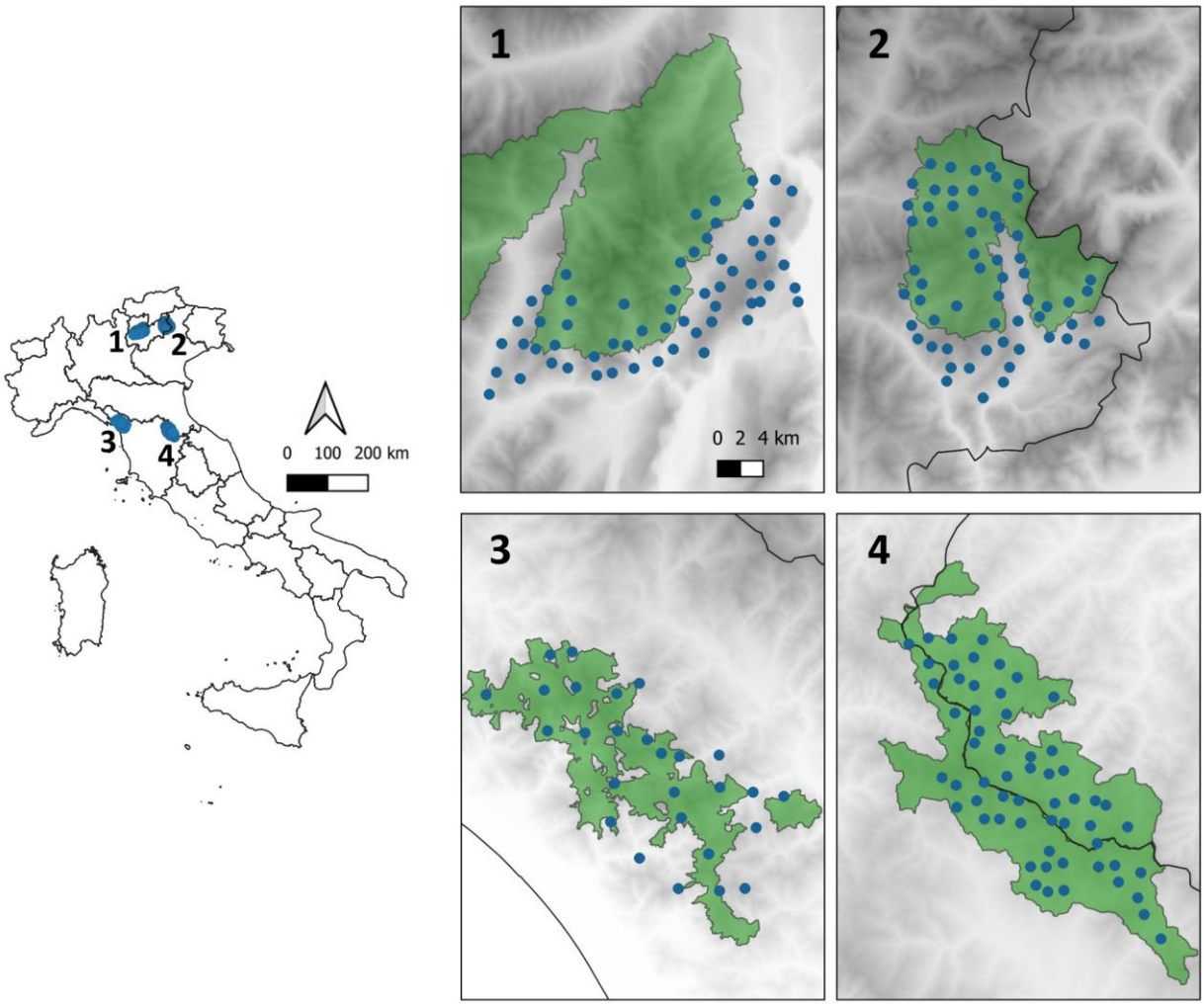

Figure 4.1. Map of the four study areas in northern and central Italy monitored with systematic camera trapping in 2020: 1 - Parco Naturale Adamello Brenta, 2 – Parco Naturale Paneveggio Pale di San Martino, 3 – Parco Naturale Regionale delle Alpi Apuane, 4 – Parco Naturale Nazionale delle Foreste Casentinesi. Protected areas are shown in green, while sampling sites are indicated by blue dots.

Data collection

The sampling design applied in the four areas has been used in Area 1 since 2015 (Oberosler et al., 2017; Salvatori et al., 2023) and is adapted from the Tropical Ecology Assessment and Monitoring Network (TEAM Network, 2011; Jansen et al., 2014), a pan-tropical biodiversity monitoring program (Rovero and Ahumada, 2017). Differences with the TEAM Network protocol include a larger spacing between camera locations to maximise the overall area

monitored and to account for the larger home range size of the mammals of temperate forests compared to species in tropical rainforests. We designed a regular grid with side of cells of 2/3 km and placed one camera-trap site per cell, evenly spaced and positioned to cover the whole altitudinal gradient (Figure 4.1). In areas 1, 2, and 4 the number of sampling sites was 60, and 45 in Area 3, due to the smaller spatial extent of this study area. Within each cell, we randomly selected one trail or forestry road and positioned a random point on it, that was then located in the field based on accessibility. Cameras were installed on trees at about 60 cm above the ground and at a distance of 3-5 metres from the target trail or road. For all areas, baits were not used, and cameras stayed active in the field for a minimum of 30 consecutive days. For this study, we used heat-in-motion triggered cameras of different brands: Reconyx (Holmen, WI, USA), Browning (Birmingham, AL, USA;), UWAY Outdoor Products (Norcross, GA, USA), Bushnell Outdoor Products (Overland Park, KA, USA), Boly Inc. (Santa Clara, CA, USA) and Apemans (Shenzhen, China). The pictures collected were classified at the species level by the authors through the software Wild.ID (Rovero and Zimmermann, 2016), apart from photographs of *Martes foina* and *Martes martes*, that were classified at genus level only, due to impossibility to distinguish these two sympatric species with certainty from camera trap detections. Since the sampling sites were positioned on trails and roads, our inference is generally related to wild mammals' and humans' use of these features only, and not of the whole study area (see Discussion). For the present study, trail-based sampling was necessary to monitor both wildlife and human site use, and thus to evaluate the potential consequences of human passage on wild mammals.

Covariates

To model large-scale effects of human frequentation on the spatial distribution and temporal behaviour of the mammalian communities in the four study areas, we extracted a set of four anthropogenic and environmental variables: i) the Relative Abundance Index (RAI) of humans at camera level (RAIHUMAN), ii) the distance from the camera to the closest settlement (SETTL), iii) elevation (ELEV), and iv) slope (SLOPE). These variables were not collinear based on the Pearson correlation coefficient (threshold = 0.5). The RAI of humans (vehicles included) represented a proxy of the diffuse presence of people in the reserves as well as a measure of the direct human passage at the camera stations. Site-level RAIs were calculated by extracting the average number of independent events and dividing it by the number of sampling days and multiplying by 100. We defined events as photographic sequences separated by at least 15

minutes (Rovero and Zimmermann, 2016). RAIs thus summarised the average number of independent events every 100 days of sampling. The distances from each camera station to the closest settlement were estimated by computing the Euclidean distance and represented proximity to towns and infrastructures and a proxy of human accessibility to forest interior (Benítez-López et al 2017). Site elevation and site slope were used to correct for possible environmental influences while investigating focal anthropogenic effects on mammals, and were extracted from Digital Elevation Models (DEMs) by using the built-in tools for geospatial analyses in QGis (QGis, 2020). Since we used a mix of camera trap brands, we categorised the photographic devices based on their technical characteristics (CAM_TYPE), with "fast" = 1 for cameras with trigger speed <0.2s, and "moderate" = 2 for the others.

Analyses

The composition of the mammalian communities in the four study areas was explored by calculating the RAI of wild mammals following the same procedure described above for the RAI of humans. Thus, for each study area, by ordering the species according to their RAI value, we could appraise the composition in terms of the number of photographic events of the mammalian species in each community.

To model global spatio-temporal variations of mammal communities across four study areas we adapted the multi-region occupancy model developed by Sutherland et al. (2016) to accommodate not only presence/absence data for estimating detection and occupancy probability but also independent events in three different time slots (day, crepuscular hours, and night) to model potential variations in mammal site use intensity in relation to time of day and anthropogenic covariates. This model extends the community occupancy model of Dorazio and Royle (2005) by linking data collected at multiple spatially independent regions, thus information is connected across sites and species, but also across different study areas (R = 4), while also accounting for different faunal species compositions. In this way, the coefficients of regressions are not only linked across species J of the same community through a random effect with a common mean, but also across regions R through a global random effect with a common mean for different study areas. This allowed us to assess the effect of covariates of interest as global effects on multiple independent communities as well as to assess covariate effects on each species in each region.

The number of diurnal, crepuscular and nocturnal photographic events were modelled through a sub-model with Poisson distribution , area-specific intercepts, and species- and area-

specific slopes drawn from a normal distribution. Response data were organised as independent tridimensional arrays, with the number of diurnal, crepuscular and nocturnal photographic events for each species *i*, at each site *j*, and in each area *r*. We superimposed communities to be of equal size, such that i_{max} represented the number of species in the community with the biggest faunal assemblage, while missing species were recorded as NA. We defined diurnal events those obtained between one hour after sunrise and one hour before sunset; crepuscular events those obtained within one hour before and after sunrise or sunset; and nocturnal events those obtained between one hour after sunset and one hour before sunrise. Sunrise and sunset time were extracted through the R package 'suncalc' (Thieurmel, 2022). The number of events in the three time intervals were then modelled as functions of covariates, such that:

$$log(\lambda day_{ijr}) = \mu\lambda day_r + \beta 1day_{ir} * RAIHUMAN_{jr} + \beta 2day_{ir} * SETTL_{jr}$$

$$log(\lambda crep_{ijr}) = \mu\lambda crep_r + \beta 1crep_{ir} * RAIHUMAN_{jr} + \beta 2crep_{ir} * SETTL_{jr}$$

$$log(\lambda night_{ijr}) = \mu\lambda night_r + \beta 1night_{ir} * RAIHUMAN_{jr} + \beta 2night_{ir} * SETTL_{jr}$$

For the occupancy sub-model, data were again organised as tridimensional array of species by sites by area (*i*J*R*). Detection/non-detection data (*Y*) corresponded to the imperfect observation of the true occupancy state (*Z*). This latter was modelled as a Bernoulli random variable such that $z_{jir} \sim$ Bernoulli(ψ_{jir}), with $z_{jir} = 1$ if site *j* was occupied by species *i* in region *r*, and $z_{jir} = 0$ if unoccupied. Here, ψ_{jir} is the species-specific occupancy probability of species *i* at site *j* in region *r*. The true occupancy states *Z* were then related to the observed data (*Y*) with the observational sub-model through a Binomial random variable $y_{jir} \sim$ Binomial(K_{ir}, p_{jir}, z_{jir}), where K_{ir} represent the number of sampling occasions, thus the number of days each camera was active in every forest, and p_{jir} is the detection probability of species *i* at site *j* of region *r*. Region-specific detection and occupancy probability were modelled as a function of covariates through a logistic link, such that:

$$logit(p_{jir}) = \alpha 0_r + \alpha 1_{ir} * SETTL_{jr} + \alpha 2_{ir} * equals\ (CAM\_TYPE_{jr}, 2)$$

$$logit(\psi_{jir}) = \beta 0_r + \beta 1_{ir} * RAIHUMAN_{jr} + \beta 2_{ir} * SETTL_{jr} + \beta 3_{ir} * ELEV_{jr} + \beta 4_{ir} * SLOPE_{jr}$$

Region-specific variations in both detection and occupancy probability were accounted for by the intercepts ($\alpha 0_r$, $\beta 0_r$), modelled as random effects drawn from normally distributed hyperparameters of common mean and variance.

Both modelling approaches were executed in JAGS (Plummer 2003) in the Bayesian framework through the package jagsUI (Kellner and Meredith 2021), in R (R Core TEAM 2022). Posterior distributions of the parameters were estimated by using 3 Markov Chain Monte Carlo of 750,000 iterations (500,000 burn-in and 250,000 post-burn in, and thinning = 10). We visually assessed model performances by inspecting the convergence of the chains for every parameter of interest, the R-hat diagnostic with R-hat $\approx$ 1 indicating good convergence, and the number of samplings from the posterior distribution. For further details on priors and the model formulation we provide the JAGS code in the supplementary material. Furthermore, to test whether the diurnal, crepuscular and nocturnal responses to human passage and proximity to urban areas changed according to body size, we regressed coefficient estimates of the three event types and two anthropogenic covariates against the log of each species body mass with post hoc linear regressions.

We discuss all our numerical results considering strength of evidence as a gradient rather than excluding parameters strictly relying on p-values and confidence intervals as in traditional significance testing (see Muffs et al., 2021).

Results

We collected a total of 359,400 pictures with a global sampling effort of 8,619 camera days, from the 204 sites that effectively sampled across the four areas (Table S4.1.1). Pictures of humans or vehicles corresponded to 74% of total pictures collected in Area 1, 59% in Area 2, 31% in Area3, and 52% in Area 4.

In all four areas the number of photographic events of humans far surpassed that of any other species, with higher values in the Alpine areas (RAI_{human} in Area 1 = 194.6; RAI_{human} in Area 2 = 250.0) compared to the Apennine ones (RAI_{human} in Area 3 = 150.9; RAI_{human} in Area 4 = 152.8; Figure 4.2). These latter areas showed a higher number of wild mammalian species (13 in Area 3 and 15 in Area 4) compared to the first two (10 in Area 1 and 9 in Area 2), with red fox and wild boar being the second and third most detected species, before domestic animals, at the fourth place. Domestic animals were instead the second most detected species

after humans in the Alpine areas. Red fox was the most detected wild species in all areas except Area 2, where red deer ranked first.

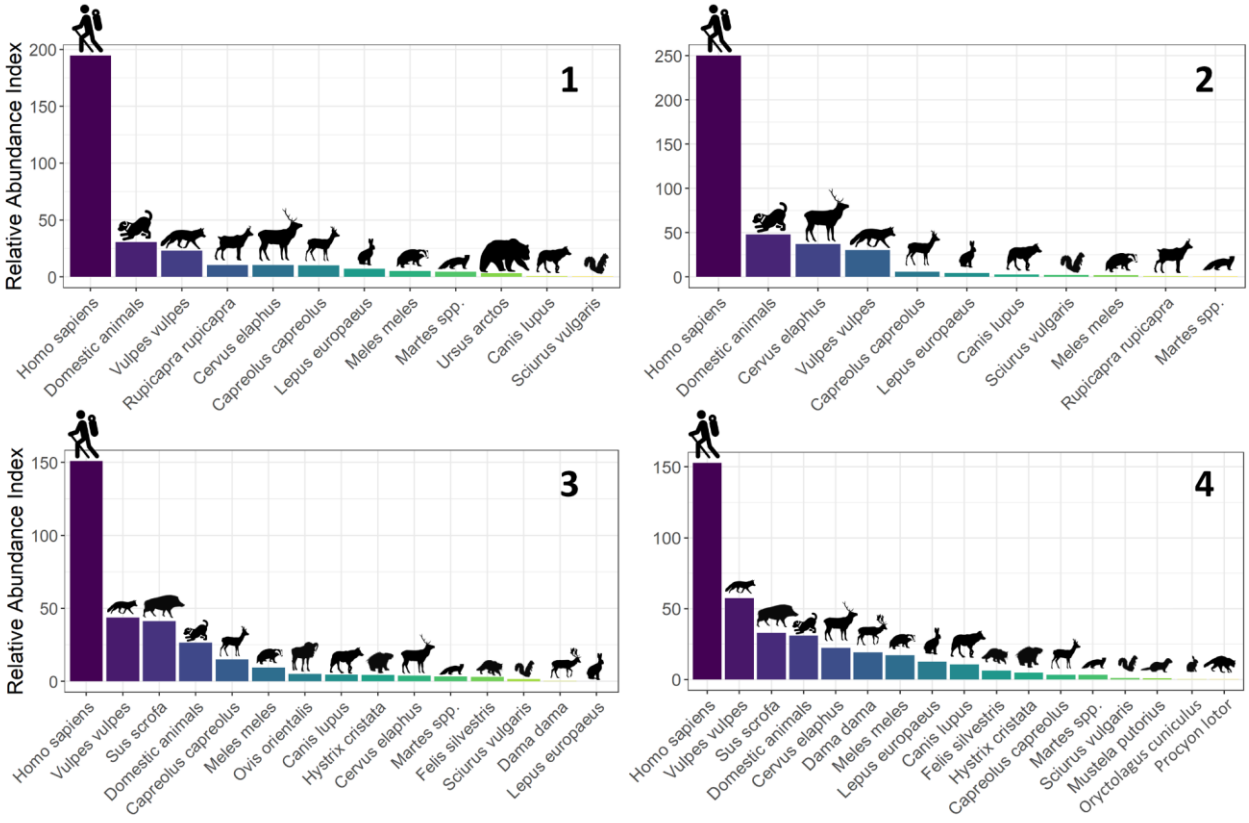

Figure 4.2. Relative Abundance Index of humans (vehicles included), domestic animals and wild mammals, ordered from the most to the least detected for each area. Species identity is indicated by its silhouette and scientific name. Data derive from systematic camera trapping in four protected areas of central and northern Italy during 2020: 1 - Parco Naturale Adamello Brenta, 2 – Parco Naturale Paneveggio Pale di San Martino, 3 – Parco Naturale Regionale delle Alpi Apuane, 4 – Parco Nazionale delle Foreste Casentinesi.

Across the four areas, we found a global consistent spatio-temporal response of mammals to human frequentation (Figure 4.3). In particular, the number of diurnal events decreased with increasing rates of human passage ($\beta 1_{day}$ = -0.57; 90% BCI: -0.79, -0.36; Figure 4.3A). Crepuscular events followed the same pattern, even though with a weaker effect size

($\beta 1_{crep}$ = -0.17; 90% BCI: -0.32, -0.04), while the number of nocturnal events did not vary with human passage ($\beta 1_{night}$ = -0.03; 90% BCI: -0.15, 0.08). Overall then, the number of total events decreased and became mostly nocturnal at increasing rates of human passage (Figure 4.3C). We found a lack of effect of distance from the closest town on diurnal ($\beta 2_{day}$ = 0.02; 90% BCI: -0.21, 0.25; Figure 4.3B), crepuscular ($\beta 2_{crep}$ = -0.14; 90% BCI: -0.32, 0.04) and nocturnal ($\beta 2_{night}$ = -0.13; 90% BCI: -0.31, 0.05) events, though the positive sign of the coefficient for diurnal events and the negative one for crepuscular and nocturnal ones may suggest a tendency for a general increase of diurnality at increasing distance from urbanised areas (Figure 4.3D).

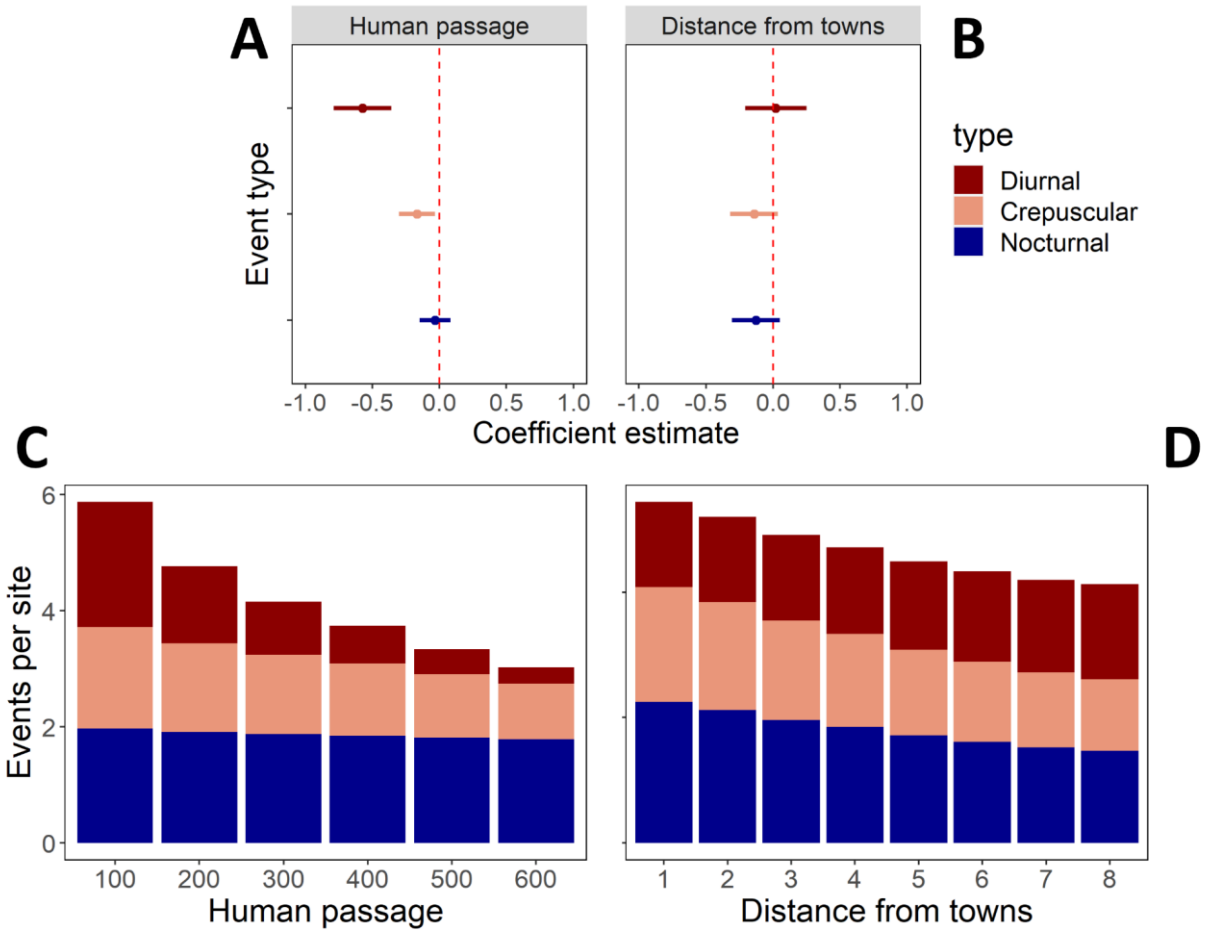

Figure 4.3. Effects of the rate of human passage and distance from towns on the number of events of wild mammals estimated with a multi-region community model. Caterpillar plots depict standardised beta coefficients of diurnal (red), crepuscular (orange) and nocturnal (blue) events in relation to human passage (Panel A) and distance from towns (Panel B). Points represent the median of the full posterior distribution, and error bars represent the 90% BCI.

Stacked bar plots show the predicted number of average diurnal (red), crepuscular (orange) and nocturnal (blue) events of the mammalian community for different rates of human passage (human RAI; Panel C) and increasing distance from towns, in kilometres (Panel D). Values on the x axes of Panel C and D indicate upper limits of each interval. Data derive from systematic camera trapping in four protected areas of central and northern Italy during 2020.

The relationship between the rate of human passage and the number of events was lower for diurnal than nocturnal ones in all species without exception, meaning that at increasing human frequentation of sites mammalian behaviour became more nocturnal and that this pattern was consistent across species (Figures 4.4 and 4.6; Appendix S4.2). However, the degree to which species shifted towards nocturnality at increasing disturbance varied: large herbivores and the brown bear showed a marked decrease in diurnal events leading to a strong disproportion towards nocturnal behaviour (e.g., Wild boar: β1day = -2.75; 90% BCI: -3.86, -1.45; Red deer: β1day = -1.04; 90% BCI: -1.71, -0.29; Roe deer: β1day = -1.00; 90% BCI: -2.71, -0.12; Figures 4.4 and 4.5). These species also showed a general tendency to decrease their total number of events in response to human frequentation, namely the coefficient was negative for diurnal, crepuscular and nocturnal events alike (e.g. Fallow deer: β1day = -0.86 ; β1crep = -0.36; β1night =-0.25; Chamois: β1day = -0.47 ; β1crep = -0.27; β1night =-0.17). The badger showed a similar tendency to decrease its average number of events at increasing human disturbance, but its activity was concentrated during night-time even at low disturbance rates (Badger: β1day = -0.27 ; β1crep = -0.02; β1night =-0.17). The wolf and the wild cat had very similar responses, both did not vary the overall number of events, but concentrated most of them during night-time at high rates of human passage (Wolf: β1day = -0.30 ; β1crep = -0.15; β1night = 0.06; Wild cat: β1day = -0.18 ; β1crep = -0.11; β1night = 0.07). Hystrix, racoon and polecat did not show pronounced variations in their number of events at differing rates of human frequentation, with the former maintaining a predominantly nocturnal and crepuscular behaviour and the latter two showing a balanced subdivision of their events in the three time categories. *Martes* spp. maintained a nearly constant number of nocturnal and crepuscular events, but slightly decreased their diurnal events (Martens: β1day = -0.26 ; β1crep = 0.00; β1night = -0.04) in relation to human passage. Red fox, hare and rabbit were the only species exhibiting an increase in events at increasing human frequentation, but while hare and rabbit conserved similar levels of diurnal events but increased nocturnal and crepuscular events

(Hare: β1day = 0.07 ; β1crep = 0.28; β1night = 0.28; Rabbit: β1day = -0.02 ; β1crep = 0.13; β1night = 0.18), red fox sharply increased nocturnal, and secondarily also crepuscular events while decreasing diurnal ones (Red fox: β1day = -0.45 ; β1crep = 0.26; β1night = 0.49). Red squirrel, though being the smallest species, displayed a pattern more similar to the largest ones, with a general decrease in all event types, especially diurnal ones (Red squirrel: β1day = -1.13; β1crep = -0.19; β1night = -0.15).

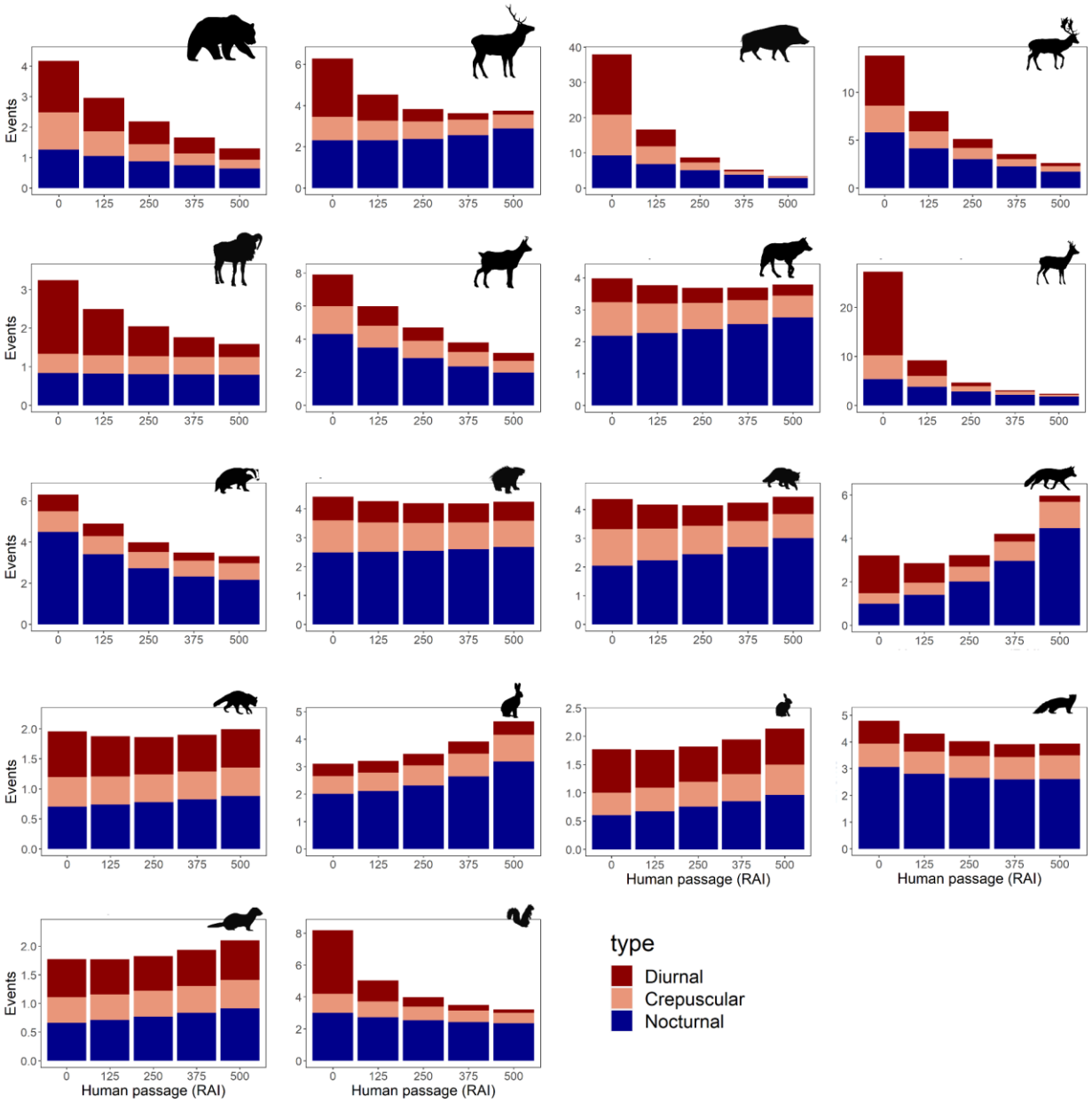

Figure 4.4. Effects of the rate of human passage on the number of events of each species of wild mammal, indicated by the silhouettes, estimated with a multi-region community model. Stacked bar plots show the predicted number of average diurnal (red), crepuscular (orange) and nocturnal (blue) events of each species for different rates of human passage (human RAI). The species have been order according to body mass from top left to bottom right as follows: *Ursus arctos*, *Cervus elaphus*, *Sus scrofa*, *Dama dama*, *Ovis musimon*, *Rupicapra rupicapra*, *Canis lupus*, *Capreolus capreolus*, *Meles meles*, *Hystrix cristata*, *Felis silvestris*, *Vulpes vulpes*, *Procyon lotor* (allochthonous species), *Lepus europaeus*, *Oryctolagus cuniculus*, *Martes* spp., *Mustela putorius*, *Sciurus vulgaris*. Data derive from systematic camera trapping in four protected areas of central and northern Italy during 2020, modelled through a multi-region community model.

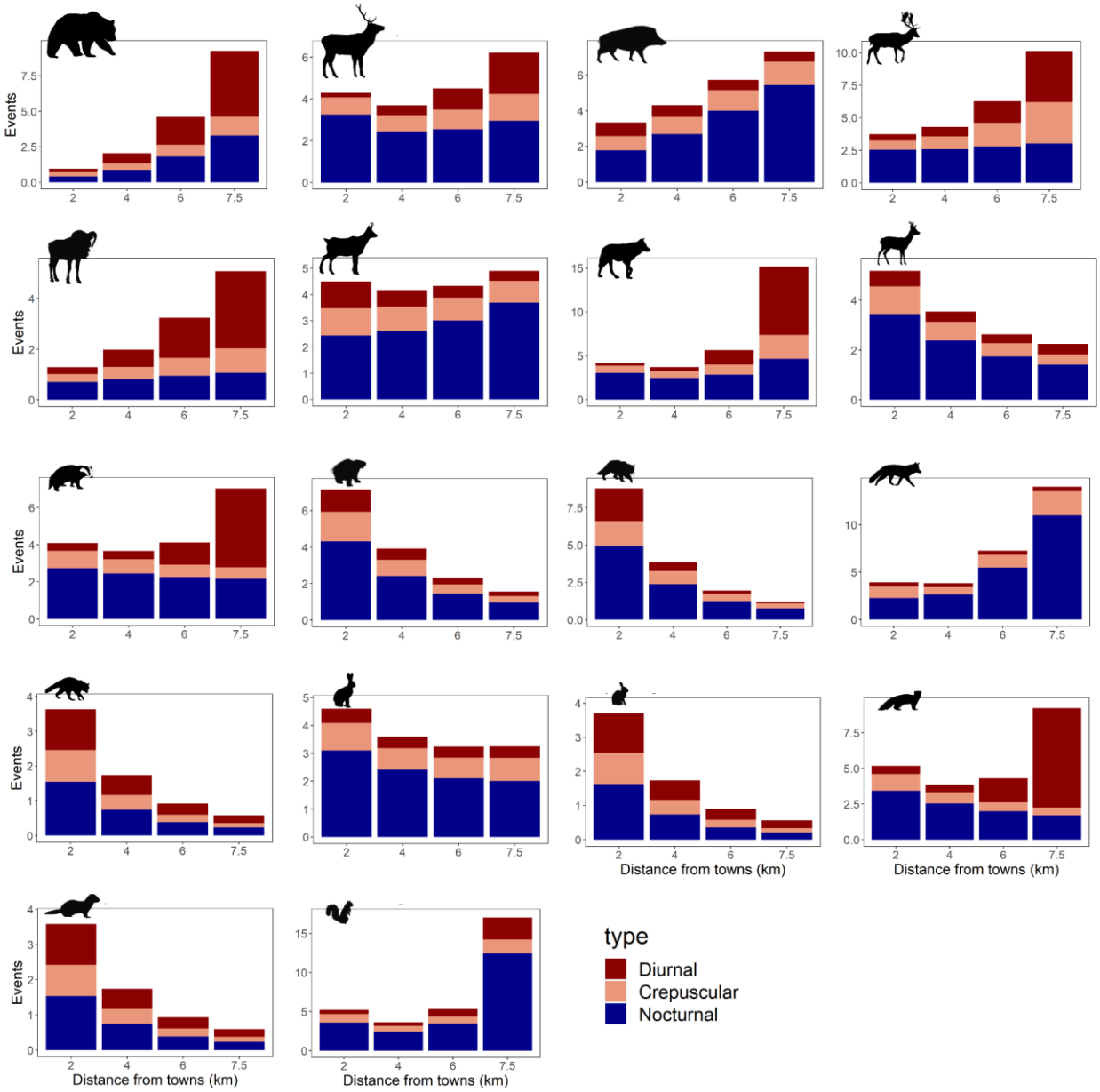

Figure 4.5. Effects of distance from the closest town on the number of events of each species of wild mammal, indicated by the silhouettes, estimated with a multi-region community model. Stacked bar plots show the predicted number of average diurnal (red), crepuscular (orange) and nocturnal (blue) events of each species for different distances from closest human settlement (in km). The species have been subdivided according to body mass from top left to bottom right as follows: *Ursus arctos*, *Cervus elaphus*, *Sus scrofa*, *Dama dama*, *Ovis musimon*, *Rupicapra rupicapra*, *Canis lupus*, *Capreolus capreolus*, *Meles meles*, *Hystrix cristata*, *Felis silvestris*, *Vulpes vulpes*, *Procyon lotor* (allochthonous species), *Lepus europaeus*, *Oryctolagus cuniculus*, *Martes* spp., *Mustela putorius*, *Sciurus vulgaris*. Data derive from systematic camera

trapping in four protected areas of central and northern Italy during 2020, modelled through a multi-region community model.

The effect of distance from the closest settlement was less consistent across species, with some species, especially larger ones, exhibiting an increase in the number of events (particularly diurnal ones) further away from towns (e.g., Brown bear: $\beta 2_{day}$ = 1.10; 90% BCI: 0.58, 1.70; Red deer: $\beta 2_{day}$ = 0.84; 90% BCI: 0.35, 1.37; Figure 4.5 and 4.6; Appendix S4.2), whereas other species, especially the small and medium sized ones, showed a general decrease in the total number of events at greater distances from towns (e.g., Wild cat: $\beta 2_{day}$ = -1.32, $\beta 2_{crep}$ = -0.70, $\beta 2_{night}$ = -0.70; Hystrix: $\beta 2_{day}$ = -0.65, $\beta 2_{crep}$ = -0.64, $\beta 2_{night}$ = -0.63). Martens and badger, however, displayed an increase in diurnal events and a decrease in crepuscular and nocturnal ones further away from human settlements (*Martes* spp.: $\beta 2_{day}$ = 0.39, $\beta 2_{crep}$ = -0.21, $\beta 2_{night}$ = -0.30; Badger: $\beta 2_{day}$ = 0.18, $\beta 2_{crep}$ = -0.17, $\beta 2_{night}$ = -0.19). Red Fox and squirrel showed instead an increase in events at greater distances from towns but concentrated in the nocturnal category (Red Fox: $\beta 2_{day}$ = 0.01, $\beta 2_{crep}$ = -0.23, $\beta 2_{night}$ = 0.03; Red squirrel: $\beta 2_{day}$ = -0.10, $\beta 2_{crep}$ = 0.00, $\beta 2_{night}$ = 0.22).

Additionally, we also estimated area and species-specific effects on occupancy. Coefficient estimates at area level were centred around zero, as expected when species within a community present contrasting effects that cancel each other out in the common mean (Appendix S4.3). Hare occupancy increased at increasing rates of human passage in Area 1, while red squirrel, rabbit, red fox, wild cat, badger, roe deer and brown bear all decreased their occupancy at increasing distance from towns (Appendix S4.3). Wolf and wild boar on the contrary increased their occupancy further from towns, whereas red deer had contrasting coefficients in the four areas, negative for the first three areas, and positive for the last one. Occupancy was also negatively correlated with terrain elevation for red squirrel, racoon, hystrix, badger and wild boar, and positively for polecat, roe deer and fallow deer. It had instead inconsistent coefficients in the four areas for *Martes* spp., hare, red fox, and red deer, indicating local responses to topography and habitat characteristics specific to each area (Appendix S4.3).

The post hoc linear regressions indicated that the coefficient estimate for number of events in relation to human passage was inversely proportional to the log of body mass, especially for diurnal (β = -0.37 ± 0.19 SE; Figure 4.6B) and crepuscular events (β = -0.29 ± 0.12 SE), and less markedly also for nocturnal events (β = -0.18 ± 0.10 SE). Symmetrically, the log of body mass was positively related to the coefficients of distance from towns on number of events, again more strongly for diurnal events (β = 0.46 ± 0.17 SE; Figure 4.6D), intermediate

for crepuscular (β = 0.32 ± 0.10 SE), and less pronouncedly for nocturnal ones (β = 0.28 ± 0.12 SE).

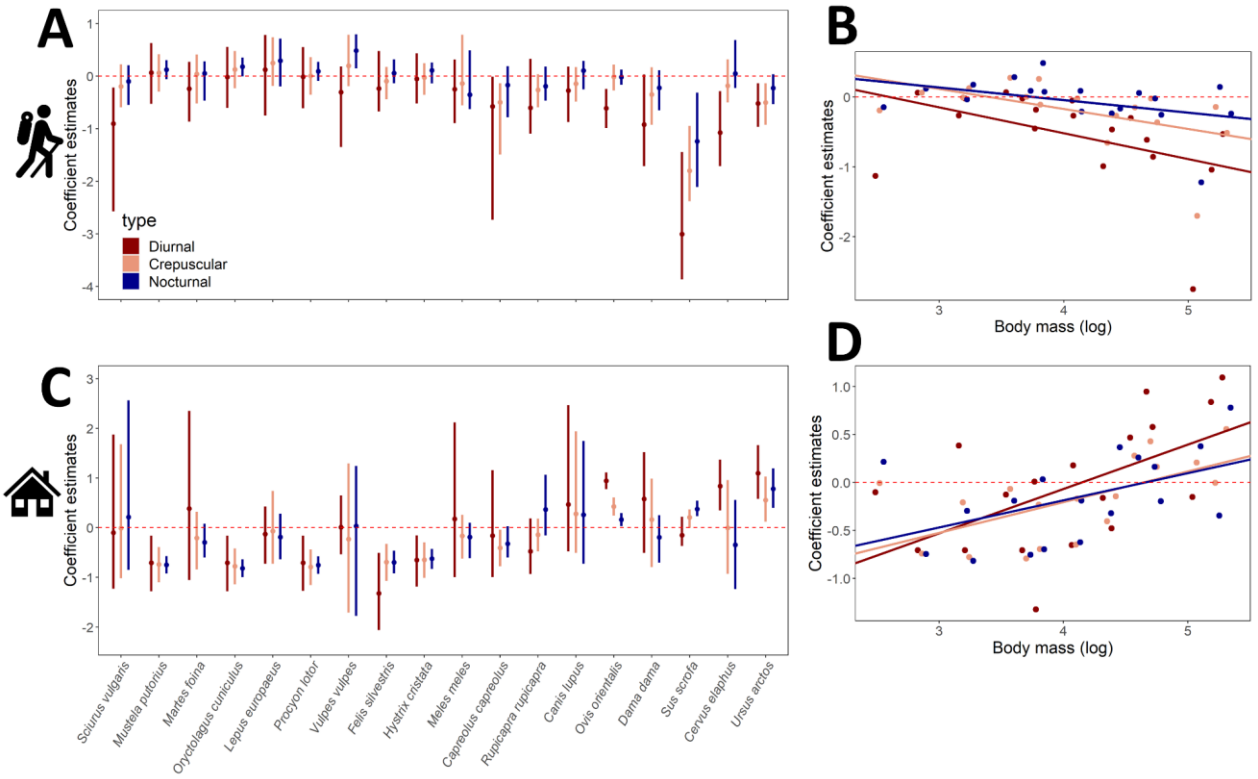

Figure 4.6. Caterpillar plots in Panel A and C show the coefficient estimates and 90% BCI of the effect of the rate of human passage (human RAI) and of the distance from the closest town, respectively, on the number of diurnal (red), crepuscular (orange) and nocturnal (blue) events for each species, ordered from the smallest (left hand side) to the largest (right hand side). Panel B and D depict the estimated relations of the coefficients to species body mass (in logarithmic scale) for human passage and distance from town respectively. Data derive from systematic camera trapping in four protected areas of central and northern Italy during 2020, modelled through a multi-region community model.

Discussion

By systematically monitoring the community of medium and large sized mammals in four PAs of the European Natura 2000 network at more than 200 camera trapping sites we found that wildlife consistently tended to decrease site use and increase nocturnality at higher rates of human passage. Indeed, the number of diurnal events decreased sharply, and crepuscular

events mildly in response to more intense human disturbance, while nocturnal events remained essentially unvaried , thus becoming the relative majority. This effect was consistent across species, since all had a response to human passage that was more negative for diurnal than for nocturnal events. However, this pattern was stronger for species with larger body mass, which in general decreased all event types at higher disturbance, but with a preeminent decrease in diurnal ones. More opportunistic species with medium and small body mass showed instead a general increase in the overall number of events with human passage that were however concentrated during night-time. Therefore, the mammalian species we studied did not differ in the tendency to increase nocturnal behaviour at higher human frequentation but more in the strategy adopted to avoid disturbance: larger species avoided humans both in space and time, by diminishing the passage at more disturbed sites and concentrating them during the night, whereas smaller species avoided humans only temporally, since their total events either remained constant or even increased at more disturbed sites, but anyway focalized at night-time, confirming results of a previous long-term study on one of our four target areas (Salvatori et al., 2023). Thus, our prediction P1A (lower site-use in response to human outdoor activities) was generally confirmed, even if most of the reduction was in diurnal and crepuscular events, supporting our prediction P1B (increased nocturnality in response to human outdoor activities). In both cases, the spatio-temporal avoidance of human passage was stronger for species with larger body mass, confirming prediction P3A.

The proximity to settlement did not have a similarly strong and general effect on mammals' spatio-temporal behaviour, given that all the three event types (diurnal, crepuscular and nocturnal) presented a community coefficient that overlapped 0 (Figure 4.3B). Predictions P2A (increased use of site further from towns) and P2B (increased diurnality further from towns) were therefore not confirmed at community level. However, prediction P3B (spatio-temporal avoidance of towns by larger species) was confirmed, since large sized species generally displayed an increase in the number of events at greater distances from human settlements, especially for diurnal events, while several small and medium mammals showed even a decrease in total number of events at more remote sampling sites. This pattern could be due to higher spatial requirements of bigger species, needing less fragmented and modified habitats, but possibly also to parallel habitat preferences if suitable environments for small sized species are more common close to towns. Hares and rabbits for example are known to favour more heterogeneous landscapes with presence of grasslands and agricultural fields (Naldi et al., 2020), that in our study areas are located around human settlements, and that give

way to dense continuous forests further away from towns, at PAs cores. Another possible explanation for the preference of small herbivores of sites closer to towns lies in the human shield hypothesis: by occupying areas closer to human settlements small prey might decrease predation probability by carnivores afraid of encountering humans (Berger et al., 2007). In turn, lower density of prey at greater distances from towns might explain the higher site use in proximity to urban areas in the case of polecat and wild cat. Yet we detected a higher variability between areas in the spatio-temporal effect of the distance from human settlements than that of human outdoor activities, suggesting that the local configuration of the urban-natural boundary and the species-specific fine-scale distribution of suitable habitat patches within each study area likely plays a role (Appendix S4.2). Ultimately, these results also indicate that human active disturbance can be a stronger driver of mammalian behavioural change than structural landscape modifications, as already found by previous research (Corradini et al., 2021; Nickel et al., 2020).

The sampling design chosen targeted trails and unpaved roads, hence the inferences we obtained must be interpreted in light of such non-random placement of detectors. Spatio-temporal responses of mammals to human passage and to proximity to towns might be different in locations outside of the trail and road network, for example with a lower tendency to nocturnality in dense forest stands where humans cannot access (Tanwar et al., 2021). However, our camera-trap placement is functional to the aim of simultaneously detecting the whole pool of larger wild mammals and humans, and previous research suggests that this sampling design is more cost-effective, more efficient at detecting rare species and species such as large carnivores that mainly travel along well established paths, and can give similar community metrics compared to random designs (Tanwar et al., 2021; Cusak et al., 2015). Interestingly moreover, the patterns we observed using photographic events as dependent variable were not evident with occupancy modelling. This is not surprising, and matches previous research highlighting that since occupancy quickly asymptotes to 1 it cannot measure a gradient of site use intensity once 100% occurrence probability has been reached, due to the binary nature of presence/absence data (Suraci et al., 2019; Salvatori et al., 2023). For these reasons occupancy might not be the ideal variable to represent gradients of animal space use in continuous habitats (Efford and Dawson, 2012; Parsons et al., 2017).

Our results suggest that human outdoor recreation and the presence of urban areas might affect the behaviour and movement patterns of large mammals more than that of smaller species, since the increase in nocturnality with more intense human frequentation was

proportional to species body mass, as was the case for the increase in diurnality moving away from urban areas. Suraci et al. (2021) found that body mass and spatial requirements were among the best predictors of the degree with which mammals used areas with high human footprint (i.e., intense structural modifications) at a continental scale, with smaller species exhibiting tolerance towards landscape modification and larger ones displaying spatial avoidance. Yet, they did not find a similar pattern regarding the intensity of human frequentation, most probably because the avoidance of human presence, largely diurnal, has a preeminent temporal component, as shown by our results. This general activity shift towards nocturnality may imply that terrestrial mammals not only have less and less room to roam (Tucker et al., 2018; Wilcove et al., 2008), but also less time to be active. By avoiding diurnal humans and seeking refuge during night-time, animals might experience greater pressure from ecological competitors and predators, all forced to exploit darkness hours (Gaynor et al., 2018; Bonnot et al., 2020).

Our data show that the four areas of the Natura 2000 ecological network, though under various protection regimes, may be partially failing to provide a safe environment for wildlife, as many PAs are likely exposed to high rates of human outdoor activities: in the two alpine areas in particular we measured a relative abundance of humans, mainly composed of outdoor recreationists, that was seven times higher than the most detected wild species. This intense human use of the PAs affected mammals' spatio-temporal behaviour, in terms of an overall reduction in the number of events and a temporal shift with fewer diurnal events in disturbed sites by imposing a landscape of human fear that consistently drove the biological communities towards nocturnality and elicited even spatial avoidance in bigger sized species, potentially affecting inter-specific interactions, like intra-guild competition, predator-prey dynamics and various ecosystem processes, like nutrient cycling and herbivory. High human risk perception in natural areas, by concentrating wild mammals within more densely covered forests, that provide more efficient shields to human disturbance, has been suggested to even modify the nitrogen biogeochemical cycle, with the potential for soil eutrophication (Segar et al., 2022). Similarly, the avoidance of human super-predators and their infrastructures can intensify forest browsing by ungulates in the less disturbed and more secluded areas, with potential negative impacts on forest dynamics (Mathisen et al., 2018). Both scenarios are in line with our findings that ungulates consistently avoided areas with high rates of human frequentation and favoured habitats at further distances from urbanised areas, possibly resulting in aggregation of herbivores in less disturbed and accessible areas. That wolf and brown bear tended to spatio-

temporally avoid humans and towns is encouraging for the large carnivore-human coexistence, thanks to a low encounter probability, but is concerning for the weakened ecological role that large carnivores can assume under an intense landscape of human fear (Ordiz et al., 2013).

As world governments pledge to protect 30% of lands and seas for ecosystems and nature conservation through the Kunming-Montreal Global biodiversity framework (CBD 2022), our work adds to an increasing body of evidence which shows that PAs need to enforce real regulations and limitations to human activities, and not only rely on mere protection on paper, to reach desired conservation outcomes (Wauchope et al., 2022). These include limitations and mitigations to urban development and infrastructures, but also regulations of human access through spatial and temporal zoning to decrease human direct disturbance on wildlife communities, thereby providing refuge habitats in which species can express natural behaviours and activity patterns (Reed et al., 2008; Whittington et al., 2019). Finally, our study underscores the need for harmonising wildlife monitoring techniques and protocols across the sites of an ecological network in order to collect comparable results and gain insight on general ecological phenomena while also accounting for local specificities.

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General conclusions

By coupling systematic camera trapping, a cost-effective sampling technique, with a wide range of statistical methods I inferred relevant information on the structure of mammalian communities, on their multi-year trends and on their spatio-temporal responses under two emergent anthropogenic pressures on natural and protected areas, namely free-ranging livestock rearing and outdoor recreation (Schulze et al., 2018). In part 1 I applied two different statistical models in the hierarchical framework to reconstruct networks of potential inter-specific interactions under widespread presence of free-ranging livestock in mountainous and dry grassland ecosystems in western Mongolia, explicitly including livestock as one of the actors at play, and even differentiating between two different livestock categories in chapter 2. While the spatial co-occurrence patterns we found might in part be the results of similar ecological preferences of species, through unmeasured environmental variability, they anyway describe the structure of this community characterised by a high number of threatened species.

In chapter 1 I discovered that the Siberian ibex seemed to spatially avoid livestock and favour steeper areas at higher elevation, and the snow leopard was revealed as strictly dependent on this large prey, as their spatial overlap was very strong. On the contrary the wolf, the other large predator in this ecosystem, preferred areas at lower elevation and had a positive spatial overlap with livestock, though avoiding the proximity of villages, with high potential for livestock depredation, human-wolf conflicts, and retaliatory killings. By widening the perspective thanks to the use of a community-level species distribution model with interspecific correlations, in chapter 2 I included more species in the frame and found out that hares, marmots, ground squirrels and the red fox were also positively co-occurring with livestock, either for a higher tolerance to the presence of domestic animals or similar environmental preferences for milder topography, or both. The nearly threatened Pallas' cat showed a strong spatial overlap with pikas and marmots, both considered important prey items for this felid. The co-occurrence of marmots with livestock herds and the dependence of this wild cat on them might force it to visit areas with high livestock densities, and higher potential anthropogenic mortality. As general ecological patterns we detected strong predator-prey relationships and ample intraguild tolerance. The spatial segregation of wild species with livestock seemed to follow a pattern loosely related to body-mass, with larger species being less prone to co-occur with the herds. Overall, domestic animals seem to cover an influential role in the system, since most species showed pronounced spatial relationships with it, confirming the

importance of taking livestock into account in conservation planning in this area, especially considering current and projected trends in cashmere wool demand and consequently goat numbers (Berger et al., 2013).

In part 2 I aimed to understand the net result of conflicting positive and negative drivers on mammalian communities in Italian mountainous PAs. The increase in forest surface, the legal protection, hunting regulations, lowered persecutions and reintroduction projects seem to result in the stable community trends in occurrence shown in chapter 3 for a community of mammals systematically monitored since 2015 in a touristic area of the central Alps. The species-specific trends in occurrence, estimated through a multi-season and multi-species occupancy model, were condensed into the Wildlife Picture Index for the whole community, which coherently indicated a positive trend too. This finding is reassuring for the long-term conservation of the mammals composing this community and others located in similar ecological and social context. However, I also detected clear signs of spatial avoidance of human presence in the bigger-sized species, like the brown bear, the red deer and the chamois, that also tended to elude the proximities of urban settlements. All the species of the target community responded to human outdoor activity by becoming more nocturnal and halving their temporal overlap with humans in most disturbed sites.

In chapter 4 I broadened the spatial extent of the analysis, including other three Italian PAs of the European Natura 2000 Network. Through multi-area and multi-species models I obtained both species- area-specific and general inferences on the spatio-temporal responses of mammals to human outdoor activities. The four mammalian communities targeted showed a general decrease in diurnal and crepuscular passage at increasing rates of human frequentation while nocturnal passages remained stable. Thus, mammals overall were less active at disturbed sites, and their activity was concentrated during night-time. A post-hoc analysis revealed again a link between the strength of spatio-temporal avoidance of humans and species body mass: larger species, especially large carnivores and ungulates, generally decreased their site use and their diurnality in areas with intense human passage and instead favoured sites at greater distances from urban settlements, where they also presented a more diurnal behaviour. The shift towards nocturnality is a general behavioural response of mammals to cope with a pervasive human presence that has been documented even at global level (Gaynor et al., 2018). This behavioural plasticity, if on one hand seems to guarantee positive trends in occurrence (hence good survival and reproductive probability), as shown in chapter 3, on the other hand may come with costs for animals. Reduced efficiency in movement,

foraging, reproduction and thermoregulation have all been reported as possible costs associated with nocturnal shifts in activity, and may negatively affect mammalian populations and communities on a longer time frame (Sih, 2013). The research included in chapter 4 provides also a robust methodological framework on which to base standardised monitoring of mammals in a PA network, with the aim of gathering systematic and directly comparable data across different areas and biological communities.

In conclusion, the collection of spatially and temporally robust data on biological communities is pivotal to infer ecological patterns, understand the consequences of anthropogenic pressures and tackle contemporary sustainability challenges (Nicholson et al., 2012). On the methodological side, this thesis shows a wide range of replicable analytical approaches to test ecological hypotheses on mammalian communities facing human impacts, and to monitor them through time. On the conservation side, the results of this thesis add to a body of knowledge on weaknesses and vulnerabilities of PAs in a rapidly changing planet (Geldmann et al., 2019), a very relevant challenge for future conservation efforts, especially as world governments recently signed for the protection of 30% of lands and oceans through the UN's Kunming-Montreal agreement (CBD, 2022).

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Appendix

S1. Appendix of chapter 1

Appendix S1.1

Table S1.1.1. Summary of the sampling design and effort of systematic camera-trapping surveys in four areas of western Mongolia. Sampling occasions are expressed as mean number of sampling days per camera ± standard deviation. The area sampled is calculated as the minimum convex polygon around the camera trap sites.

Area	Year	Protection status	Area sampled (km^2)	Elevation range sampled (m a.s.l.)	Number of camera-trapping sites	Survey period	Effort (camera days)
Siilkhem B	2015	National Park	513	2231-3123	48	19/03 – 23/06	46.5 ± 6.6
Tavan Bogd	2017	National Park	720	2488-3489	44	07/04 – 2/06	48.2 ± 1.6
Khork Serkhe	2018	Strictly Protected Area	1110	1965-3072	63	18/03 – 20/06	65.2 ± 5.8
Sutai	2019	Not protected	843	2115-3527	61	18/03 – 29/06	92.1 ± 15.3

Appendix S1.2.

Table S1.2.1. Summary of naïve and predicted occupancy (estimated from single-specie occupancy models) for livestock, snow leopard, wolf and ibex in four areas of western Mongolia from systematic camera-trapping data.

	Silkhem B		Tavan-Bogd		Korkh Serkhe		Sutai	
	naive ψ	**ψ**	**naive ψ**	**ψ**	**naive ψ**	**ψ**	**naive ψ**	**ψ**
Livestock	0.44	0.44	0.29	0.30	0.60	0.61	0.62	0.65
Snow leopard	0.27	0.51	0.05	0.08	0.27	0.34	0.80	0.83
Wolf	0.17	0.33	0.20	0.31	0.16	0.31	0.36	0.40
Siberian ibex	0.19	0.21	0.11	0.13	0.30	0.34	0.34	0.42

Appendix S1.3.

Table S1.3.1. List of the most supported (with ΔAIC < 2) single-species occupancy models for systematic camera-trapping data from four areas of western Mongolia for snow leopard, wolf, Siberian ibex and livestock.

Model	logL	No. parameters	AIC	ΔAIC	AICwt
Snow leopard					
ψ(Area+Slope), p(sampling days)	-720.56	7	1455.13	0.00	0.18
ψ(Area), p(sampling days)	-721.62	6	1455.24	0.11	0.17
ψ(Area+Slope+Distance), p(sampling days)	-719.88	8	1455.77	0.64	0.13
ψ(Area +Distance), p(sampling days)	-720.99	7	1455.97	0.85	0.12
ψ(.), p(.)	-768.61	2	1541.22	86.1	0.00
Wolf					
ψ(Elevation+Distance), p(.)	-356.95	4	719.81	0.00	0.19

ψ(Distance), p(.)	-355.90	3	719.89	0.09	0.18
ψ(Slope+Elevation+Distance), p(.)	-355.84	5	721.67	1.87	0.08
ψ(Slope +Distance), p(.)	-356.90	4	721.79	1.98	0.07
ψ(.), p(.)	-359.65	2	723.31	3.50	0.03
Siberian ibex					
ψ(Area+Elevation+Slope), p(sampling days)	-434.47	8	884.93	0.00	0.21
ψ(Area+Slope), p(sampling days)	-435.76	7	885.51	0.58	0.15
ψ(Area+Elevation+Slope+Distance), p(sampling days)	-434.47	9	886.91	1.99	0.07
ψ(.), p(.)	-447.10	2	898.19	13.4	0.00
Livestock					
ψ(Area+Elevation+Distance), p(sampling days + Distance)	-1050.66	9	2119.33	0.00	0.38
ψ(Area+Elevation+Slope+Distance), p(sampling days + Distance)	-1050.44	10	2120.89	1.56	0.18
ψ(.), p(.)	-1122.2	2	2248.58	129	0.00

Table S1.3.2. Output of the most parsimonious single-species occupancy model for snow leopard, wolf, Siberian ibex and livestock from camera trap surveys in four areas of western Mongolia.

Species	Best model parameter	Estimate	SE	Z	P(>|z|)	
Snow leopard						
	Ψ Area KS	-0.68	0.33	-2.1	0.04	*
	Ψ Area SB	0.72	0.62	1.2	0.24	
	Ψ Area SU	2.23	0.48	4.66	< 0.001	***
	Ψ Area TB	-1.74	0.82	-2.1	0.04	*
	p Intercept	-2.1	0.16	-12.9	< 0.001	***
	p sampling effort	0.49	0.12	4.22	< 0.001	***

Wolf						
	Ψ Intercept	-0.69	0.23	-2.9	< 0.01	**
	Ψ *Distance from settlement*	0.43	0.19	2.22	0.03	*
	p Intercept	-2.45	0.16	-15	< 0.001	***
Siberian ibex						
	Ψ Area KS	-0.75	0.30	-2.5	0.01	*
	Ψ Area SB	-0.57	0.48	-1.2	0.24	
	Ψ Area SU	0.45	0.44	1.0	0.31	
	Ψ Area TB	-1.22	0.57	-2.1	0.03	*
	Ψ *Slope*	0.35	0.17	2.1	0.04	*
	p Intercept	-1.78	0.13	-13.6	< 0.001	***
	p sampling effort	-0.45	0.13	-3.5	< 0.001	***
Livestock						
	Ψ Area KS	0.15	0.28	0.54	0.60	
	Ψ Area SB	-0.68	0.42	-1.6	0.10	
	Ψ Area SU	1.05	0.49	2.1	0.03	*
	Ψ Area TB	-0.83	0.46	-1.8	0.07	.
	Ψ *Elevation*	-0.58	0.19	-3.0	< 0.01	**
	Ψ *Distance from settlement*	-0.59	0.19	-3.0	< 0.01	**
	p Intercept	-0.92	0.07	-13.0	< 0.001	***
	p sampling effort	-0.37	0.06	-6.0	<0.001	***
	p Distance from settlement	-0.45	0.08	-5.56	< 0.001	***

Appendix S1.4.

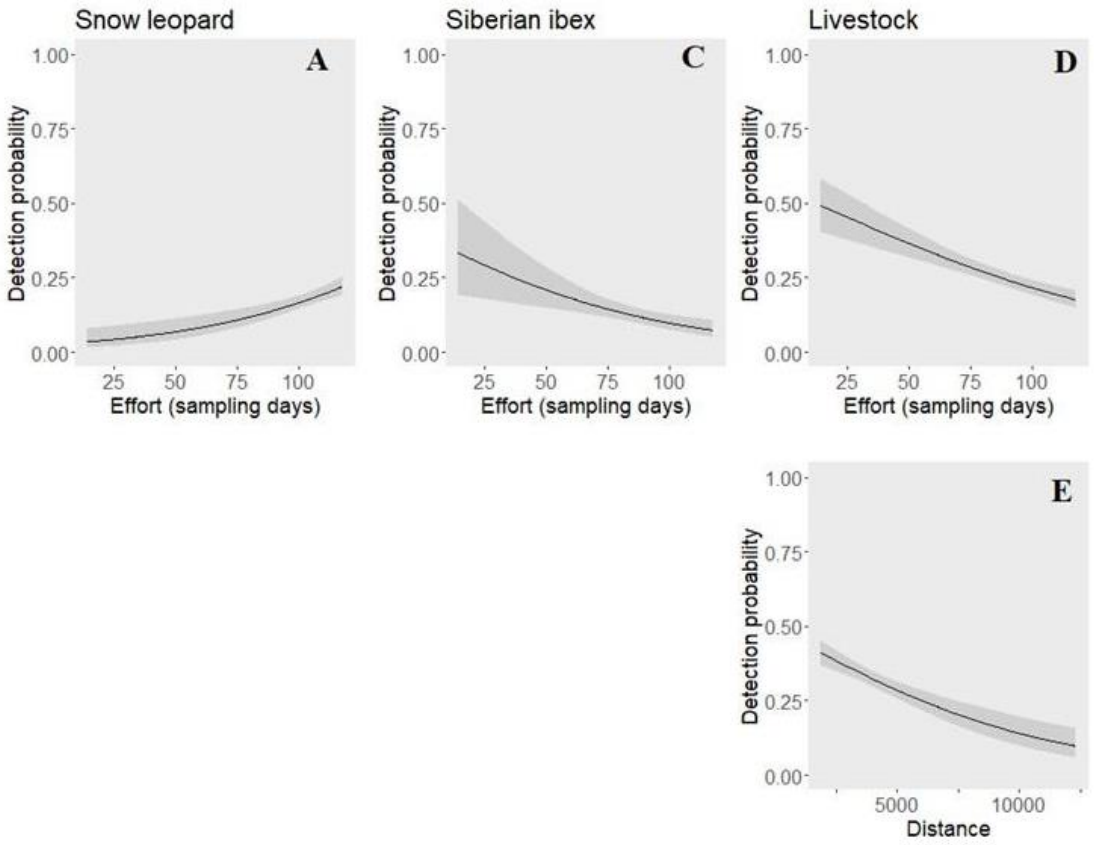

Figure S1.4.1. Relationships between single species detection probability and the significant covariates in the selected single-species occupancy models from camera-trapping surveys in four areas of western Mongolia

Appendix S1.5.

Table S1.5.1. Output of the best three co-occurrence models (i.e. with ΔAIC < 2) for snow leopard, wolf, Siberian ibex and livestock from camera trap surveys of four areas in western Mongolia.

Multi-species model	Co-occurrence parameter	Estimate	SE	Z	P(>|z|)	
M1						
	Livestock - snow leopard	-1.13	0.51	-2.2	0.03	*
	Livestock - wolf	1.14	0.46	2.5	0.01	*
	Siberian ibex – snow leopard	1.97	0.64	3.1	0.002	**
	Siberian ibex - wolf	-1.20	0.57	-2.1	0.04	*
	Snow leopard - wolf	1.24	0.58	2.1	0.03	*
M2						
	Livestock – Siberian ibex	-0.44	0.45	-0.98	0.33	
	Livestock - snow leopard	-0.87	0.56	-1.56	0.12	
	Livestock - wolf	1.02	0.47	2.2	0.03	*
	Siberian ibex – snow leopard	1.83	0.64	2.8	< 0.01	**
	Siberian ibex - wolf	-1.13	0.57	-2.0	0.04	*
	Snow leopard - wolf	1.17	0.57	2.1	0.04	*
M3						
	Livestock – Siberian ibex	-0.78	0.41	-1.9	0.06	·
	Livestock - wolf	0.83	0.46	1.8	0.07	·
	Siberian ibex – snow leopard	1.93	0.68	2.8	< 0.01	**
	Siberian ibex - wolf	-1.14	0.59	-1.9	0.05	·
	Snow leopard - wolf	1.06	0.57	1.9	0.06	·

Appendix S1.6

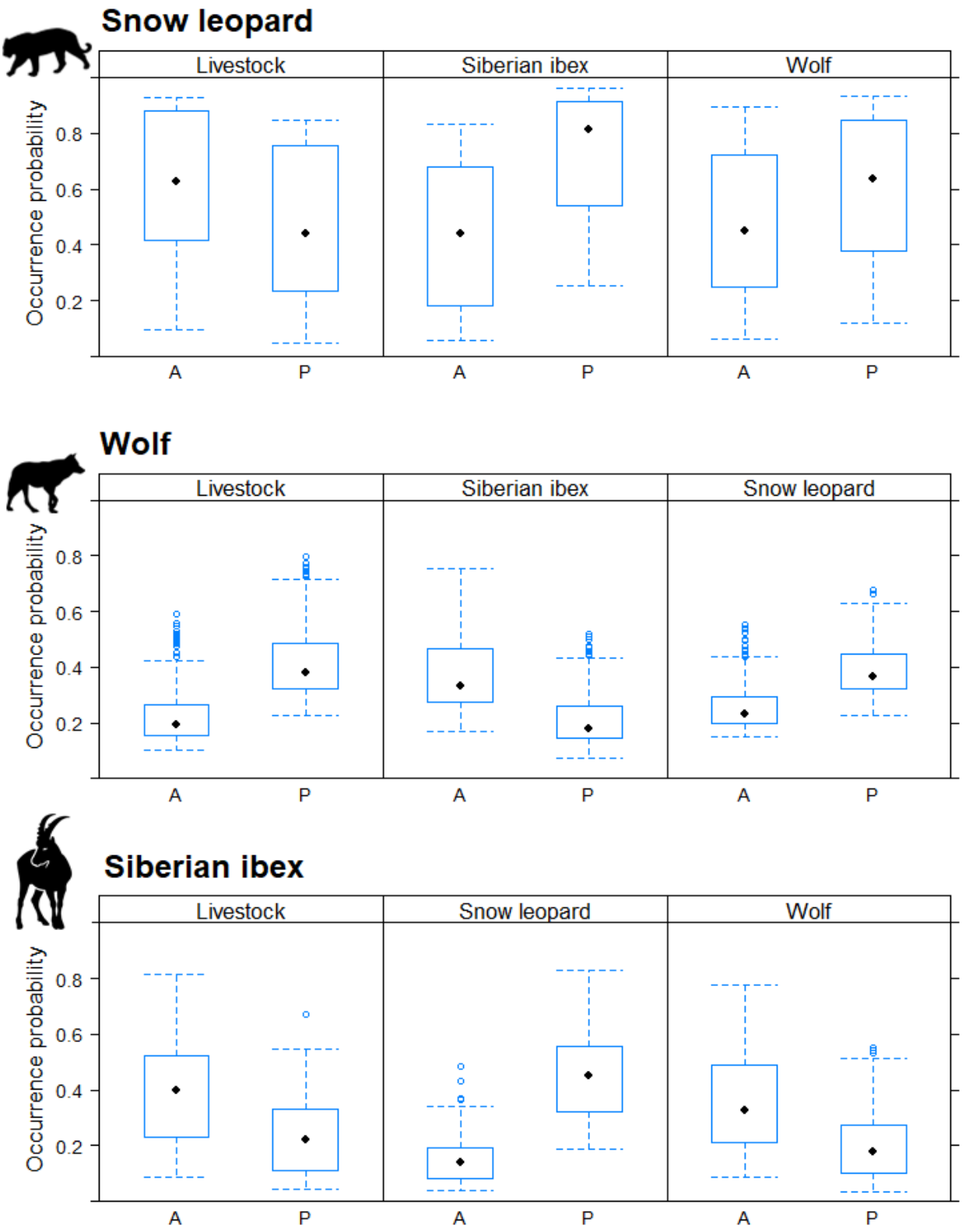

Figure S1.6.1. Predicted occurrence probabilities from the second ranked co-occurrence model M2, developed on camera-trapping data from four areas of western Mongolia. Each

species occupancy (y axis) is predicted conditional on the presence (P) or absence (A) of another (x axis), reported in each box title.

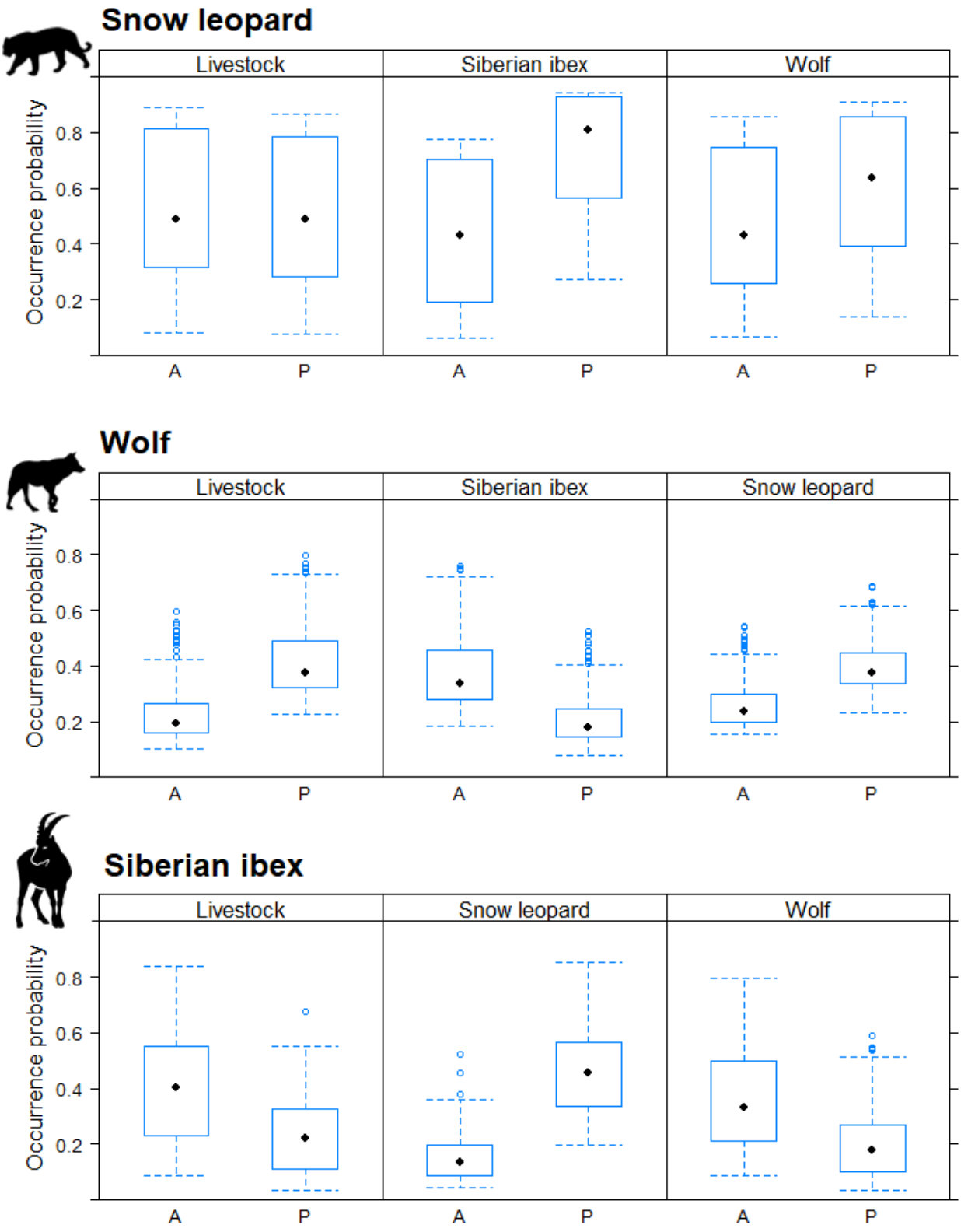

Figure S1.6.2. Predicted occurrence probabilities from the third ranked co-occurrence model M3, developed on camera-trapping data from four areas of western Mongolia. Each species occupancy (y axis) is predicted conditional on the presence (P) or absence (A) of another (x axis), reported in each box title

S2. Appendix of chapter 2

Appendix S2.1 – Sampling effort and resulting detections

Table S2.1.1. Summary of the sampling design and effort of systematic camera-trapping surveys in four areas of western Mongolia. Effort is expressed as mean number of sampling days per camera ± standard deviation. The area sampled is calculated as the minimum convex polygon around the camera-trap sites.

Area	Year	Protection status (PA extent)	Area sampled (km^2)	Elevation range sampled (m a.s.l.)	Nº of camera-trapping sites	Survey period	Effort (camera days)
Siilkhem-B	2015	National Park (760 km^2)	513	2231-3123	48	19/03 – 23/06	46.5 ± 6.6
Tavan Bogd	2017	National Park (3600 km^2)	720	2488-3489	44	07/04 – 2/06	48.2 ± 1.6
Khork Serkhe	2018	Strictly Protected Area (750 km^2)	1110	1965-3072	63	18/03 – 20/06	65.2 ± 5.8
Sutai	2019	Not protected	843	2115-3527	61	18/03 – 29/06	92.1 ± 15.3

Table S2.1.2. Checklist of wild and domestic species of mammals detected by area. Values are detections at the resolution of 1 day. Asterisks indicate species not included in the analysis because of a low number of detections and NAs indicate areas outside the distribution range of that species. The two species of *Lepus* and of *Marmota* were merged for statistical analyses.

Order	Species	Siilkhem-B	Tavan Bogd	Khork Serkhe	Sutai
Carnivora	*Canis lupus*	9	16	21	44
Artiodactyla	*Capra sibirica*	27	21	51	43
Carnivora	*Gulo gulo*	6	44	4	NA
Lagomorpha	*Lepus timidus*	15	34	NA	NA
Lagomorpha	*Lepus tolai*	NA	NA	27	52
Carnivora	*Lynx lynx**	0	0	1	0
Rodentia	*Marmota baibacina*	0	238	NA	NA
Rodentia	*Marmota sibirica*	207	NA	370	846
Carnivora	*Martes foina*	10	30	7	65
Carnivora	*Mustela erminea**	0	0	4	1
Carnivora	*Mustela eversmanii*	22	9	17	7
Lagomorpha	*Ochotona* spp.	0	4	119	43
Carnivora	*Otocolobus manul*	11	10	62	24
Artiodactyla	*Ovis ammon**	0	7	18	NA
Carnivora	*Panthera uncia*	14	2	39	224
Rodentia	*Sciurus vulgaris**	1	0	NA	NA
Rodentia	*Spermophilus* spp.	0	54	13	92
Carnivora	*Ursus arctos**	NA	2	NA	NA
Carnivora	*Vulpes vulpes*	75	61	191	288
Domestic species:	*Small-sized livestock*	134	45	140	144

Large-sized livestock	106	74	239	65

Appendix S2.2 – Modelling approach

The model includes a latent occupancy state (Z_{si}) for each of the s = 1, 2, …, S species at site i = 1,2, …, I, where Z_{si} is represented by a sequence of 0/1 values indicating whether each species s is present (1) or absent (0) at site i. The latent state is modelled using a probit distribution through an indicator function and a normally distributed random variable, $Z_{si} = \boldsymbol{I}(u_{si} > 0)$, where $\boldsymbol{I}$ is the indicator function which takes value 1 if the condition in brackets holds and 0 otherwise, and u_{si} is the random variable governing the occurrence z of species s at site i. Species occurrence u_{si} can then be modelled as a function of covariates $u_{si} = Xocc_i\beta occ_s + l_i\,\theta_s + \varepsilon_{si}$ where $Xocc_i$ is a vector of environmental covariates for site i, and βocc_s is the corresponding vector of species-specific regression coefficients for species s, treated as random effects from a common distribution of each βocc parameter in the community. A number T of latent variables $l_i = (l_{i1}, l_{i2}, \ldots, l_{iT})$ is introduced as unmeasured site-level covariates to account for residual correlation among species occupancy, with a corresponding species-specific vector of latent variable coefficients $\theta_s = (\theta_{s1}, \theta_{s2}, \ldots, \theta_{sT})$. The variance of the residuals ε_{si} is adjusted to account for the variance absorbed by the latent variables, calculating an adjusted variance $\sigma^2{}_s$ for each of the s species, so that $\sigma^2{}_s = 1 - \sum_{t=1}^{T} \theta_{st}^2$ and $\varepsilon_{si} \sim \text{Normal}(0, \sigma^2{}_s)$. The matrix M of inter-specific correlation c in occupancy can then be obtained from the correlation in the latent variables as $M = \theta\theta^T + diag(\sigma^2{}_1, \sigma^2{}_2, \ldots, \sigma^2{}_S)$. As suggested by Tobler et al. (2019) we used a number of latent variables equal to half the number of species, i.e. T = 7.

The observation component of the model relates the true underlying occupancy states Z_{si} to the observed detection frequencies y_{si} following a binomial distribution governed by the probability of detection p_{si} : $y_{si} \sim \text{Binomial}(K_i, Z_{si} \times p_{si})$, with y_{si} effectively representing the number of daily sampling occasions out of the total sampling days K_i when species s was detected at site i. Hence, $y_{si} \geq 1$ if the species s was detected at site i and $y_{si} = 0$ if it was not detected. Detection probability too was expressed as a function of site covariates, using a linear predictor in logit-scale: $\text{logit}(p_{si}) = Xobs_i\beta obs_s$, where $Xobs_i$ is a vector of detection covariates and βobs_s is a vector of species-specific regression coefficients related to the detection submodel.

Appendix S2.3 - Model coefficients estimates

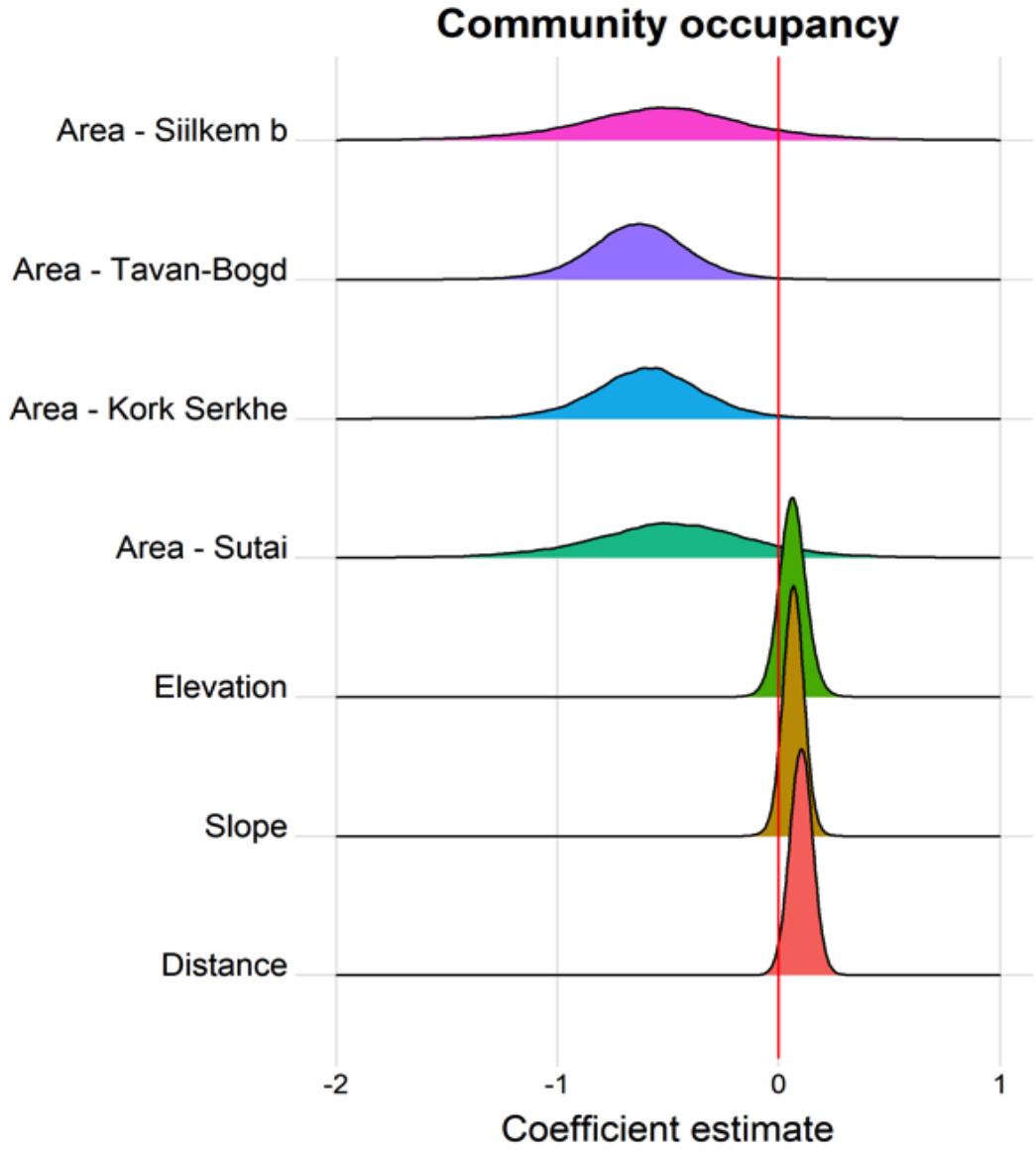

Figure S2.3.1. Parameter estimates of beta coefficients (x axis) for community occupancy covariates (y axis).

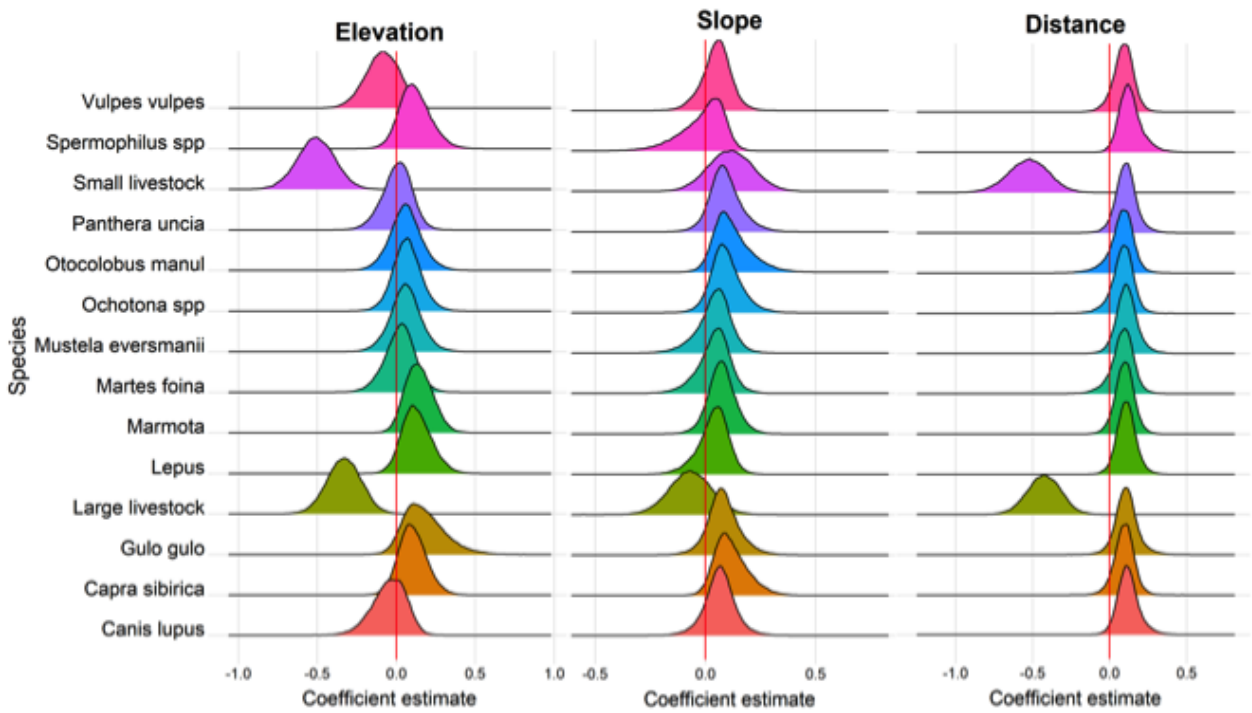

Figure S2.3.2. Parameter estimates of beta coefficients (x axis) for species-specific occupancy covariates. Species are listed in alphabetic order (y axis) for each covariate.

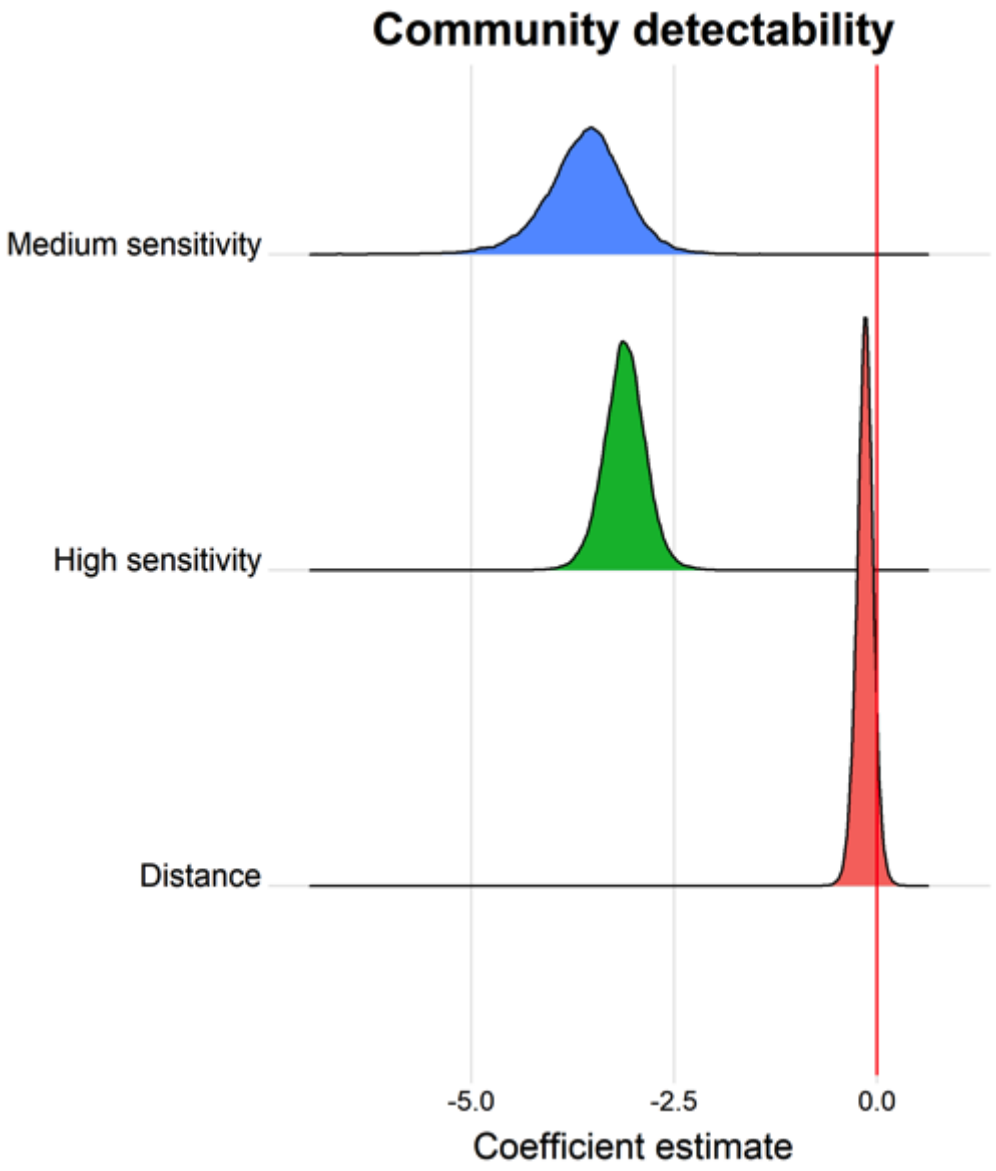

Figure S2.3.3. Parameter estimates of beta coefficients (x axis) for community detectability covariates (y axis).

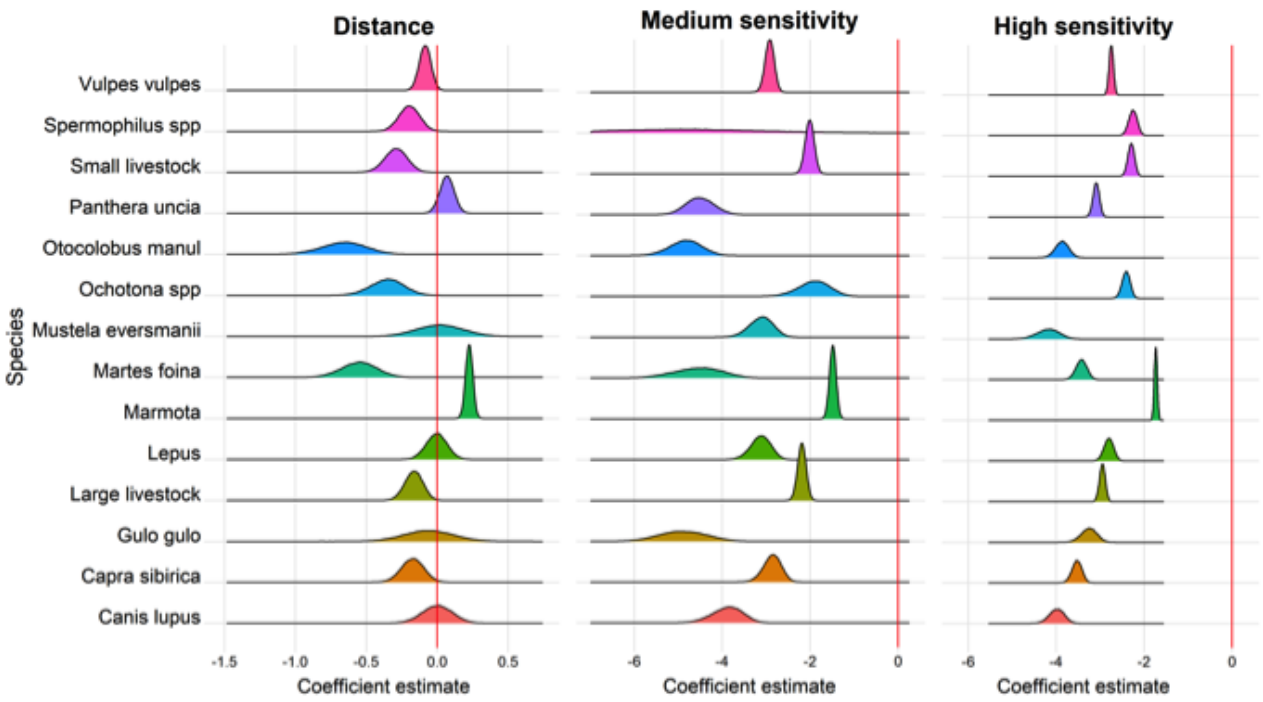

Figure S2.3.4. Parameter estimates of beta coefficients (x axis) for species-specific detectability covariates. Species are listed in alphabetic order (y axis) for each covariate.

S3. Appendix of chapter 3

Appendix S3.1

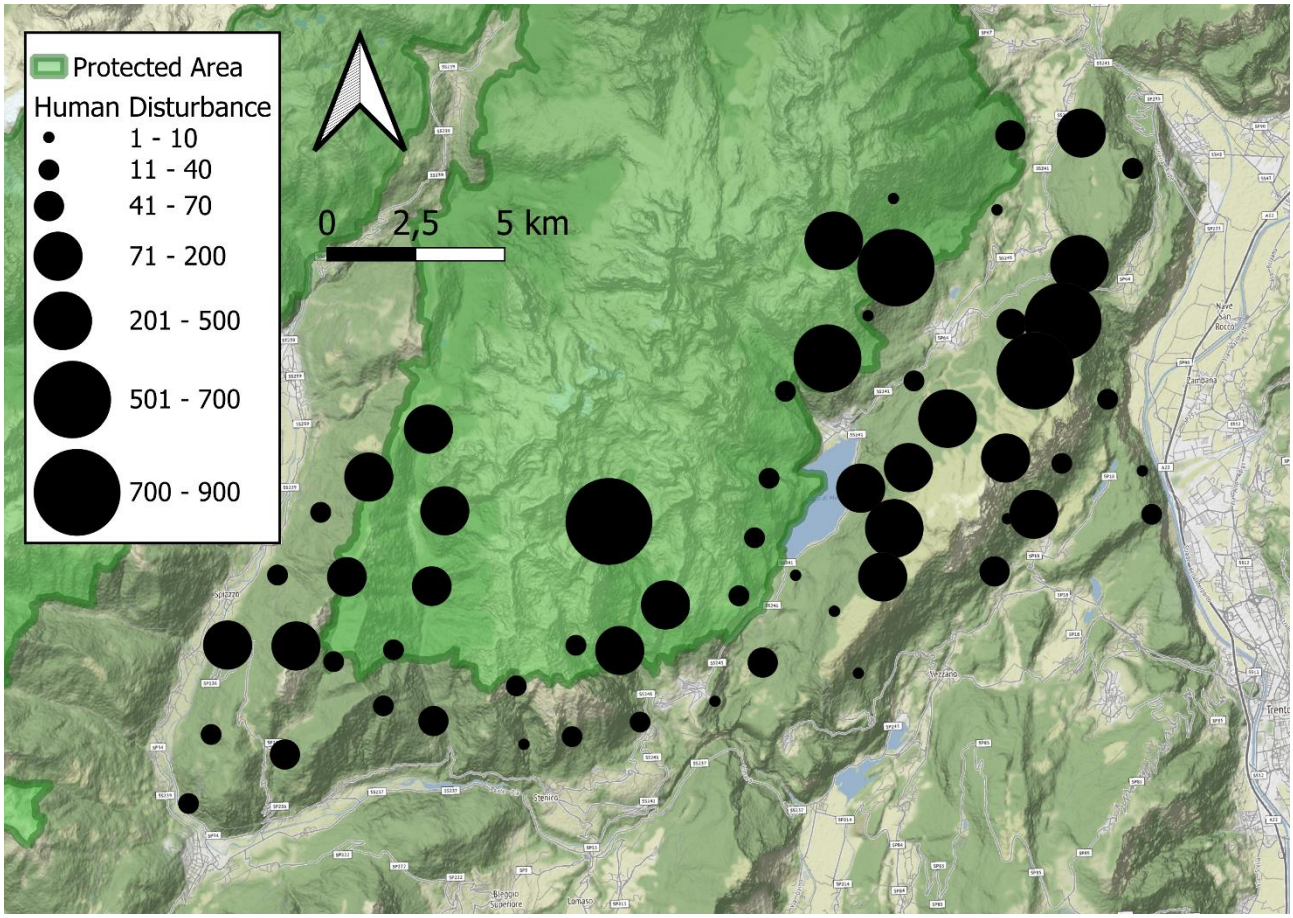

Figure S3.1.1. Map of the rate of human disturbance in the study area in the central Alps. Each dot indicates a camera-trapping site monitored in 7 consecutive summers from 2015 to 2021, and its size is proportional to the average RAI (events normalized by sampling effort) of humans (vehicles included). The PNAB protected area is denoted by the light green color and dark green borders.

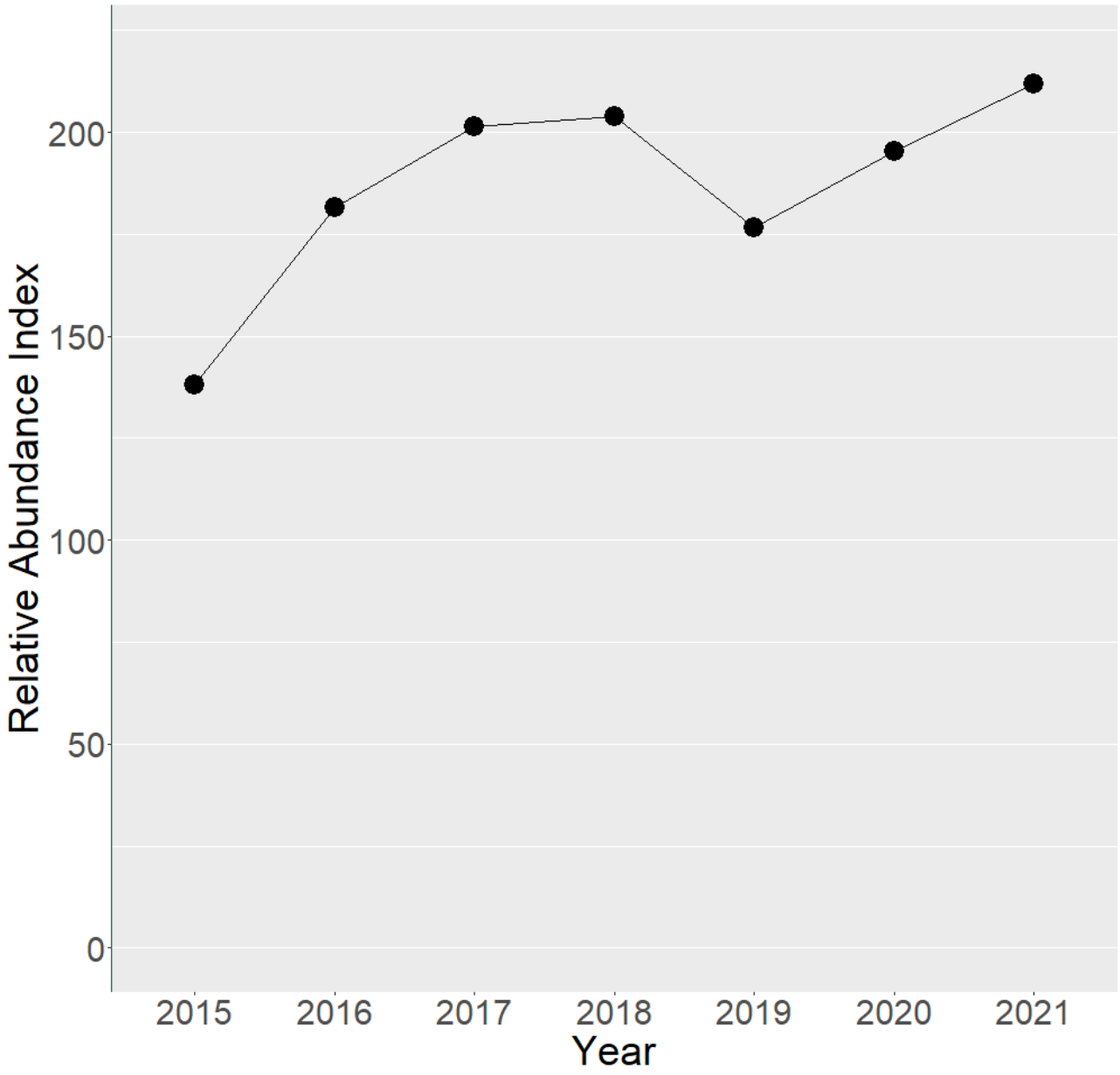

Figure S3.1.2. RAI of humans and vehicles derived from seven years of systematic camera-trapping in the central Alps. The relative abundance index (RAI) of each year was calculated as the total number of independent events divided by the total number of sampling days and multiplied by 100.

Appendix S3.2

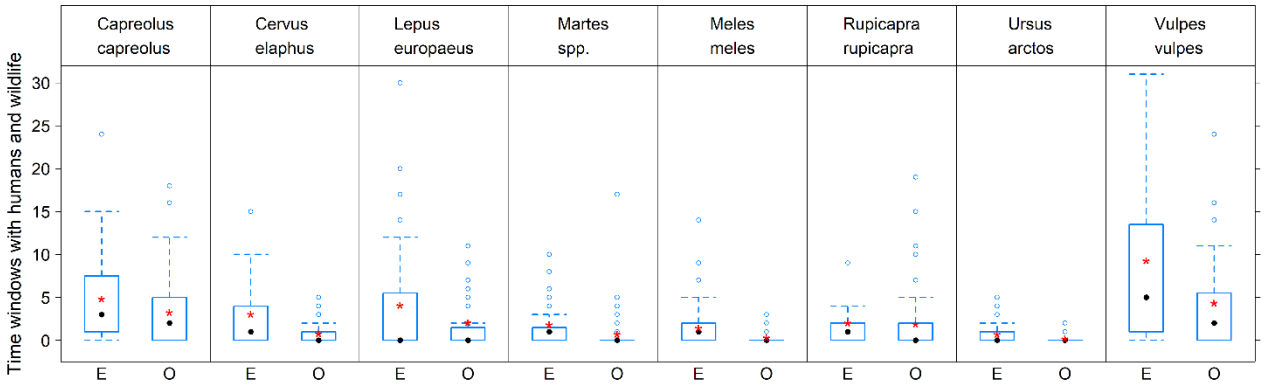

Figure S3.2.1. Observed (O) and expected (E) number of time windows with both humans and each mammal species from seven years of systematic camera-trapping in the central Alps. Species are indicated on the top labels.

Appendix S3.3

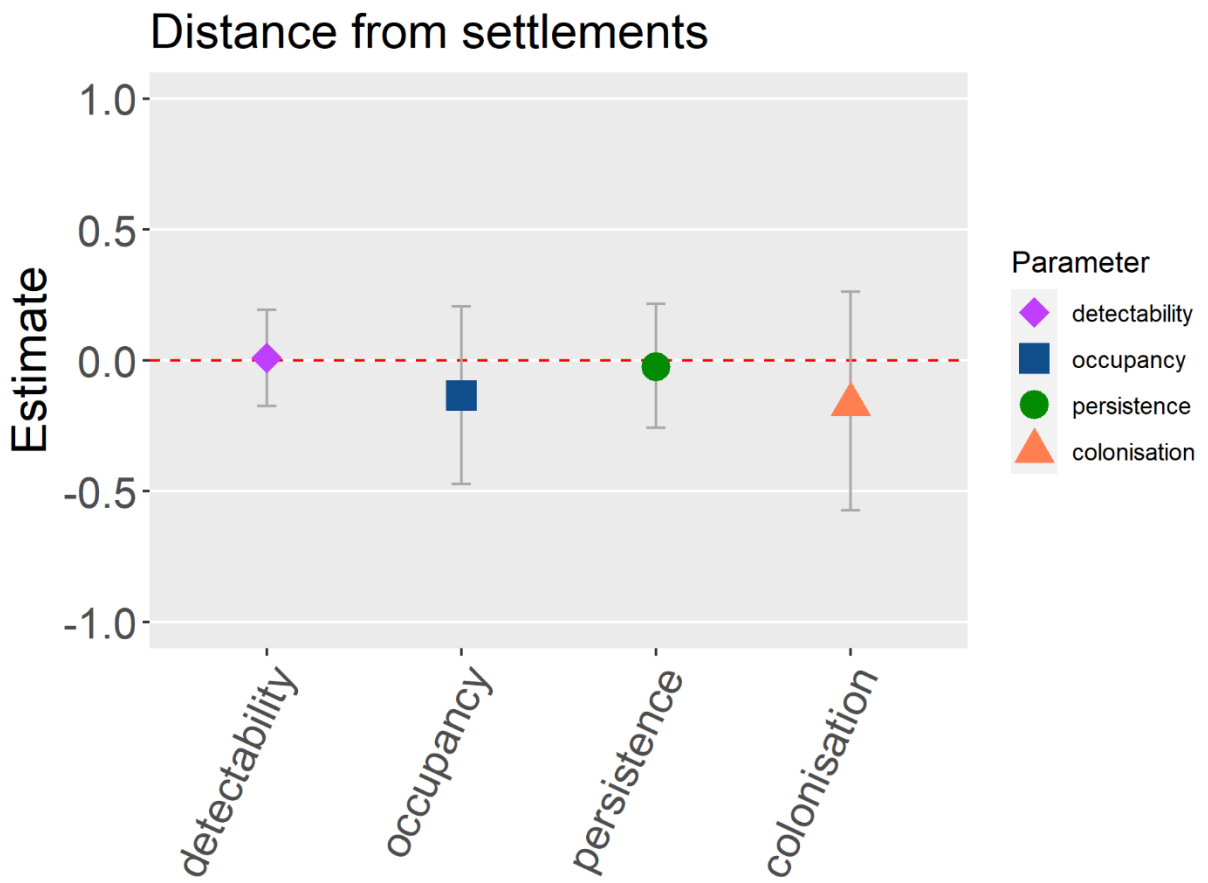

Figure S3.3.1. Estimates of the effect of distance from the closest human settlement on community-level detection probability (pink diamond), occupancy (blue square), persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals.

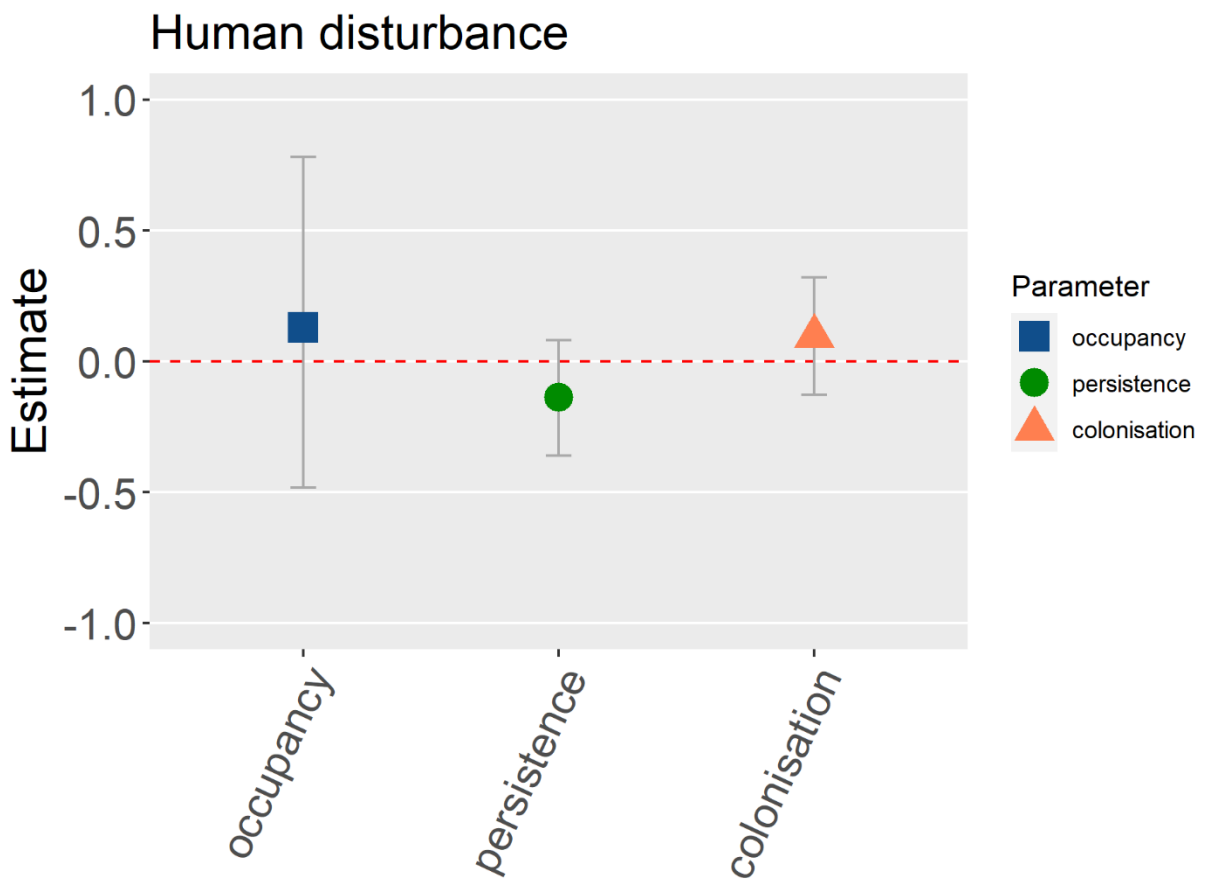

Figure S3.3.2. Estimates of the effect of human disturbance (as RAI, i.e. number of photographic events normalized on sampling effort) on community-level occupancy (blue square), persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals.

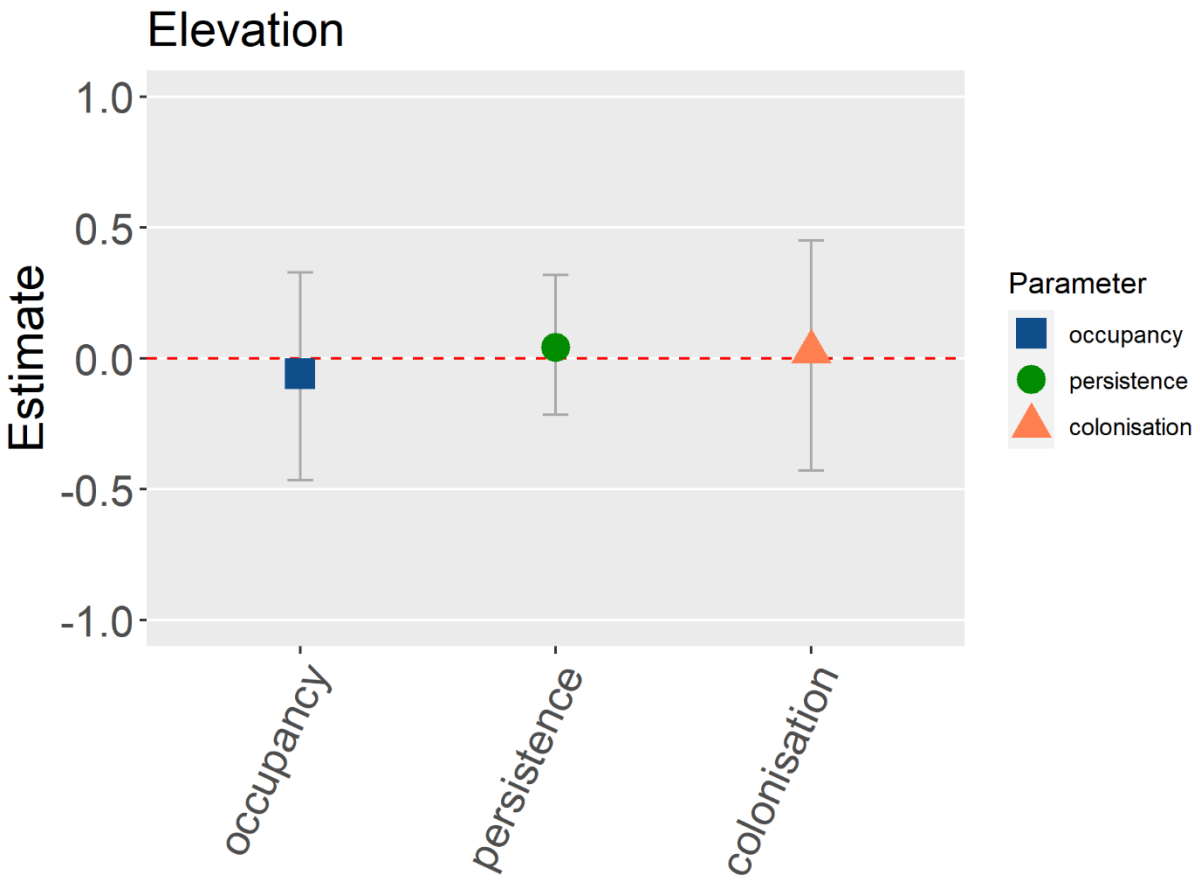

Figure S3.3.3. Estimates of the effect of elevation on community-level occupancy (blue square), persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals.

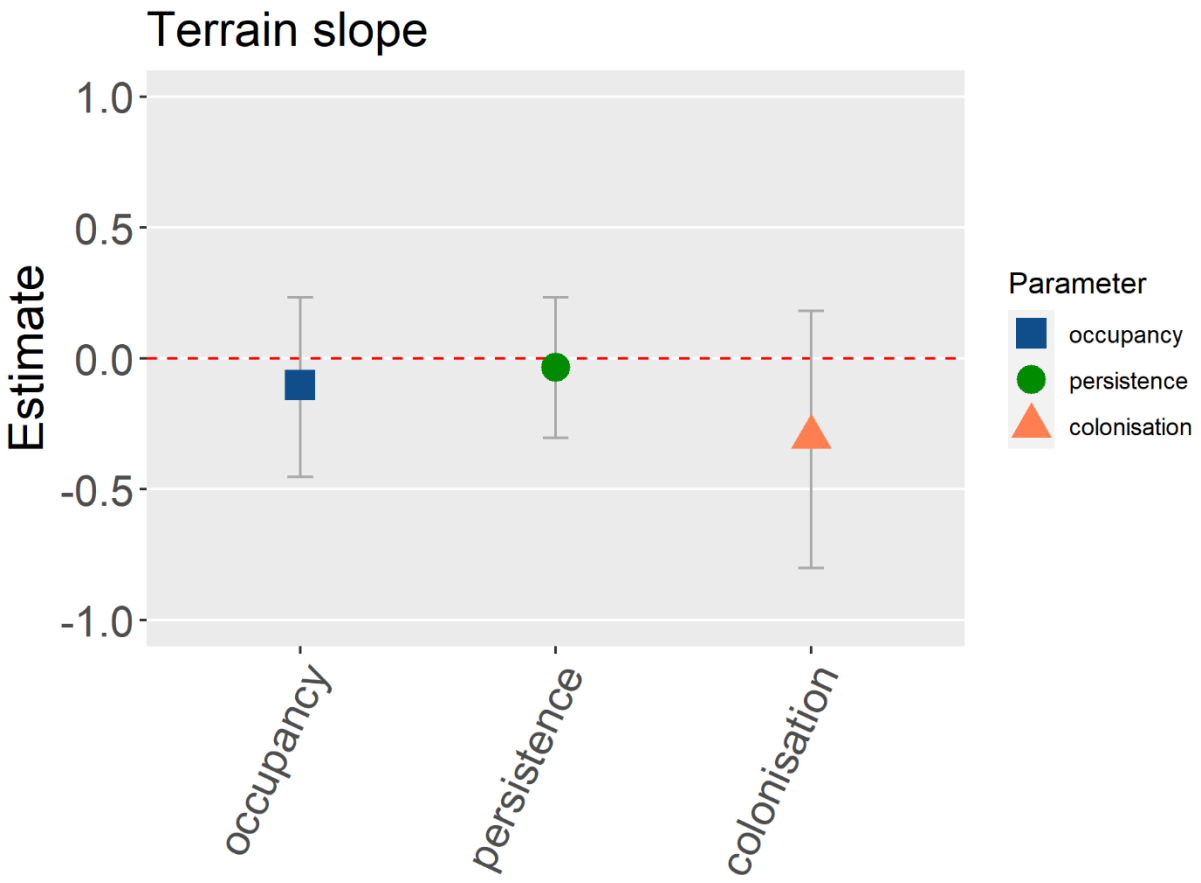

Figure S3.3.4. Estimates of the effect of terrain slope on community-level occupancy (blue square), persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals.

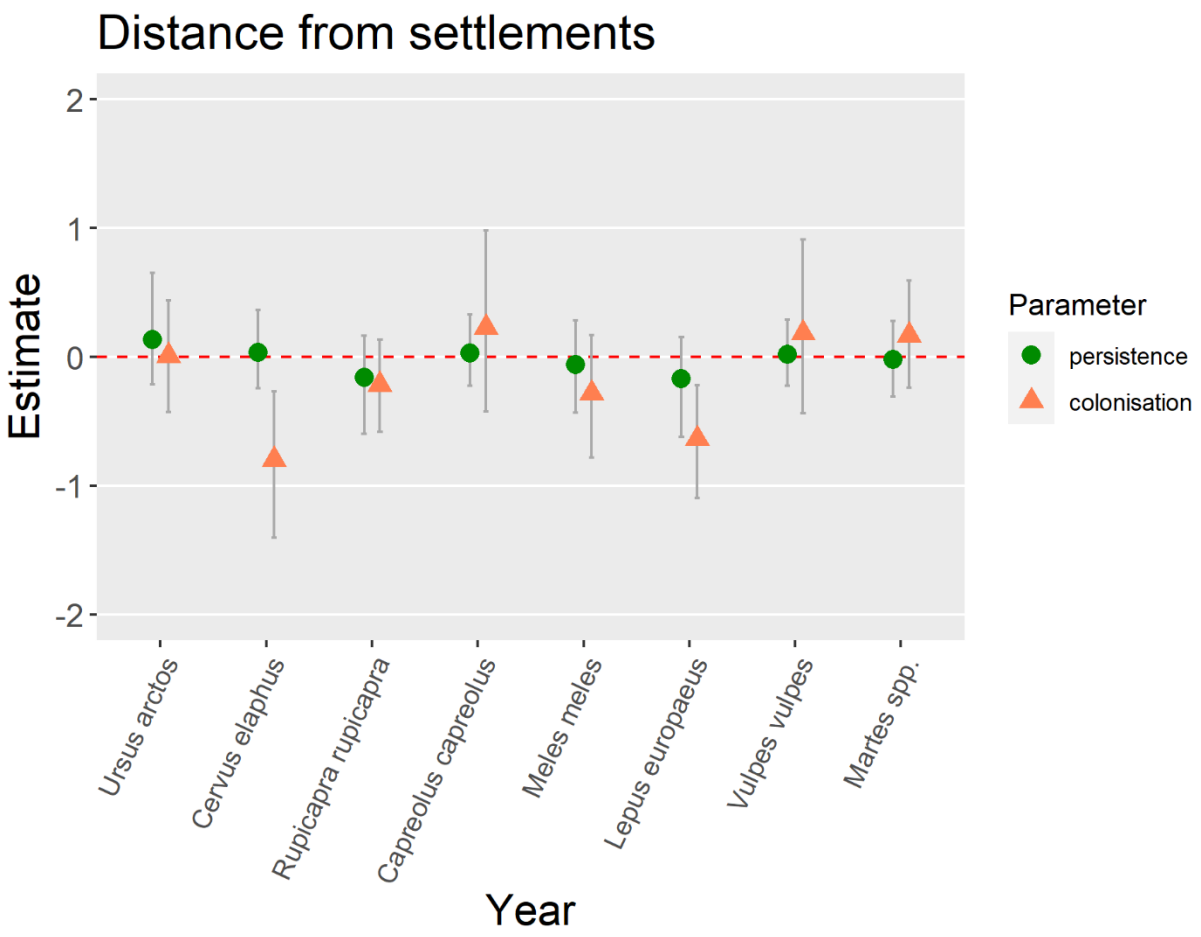

Figure S3.3.5. Estimates of the effect of distance from the closest human settlement on species-level persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals, and species are shown on the x axis, ordered by body mass.

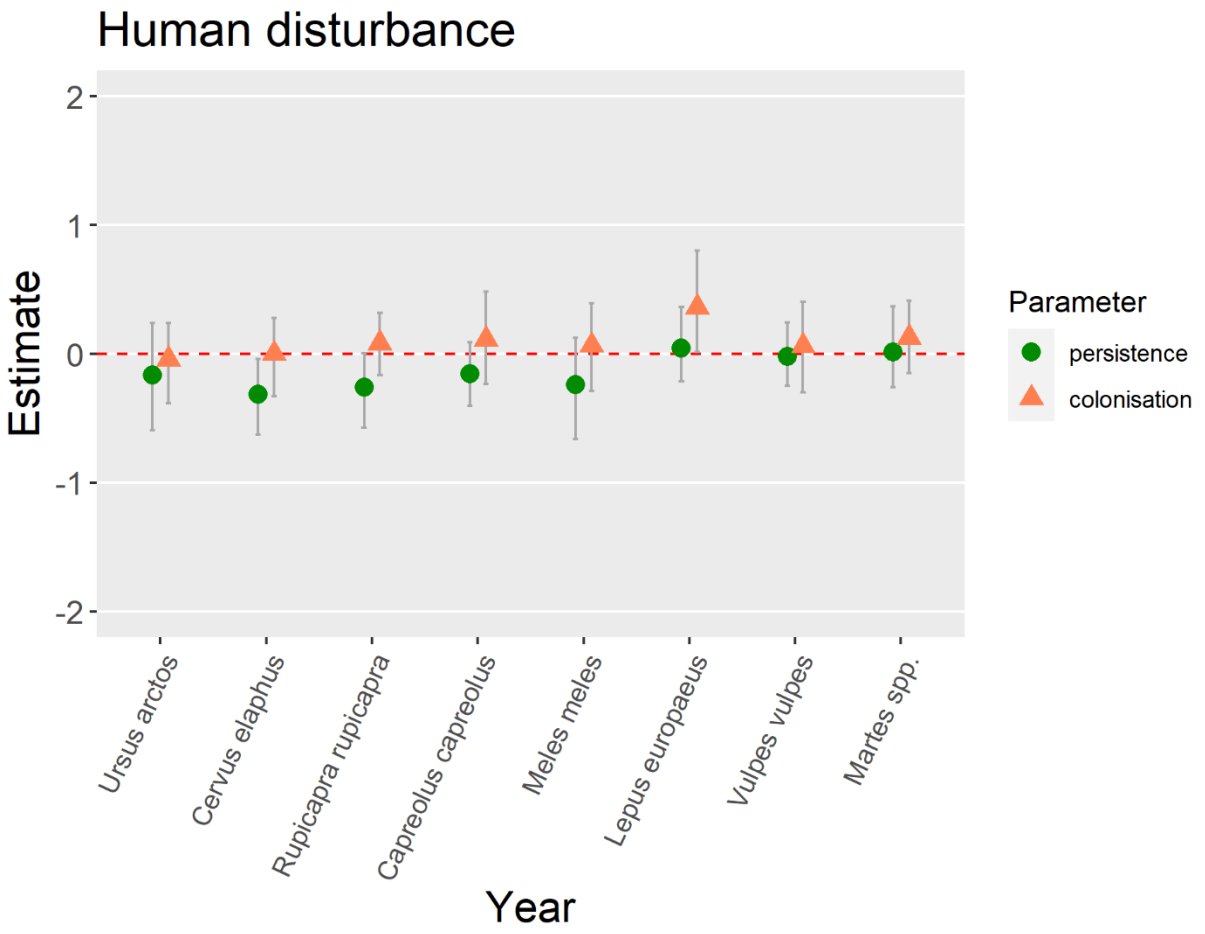

Figure S3.3.6. Estimates of the effect of human disturbance (as RAI, i.e. number of photographic events normalized on sampling effort) on species-level persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals, and species are shown on the x axis, ordered by body mass.

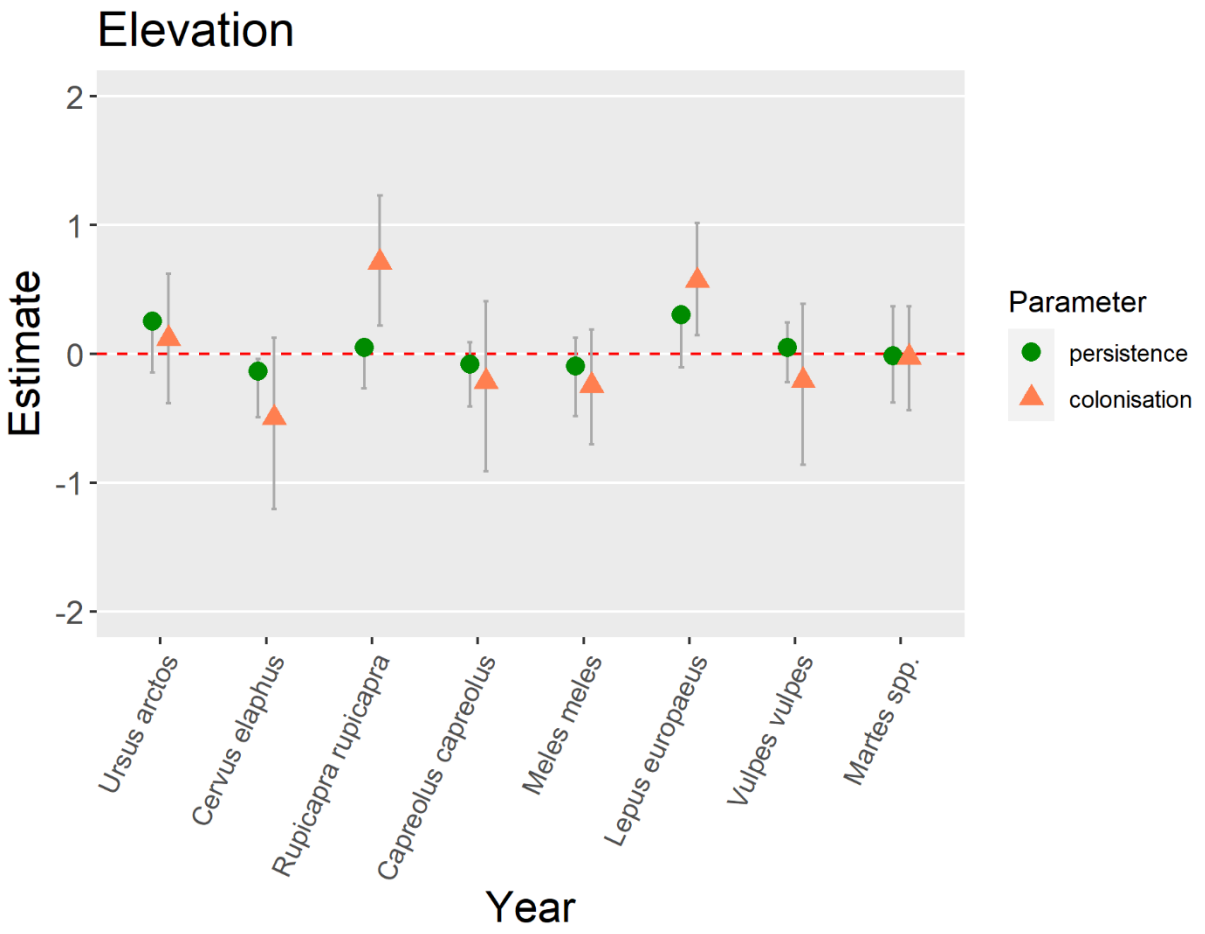

Figure S3.3.7. Estimates of the effect of elevation on species-level persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals, and species are shown on the x axis, ordered by body mass.

Figure S3.3.8. Estimates of the effect of terrain slope on species-level persistence probability (green circle) and colonization probability (orange triangle), from 7 years of systematic camera-trapping in the central Alps. Grey bars indicate 90% credible intervals, and species are shown on the x axis, ordered by body mass.

Table S3.3.1. Estimates of regression coefficients for community-level parameters from the dynamic community occupancy model applied on 7 years of systematic camera-trapping data in the Central Alps. 'Human' stands for the number of photographic events of humans, 'Distance' for distance from the closest human settlement, while 'Road dirt' refers to the categorical variable track type and 'Camera' to the camera-trap model.

species	parameter	variable	estimate	5%	95%
community	occupancy	Distance	-0.13	-0.47	0.21
community	occupancy	Humans	0.13	-0.48	0.78
community	occupancy	Elevation	-0.06	-0.47	0.33
community	occupancy	Slope	-0.10	-0.45	0.23
community	persistence	Distance	-0.02	-0.26	0.22
community	persistence	Humans	-0.14	-0.36	0.08
community	persistence	Elevation	0.04	-0.22	0.32
community	persistence	Slope	-0.03	-0.30	0.23
community	colonisation	Distance	-0.17	-0.57	0.26
community	colonisation	Humans	0.10	-0.13	0.32
community	colonisation	Elevation	0.03	-0.43	0.45
community	colonisation	Slope	-0.30	-0.80	0.18
community	detectability	Road dirt	-0.02	-0.33	0.29
community	detectability	Distance	0.01	-0.17	0.19
community	detectability	Camera	1.29	0.50	2.10

Table S3.3.2. Estimates of regression coefficients for species-level parameters from the dynamic community occupancy model applied on 7 years of systematic camera-trapping data in the Central Alps. 'Humans' stands for the number of photographic events of humans,

'Distance' for distance from the closest human settlement, while 'Road dirt' refers to the categorical variable track type and 'Camera' to the camera-trap model.

species	parameter	variable	estimate	5%	95%
Bear	occupancy	Distance	-0.13	-0.60	0.34
Bear	occupancy	Humans	-0.41	-1.30	0.34
Bear	occupancy	Elevation	-0.19	-0.85	0.34
Bear	occupancy	Slope	-0.25	-0.84	0.23
Red deer	occupancy	Distance	-0.14	-0.54	0.27
Red deer	occupancy	Humans	-0.75	-1.58	-0.02
Red deer	occupancy	Elevation	-0.18	-0.72	0.28
Red deer	occupancy	Slope	-0.25	-0.70	0.14
Chamois	occupancy	Distance	-0.06	-0.45	0.37
Chamois	occupancy	Humans	-0.30	-0.97	0.30
Chamois	occupancy	Elevation	0.27	-0.21	0.84
Chamois	occupancy	Slope	0.26	-0.17	0.77
Roe deer	occupancy	Distance	-0.05	-0.47	0.46
Roe deer	occupancy	Humans	0.04	-0.63	0.75
Roe deer	occupancy	Elevation	-0.08	-0.61	0.41
Roe deer	occupancy	Slope	-0.27	-0.83	0.18
Badger	occupancy	Distance	-0.24	-0.76	0.19
Badger	occupancy	Humans	0.67	-0.08	1.56
Badger	occupancy	Elevation	-0.32	-0.99	0.21
Badger	occupancy	Slope	-0.04	-0.48	0.43
Hare	occupancy	Distance	-0.29	-0.82	0.13
Hare	occupancy	Humans	0.75	0.05	1.55

Hare	occupancy	Elevation	0.07	-0.39	0.60
Hare	occupancy	Slope	-0.26	-0.75	0.14
Red fox	occupancy	Distance	-0.11	-0.60	0.42
Red fox	occupancy	Humans	0.56	-0.50	1.91
Red fox	occupancy	Elevation	-0.08	-0.75	0.55
Red fox	occupancy	Slope	-0.10	-0.75	0.53
Martes	occupancy	Distance	-0.06	-0.48	0.42
Martes	occupancy	Humans	0.51	-0.22	1.37
Martes	occupancy	Elevation	0.04	-0.49	0.61
Martes	occupancy	Slope	0.09	-0.35	0.62
Bear	persistence	Distance	0.13	-0.21	0.65
Bear	persistence	Humans	-0.16	-0.59	0.24
Bear	persistence	Elevation	0.25	-0.15	0.81
Bear	persistence	Slope	0.16	-0.21	0.60
Red deer	persistence	Distance	0.03	-0.25	0.36
Red deer	persistence	Humans	-0.31	-0.62	-0.04
Red deer	persistence	Elevation	-0.13	-0.49	0.17
Red deer	persistence	Slope	0.06	-0.23	0.35
Chamois	persistence	Distance	-0.16	-0.60	0.17
Chamois	persistence	Humans	-0.26	-0.57	0.00
Chamois	persistence	Elevation	0.05	-0.27	0.39
Chamois	persistence	Slope	0.36	-0.02	0.76
Roe deer	persistence	Distance	0.03	-0.22	0.33
Roe deer	persistence	Humans	-0.16	-0.41	0.09
Roe deer	persistence	Elevation	-0.08	-0.41	0.21

Roe deer	persistence	Slope	-0.24	-0.56	0.04
Badger	persistence	Distance	-0.06	-0.43	0.28
Badger	persistence	Humans	-0.24	-0.66	0.12
Badger	persistence	Elevation	-0.09	-0.48	0.23
Badger	persistence	Slope	-0.30	-0.69	0.04
Hare	persistence	Distance	-0.17	-0.62	0.15
Hare	persistence	Humans	0.05	-0.21	0.36
Hare	persistence	Elevation	0.30	-0.11	0.85
Hare	persistence	Slope	-0.33	-0.76	0.04
Red fox	persistence	Distance	0.02	-0.22	0.29
Red fox	persistence	Humans	-0.02	-0.25	0.24
Red fox	persistence	Elevation	0.05	-0.22	0.33
Red fox	persistence	Slope	0.04	-0.21	0.30
Martes	persistence	Distance	-0.02	-0.31	0.28
Martes	persistence	Humans	0.01	-0.26	0.37
Martes	persistence	Elevation	-0.01	-0.38	0.33
Martes	persistence	Slope	-0.03	-0.36	0.30
Bear	colonisation	Distance	0.01	-0.43	0.44
Bear	colonisation	Humans	-0.04	-0.38	0.24
Bear	colonisation	Elevation	0.12	-0.38	0.62
Bear	colonisation	Slope	0.26	-0.14	0.69
Red deer	colonisation	Distance	-0.80	-1.40	-0.27
Red deer	colonisation	Humans	0.00	-0.33	0.28
Red deer	colonisation	Elevation	-0.50	-1.20	0.13
Red deer	colonisation	Slope	-1.07	-1.63	-0.58

Chamois	colonisation	Distance	-0.22	-0.58	0.13
Chamois	colonisation	Humans	0.08	-0.16	0.32
Chamois	colonisation	Elevation	0.71	0.22	1.23
Chamois	colonisation	Slope	-0.13	-0.52	0.25
Roe deer	colonisation	Distance	0.23	-0.42	0.98
Roe deer	colonisation	Humans	0.11	-0.23	0.48
Roe deer	colonisation	Elevation	-0.21	-0.91	0.41
Roe deer	colonisation	Slope	-1.12	-1.75	-0.55
Badger	colonisation	Distance	-0.28	-0.78	0.17
Badger	colonisation	Humans	0.07	-0.29	0.39
Badger	colonisation	Elevation	-0.25	-0.70	0.19
Badger	colonisation	Slope	-0.12	-0.49	0.24
Hare	colonisation	Distance	-0.64	-1.10	-0.22
Hare	colonisation	Humans	0.36	0.01	0.80
Hare	colonisation	Elevation	0.57	0.15	1.02
Hare	colonisation	Slope	-0.29	-0.59	0.00
Red fox	colonisation	Distance	0.19	-0.44	0.91
Red fox	colonisation	Humans	0.06	-0.30	0.40
Red fox	colonisation	Elevation	-0.20	-0.86	0.39
Red fox	colonisation	Slope	-0.48	-0.96	-0.02
Martes	colonisation	Distance	0.17	-0.24	0.59
Martes	colonisation	Humans	0.13	-0.15	0.41
Martes	colonisation	Elevation	-0.03	-0.44	0.37
Martes	colonisation	Slope	0.53	0.21	0.87
Bear	detectability	Road dirt	-0.54	-0.79	-0.30

Bear	detectability	Distance	0.29	0.16	0.42
Bear	detectability	Camera	0.82	0.20	1.43
Red deer	detectability	Road dirt	0.32	0.22	0.42
Red deer	detectability	Distance	0.16	0.11	0.22
Red deer	detectability	Camera	0.36	0.08	0.65
Chamois	detectability	Road dirt	0.35	0.23	0.47
Chamois	detectability	Distance	0.32	0.24	0.40
Chamois	detectability	Camera	-0.25	-0.59	0.10
Roe deer	detectability	Road dirt	-0.41	-0.49	-0.32
Roe deer	detectability	Distance	-0.22	-0.26	-0.17
Roe deer	detectability	Camera	0.87	0.62	1.12
Badger	detectability	Road dirt	-0.24	-0.42	-0.06
Badger	detectability	Distance	-0.27	-0.37	-0.18
Badger	detectability	Camera	2.17	1.44	2.91
Hare	detectability	Road dirt	0.54	0.38	0.70
Hare	detectability	Distance	0.12	0.05	0.20
Hare	detectability	Camera	1.60	0.95	2.26
Red fox	detectability	Road dirt	0.12	0.05	0.20
Red fox	detectability	Distance	-0.22	-0.26	-0.18
Red fox	detectability	Camera	2.73	2.19	3.20
Martes	detectability	Road dirt	-0.29	-0.47	-0.11
Martes	detectability	Distance	-0.10	-0.19	-0.02
Martes	detectability	Camera	2.26	1.34	3.19

Appendix S3.4

Table S3.4.1. Table of the model selection for the number of photographic events of eight mammalian species from 7 years of systematic camera-trapping in the central Alps. For each species the models within ΔAIC<2, that were used for model averaging, are listed together with the null model with sampling effort (total number of camera-trap days) as only covariate, shown as a reference. 'Human' stands for the number of photographic events of humans, 'Distance' for distance from the closest human settlement, while 'Elevation' and 'Slope' are topographic variables.

species	model	AIC	ΔAIC
Bear	Effort+Human+Elevation	337.0	0
Bear	Effort+Human +Elevation+Slope	337.3	0.3
Bear	Effort+Human +Distance+Elevation	337.3	0.4
Bear	Effort+Human +Distance+Elevation+Slope	337.7	0.7
Bear	Effort +Elevation+Slope	338.4	1.4
Bear	Effort+Distance +Elevation+Slope	338.7	1.7
Bear	Effort+Distance+Slope	338.8	1.9
Bear	Effort+Human +Distance	338.9	1.9
Bear	…		
Bear	Effort	345	8.0
Red Deer	Effort+Human	519.6	0
Red Deer	Effort+Human+Elevation	519.9	0.4
Red Deer	Effort+Human+Distance+Elevation	520.2	0.7
Red Deer	Effort+Human+Slope	521.0	1.4
Red Deer	Effort+Human +Elevation+Slope	521.4	1.8
Red Deer	Effort+Human+Distance	521.5	2.0

Red Deer	…		
Red Deer	Effort	525.0	5.4
Chamois	Effort+Human +Elevation+Slope	435.4	0
Chamois	Effort+Human+Distance+Slope	436.7	1.4
Chamois	Effort+Human+Elevation	437.1	1.7
Chamois	Effort+Human+Distance+Elevation+Slope	437.2	1.8
Chamois	Effort+Human+Slope	437.3	1.9
Chamois	Effort+Human+Distance	437.4	1.9
Chamois	…		
Chamois	Effort	440.0	4.6
Roe Deer	Effort+Elevation+Slope	553.0	0
Roe Deer	Effort+Human+Elevation+Slope	553.6	0.6
Roe Deer	Effort+Distance+Elevation+Slope	555.0	1.9
Roe Deer	…		
Roe Deer	Effort	562.6	9.6
Badger	Effort+Distance+Elevation	383.7	0
Badger	Effort +Distance	383.7	0.1
Badger	Effort+Elevation	385.0	1.3
Badger	Effort+Distance+Slope	385.2	1.5
Badger	Effort +Distance+Elevation+Slope	385.2	1.5
Badger	Effort+Human+Distance	385.7	1.9
Badger	Effort+Human+Distance+Elevation	385.7	1.9
Badger	…		
Badger	Effort	393.2	9.5
Hare	Effort+Human+Distance+Elevation+Slope	365.9	0

Hare	Effort+Human+Distance+Slope	367.7	1.7
Hare	…		
Hare	Effort	380.6	14.7
Red Fox	Effort+Human+Distance+Slope	602.5	0
Red Fox	Effort+Human+Distance+Elevation+Slope	602.7	0.2
Red Fox	Effort+Human+Distance+Elevation	602.8	0.3
Red Fox	Effort+Human+Distance	603.0	0.5
Red Fox	Effort+Human+Elevation+Slope	603.1	0.6
Red Fox	Effort+Human+Elevation	603.2	0.7
Red Fox	…		
Red Fox	Effort	613.0	10.6
Martes spp.	Effort+Slope	388.1	0
Martes spp.	Effort+Human+Slope	389.2	1.1
Martes spp.	Effort+Distance+Slope	389.8	1.7
Martes spp.	Effort+Elevation+Slope	389.9	1.8
Martes spp.	…		
Martes spp.	Effort	391.5	3.4

S4. Appendix of chapter 4

Appendix S4.1

Table S4.1.1. Summary of the number of active sampling sites and effort (expressed as number of the cumulative number of days cameras were active) for each area, with the resulting number of pictures collected, in total and divided by category (humans, vehicles, domestic animals and wild mammals).

Area	1	2	3	4
Sites	58	60	27	59
Effort (camera days)	2032	2100	2519	1968
All photos	81420	86154	66852	124974
Humans	53971	45772	20106	55446
Vehicles	5901	4874	562	9252
Domestic animals	10032	9546	2569	21480
Wild mammals	12082	15129	24428	57421

Table S4.1.2. Summary of the global parameters of interest from the multi-region regression model on number of events and the multi-region occupancy model. β_{day}- coefficients are parameters used to model diurnality, β_{night}- coefficients are parameters used to model nocturnality, β_{crep}- coefficients are parameters used to model crepuscularity, α-coefficients represent variables used to model the detection probability (*p*), β- coefficients represent

parameters used to model community occupancy probability (ψ). Table depicts the mean of the full posterior distribution, the related SD, and the 90% Bayesian Credible Interval (BCI).

Submodel	Parameter	Variable	mean	SE	2.5% BCI	97.5% BCI
Diurnality	μλday[1]	intercept diurnality Area 1	-0.5	0.11	-0.72	-0.28
	μλday[2]	intercept diurnality Area 2	-0.34	0.08	-0.49	-0.19
	μλday[3]	intercept diurnality Area 3	-1.57	0.08	-1.74	-1.41
	μλday[4]	intercept diurnality Area 4	-1.81	0.11	-2.03	-1.59
	μβ1day global	RAI Human	-0.57	0.13	-0.79	-0.36
	μβ2day global	Dist. To Settlements	0.02	0.14	-0.21	0.25
Nocturnality	μλnight[1]	intercept nocturnality Area 1	-0.22	0.09	-0.39	-0.06
	μλnight[2]	intercept nocturnality Area 2	1.47	0.03	1.41	1.52
	μλnight[3]	intercept nocturnality Area 3	0.99	0.02	0.94	1.04
	μλnight[4]	intercept nocturnality Area 4	0.72	0.03	0.65	0.78
	μβ1night global	RAI Human	-0.03	0.07	-0.15	0.08
	μβ2night global	Dist. To Settlements	-0.13	0.11	-0.31	0.05

Crepuscularity	μλcrep[1]	intercept crepuscularity Area 1	-0.78	0.11	-1.00	-0.57
	μλcrep[2]	intercept crepuscularity Area 2	0.35	0.05	0.25	0.45
	μλcrep[3]	intercept crepuscularity Area 3	-0.52	0.05	-0.62	-0.42
	μλcrep[4]	intercept crepuscularity Area 4	-0.44	0.06	-0.55	-0.33
	μβ1crep global	RAI Human	-0.17	0.08	-0.32	-0.04
	μβ2crep global	Dist. To Settlements	-0.14	0.11	-0.32	0.04
Detection probability	α0[1]	intercept detection Area 1	-1.95	0.07	-2.10	-1.81
	α0[2]	intercept detection Area 2	-2.02	0.38	-2.96	-1.41
	α0[3]	intercept detection Area 3	-1.81	0.05	-1.91	-1.72
	α0[4]	intercept detection Area 4	-1.59	0.03	-1.64	-1.52
	μα1 global	Dist. To Settlements	0.07	0.11	-0.14	0.29
	μα2 global	RAI Human	-0.07	0.07	-0.21	0.06
	μα3 global	Camera	-0.8	0.31	-1.41	-0.19
	μα4 global	Camera	-1.19	0.60	-2.36	0.05
Occupancy probability	β0[1]	intercept occupancy Area 1	-0.40	0.21	-0.81	0.00
	β0[2]	intercept occupancy Area 2	0.68	0.27	0.18	1.21

	β0[3]	intercept occupancy Area 3	0.41	0.15	0.12	0.71
	β0[4]	intercept occupancy Area 4	-0.37	0.15	-0.67	-0.08
	μβ1 global	RAI Human	0.11	0.09	-0.07	0.30
	μβ2 global	Dist. To Settlements	-0.27	0.16	-0.58	0.04
	μβ3 global	Elevation	0.00	0.20	-0.40	0.40
	μβ4 global	Slope	0.01	0.09	-0.16	0.18

Appendix S4.2

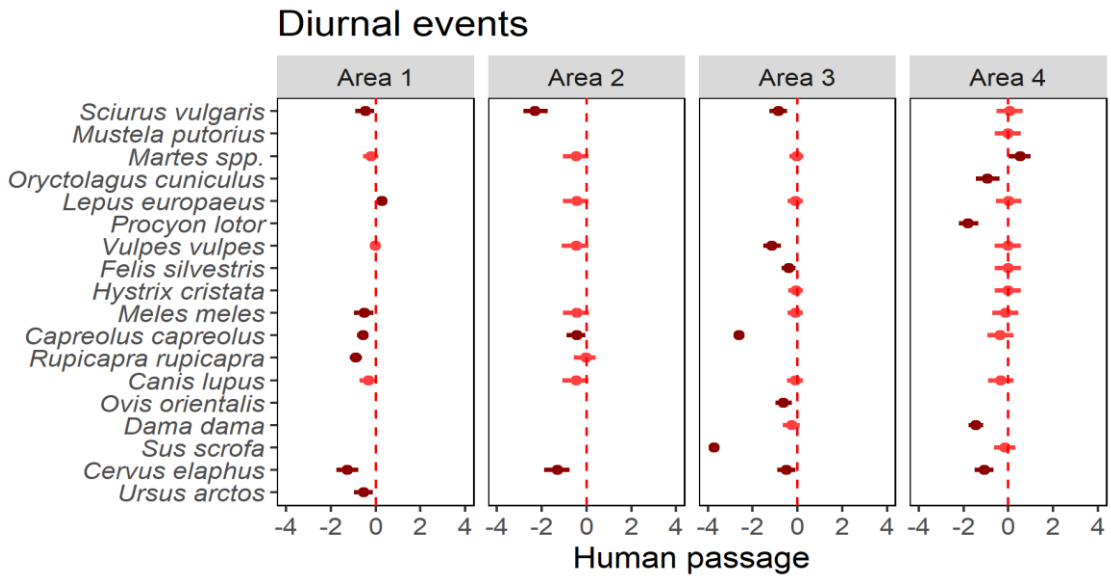

Figure S4.2.1. Species- and region-specific diurnal site-use probabilities in relation to human passage (RAI of humans), estimated from the multi-region regression model. Caterpillar plots depict beta coefficients with mean and 90% BCI. Darker red color indicates coefficients whose 90% BCI does not overlap 0, whereas coefficients in light red present a 90% BCI that does overlap 0.

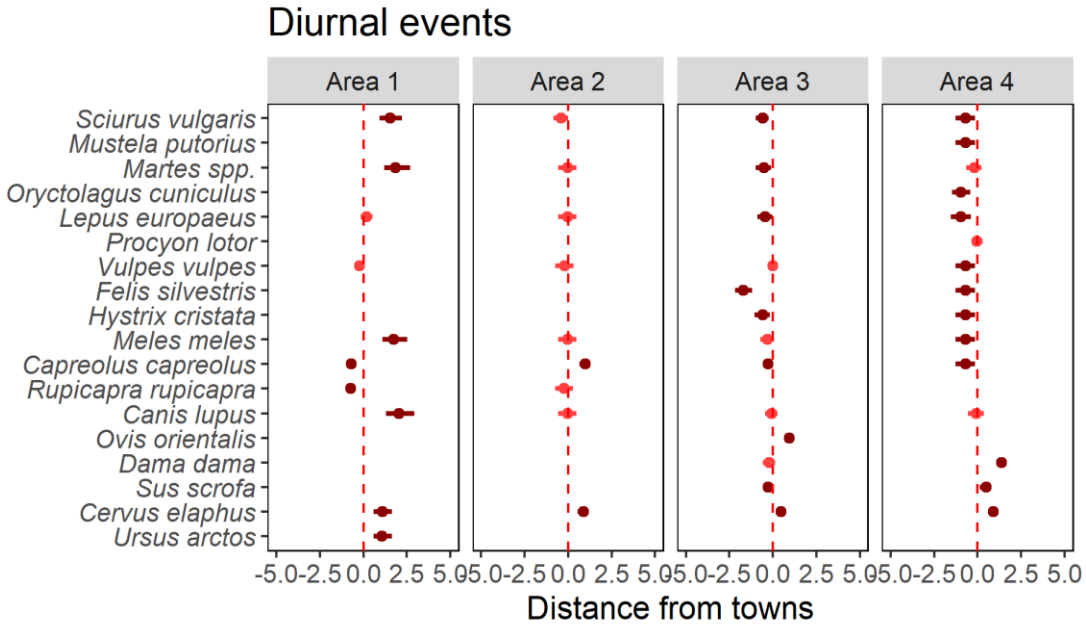

Figure S4.2.2. Species- and region-specific diurnal site-use probabilities in relation to distance from closest town, estimated from the multi-region regression model. Caterpillar plots depict beta coefficients with mean and 90% BCI. Darker red color indicates coefficients whose 90% BCI does not overlap 0, whereas coefficients in light red present a 90% BCI that does overlap 0.

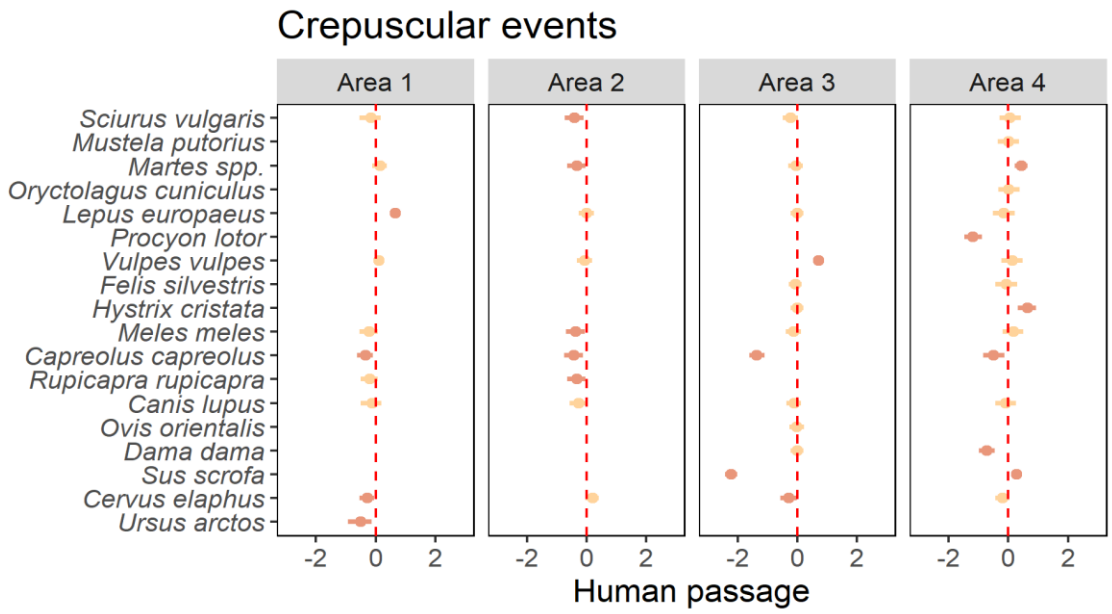

Figure S4.2.3. Species- and region-specific crepuscular site-use probabilities in relation to human passage (RAI of humans), estimated from the multi-region regression model. Caterpillar plots depict beta coefficients with mean and 90% BCI. Darker orange color indicates coefficients whose 90% BCI does not overlap 0, whereas coefficients in light orange present a 90% BCI that does overlap 0.

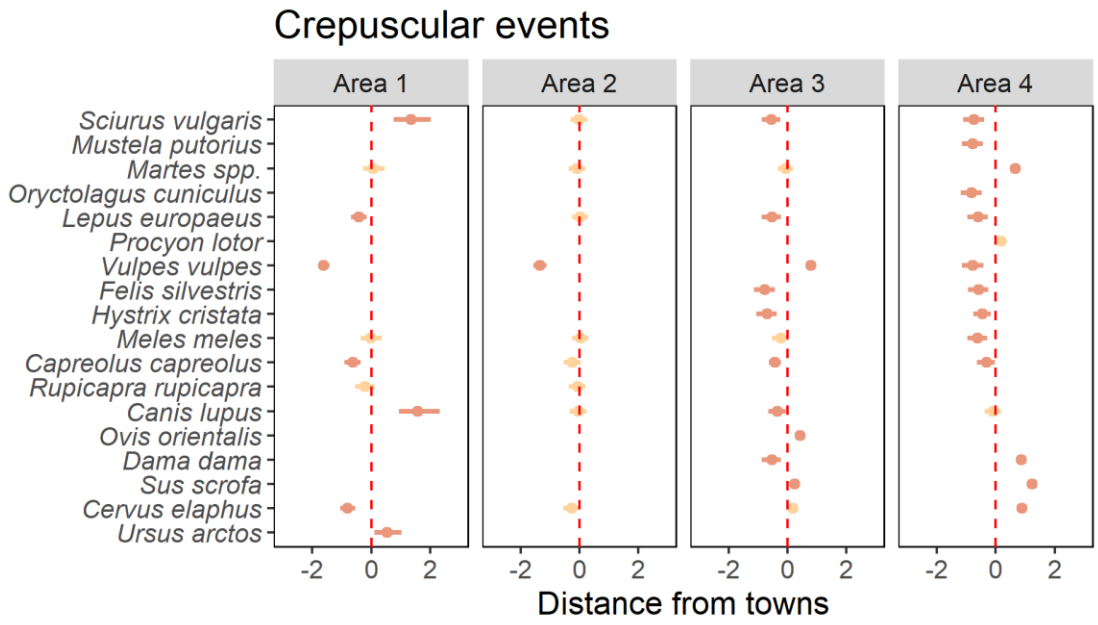

Figure S4.2.4. Species- and region-specific crepuscular site-use probabilities in relation to distance to the closest town, estimated from the multi-region regression model. Caterpillar plots depict beta coefficients with mean and 90% BCI. Darker orange color indicates coefficients whose 90% BCI does not overlap 0, whereas coefficients in light orange present a 90% BCI that does overlap 0.

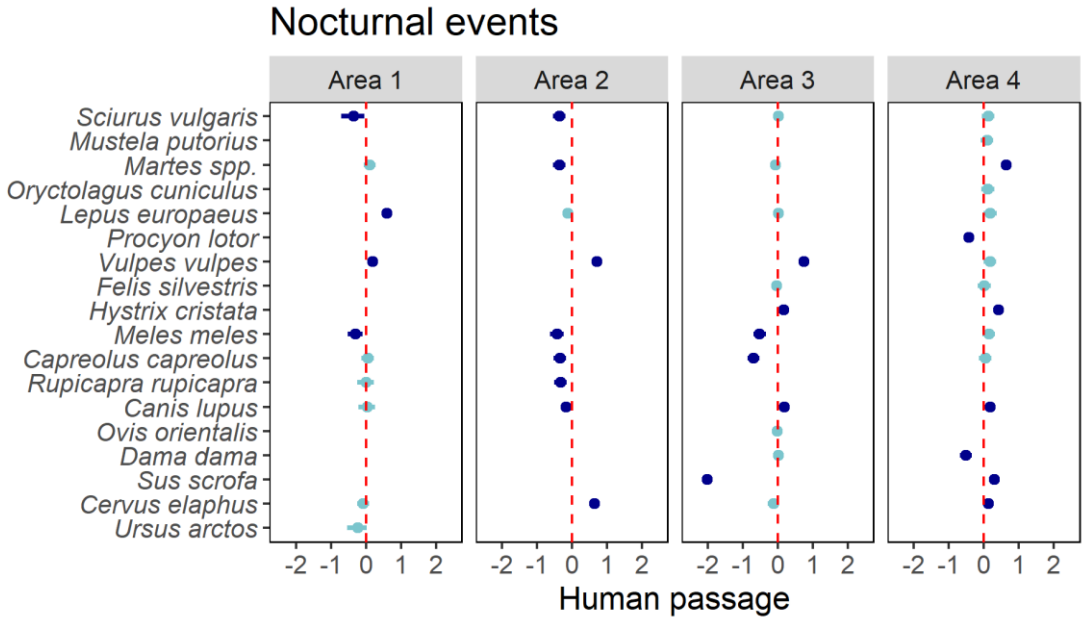

Figure S4.2.5. Species- and region-specific nocturnal site-use probabilities in relation to human passage (RAI of humans), estimated from the multi-region regression model. Caterpillar plots depict beta coefficients with mean and 90% BCI. Darker blue color indicates

coefficients whose 90% BCI does not overlap 0, whereas coefficients in light blue present a 90% BCI that does overlap 0.

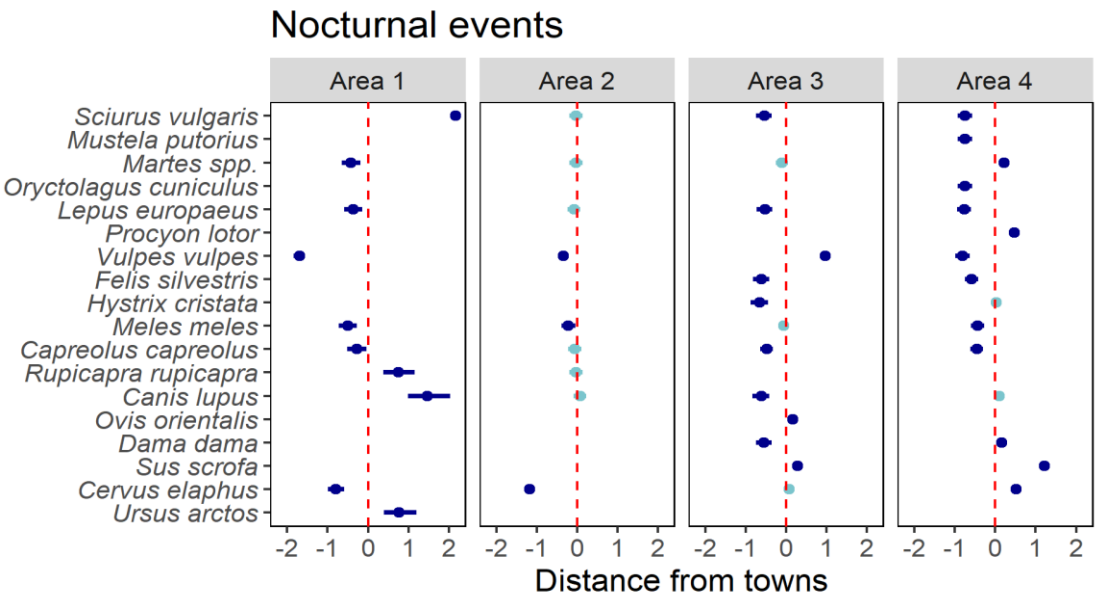

Figure S4.2.6. Species- and region-specific nocturnal site-use probabilities in relation to distance to the closest town, estimated from the multi-region regression model. Caterpillar plots depict beta coefficients with mean and 90% BCI. Darker blue color indicates coefficients whose 90% BCI does not overlap 0, whereas coefficients in light blue present a 90% BCI that does overlap 0.

Appendix S4.3

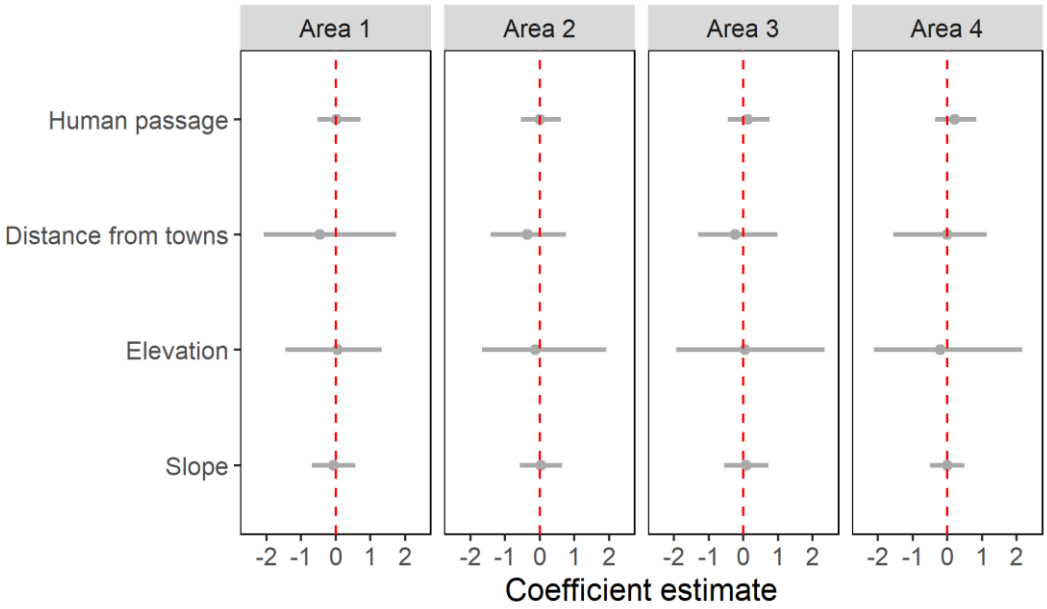

Figure S4.3.1. Region- specific coefficient estimates for the effect of anthropogenic and environmental variables on community occupancy. Caterpillar plots show mean estimates and 90% BCI.

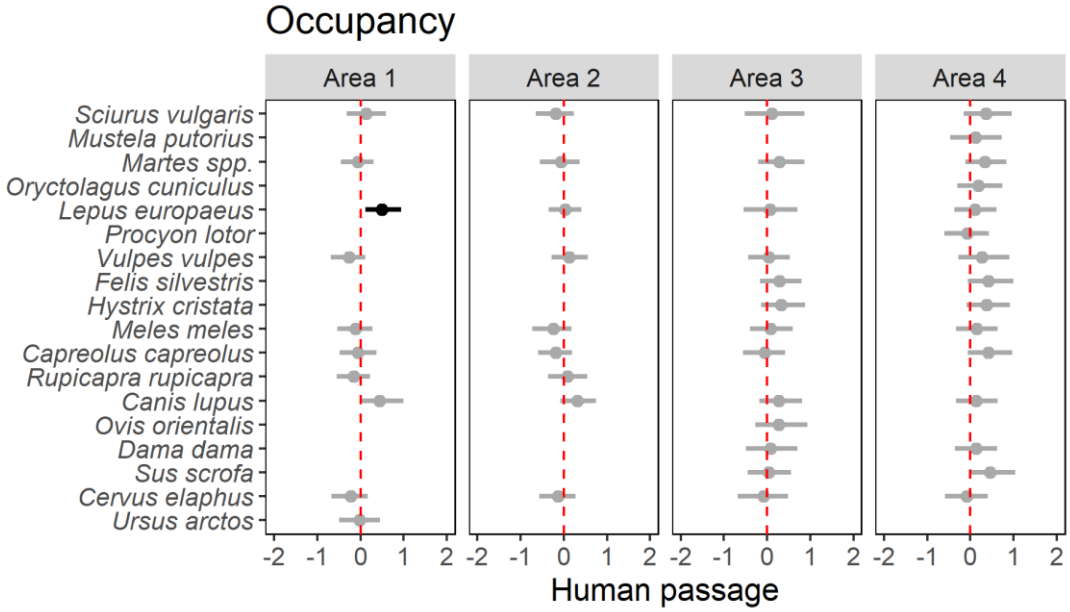

Figure S4.3.2. Region- and species- specific coefficient estimates for the effect of human passage (RAI of humans) on occupancy. Caterpillar plots show mean estimates and 90% BCI.

Black color indicates coefficients whose 90% BCI does not overlap 0, whereas gray color indicates coefficients whose 90% BCI does overlap 0.

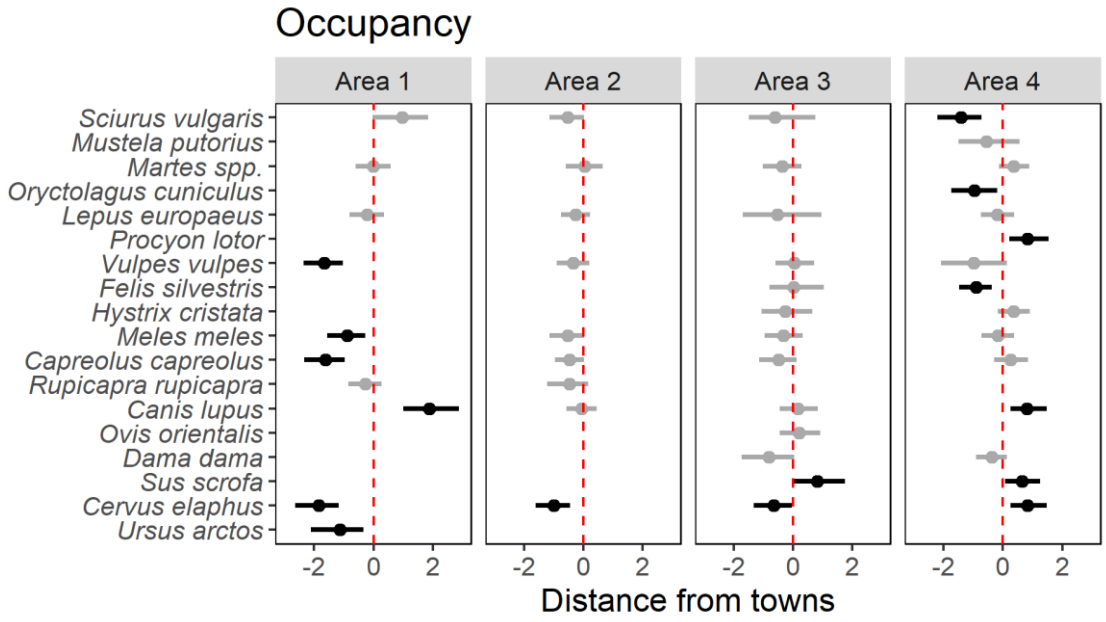

Figure S4.3.3. Region- and species- specific coefficient estimates for the effect of distance from closest town on occupancy. Caterpillar plots show mean estimates and 90% BCI. Black color indicates coefficients whose 90% BCI does not overlap 0, whereas gray color indicates coefficients whose 90% BCI does overlap 0.

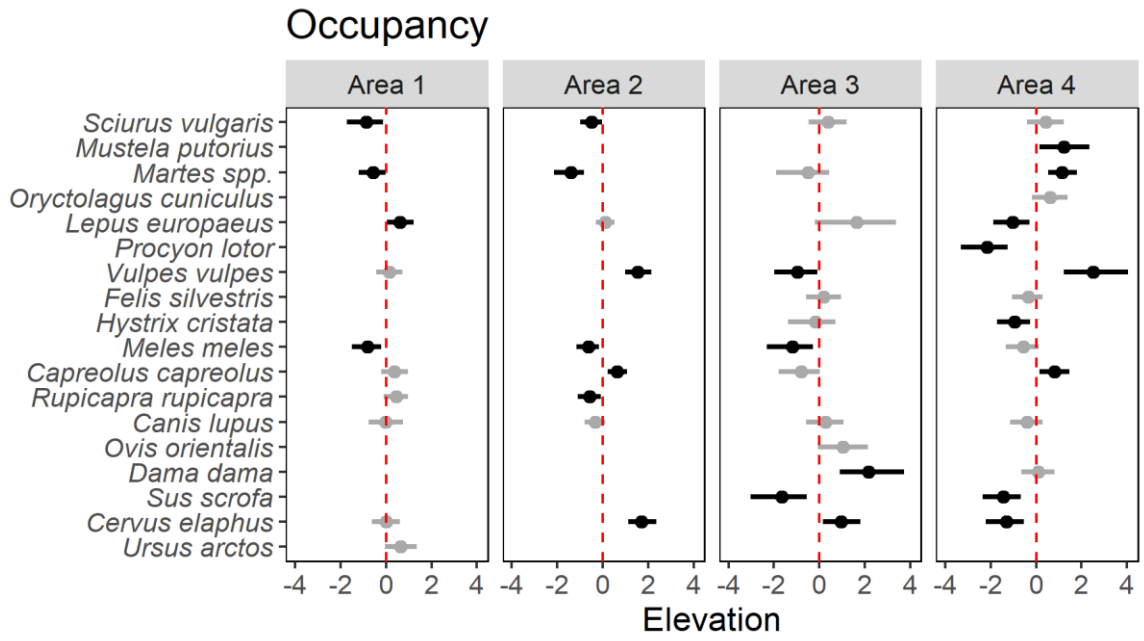

Figure S4.3.4. Region- and species- specific coefficient estimates for the effect of site elevation on occupancy. Caterpillar plots show mean estimates and 90% BCI. Black color indicates coefficients whose 90% BCI does not overlap 0, whereas gray color indicates coefficients whose 90% BCI does overlap 0.

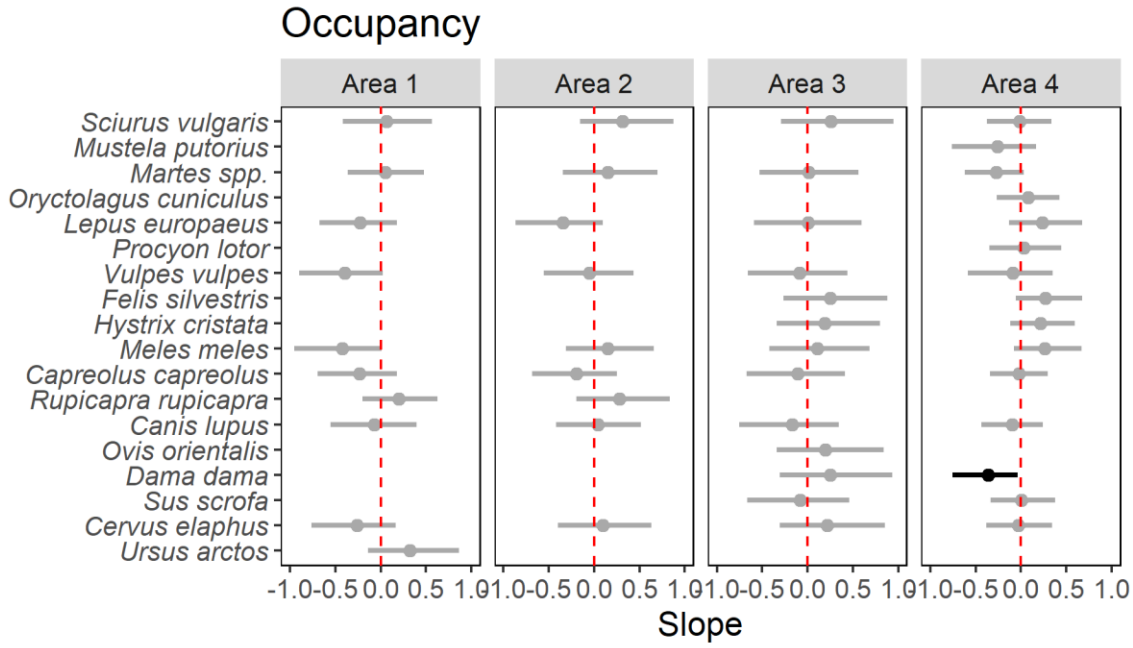

Figure S4.3.5. Region- and species- specific coefficient estimates for the effect of terrain slope on occupancy. Caterpillar plots show mean estimates and 90% BCI. Black color indicates coefficients whose 90% BCI does not overlap 0, whereas gray color indicates coefficients whose 90% BCI does overlap 0.