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**Mammals in a changing planet**  
**Using camera-trapping data with hierarchical modelling**  
**to assess and monitor populations and communities**

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## **Thesis abstract**

There is growing awareness that biodiversity is a global asset of outstanding value to present and future generations. At the same time, however, threats from species to ecosystem level have never been so disruptive as today, not only leading to biodiversity loss, but also to large alterations of biodiversity distribution, composition, and abundance. In this context, the reliable assessment of wildlife populations and the ability to monitor changes in their occurrence and abundance becomes critical. Ideally, information for monitoring progresses against indicators such as the 2020 Aichi Targets should come from primary data collected using consistent methodologies across spatial and temporal scales. Towards this end, camera trapping is an easily replicable, low-cost, highly efficient field sampling method, well suited to standardization. This methodology has evolved impressively in the last decades and encompasses a wide range of relevant ecological applications to survey and assess wildlife distribution, abundance, behaviour and community structure. Camera trapping targets primarily ground-dwelling, medium-to-large mammals. These species are widely recognized as playing a key role in numerous ecological functions. Notwithstanding their iconic appeal, the overall conservation status of the world's mammals is precarious, yet our knowledge of mammalian diversity is still surprisingly disparate, with many of the drivers and consequences of this decline still poorly understood.

This thesis addresses different ecological hypotheses in the population and community ecology field, by using camera-trapping data and the conceptual clarity of the hierarchical occupancy modelling framework, in most cases together with the benefits of Bayesian methods. Occupancy analysis, which accounts for imperfect detection and can explicitly incorporate ecological and anthropogenic factors, is particularly well suited to standardized camera trapping data and can yield useful biodiversity metrics.

The five Chapters composing this thesis investigate spatio-temporal patterns of various mammal species and communities of protected mountain ecosystems. Thus, I investigated the effect of human disturbance on occurrence probability and daily activity pattern of a set of mammals in the central Italian Alps, and found an effect on their detectability and activity pattern (Chapter 1). For the small brown bear population of the central Italian Alps, of remarkable importance for conservation, results suggested that human activity and settlements affect bears through temporal and spatial displacement. This provides more evidence that bears living in human-modified landscapes have developed a solid pattern of human avoidance (Chapter 2). Analyses of a standardized dataset of tropical forest mammals from Tanzania provided evidence that effective ground protection is associated with stability over time in the occurrence probability of the camera-trapped species (Chapter 3). In particular, the analysis of mammal communities in two ecologically comparable protected areas in the Udzungwa Mountains with contrasting management regimes revealed lower species richness, altered trophic composition and reduced occurrence probabilities for most mammal species in the forest with high disturbance. This study suggests that legal protection needs to be backed up by on ground protection to play a determinant role in maintaining diverse mammal communities in tropical forests (Chapter 4). Finally, the study of co-occurrence patterns between the snow leopard, its wild preys and livestock in the Altai Mountains of Mongolia showed that livestock may negatively impact wild ungulates. These findings deserve further research based on larger sample size (Chapter 5).

Overall, this thesis shows how camera trap data using a combination of consistent field methodology and appropriate statistical models can yield useful indicators for species and community assessments. It also offers new insights on the spatial-temporal distribution patterns of the analysed species and communities, especially in relation to different sources of human disturbance, a unifying topic in all the analysed contexts. The current epoch of biodiversity loss calls for robust indicators produced from standardized monitoring infrastructure, as critical means to accurately assess populations and identify effective conservation strategies. The work presented in this thesis ultimately aims at contributing to this goal. Finally, it can be generalized and applied to other species or ecological contexts, also as a way to inform decision-making processes.

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## **Introduction and thesis aims**

There is growing awareness that biodiversity is a global asset of outstanding value to present and future generations. At the same time, however, threats to species and ecosystems have never been so disruptive as today (Laurance *et al.*, 2012; Tilman *et al.*, 2017). Species extinction caused by human activities continues at an alarming rate and loss of biodiversity is one of the most serious phenomena in the current environmental crisis of our planet (Barnosky *et al.*, 2011; Dirzo *et al.*, 2014). The human erosion of Earth's natural resources is not only leading to biodiversity loss but also to large alterations of biodiversity distribution, composition, and abundance (Pereira *et al.*, 2012). The agreement on the Aichi Biodiversity Targets by the Parties of the Convention on Biological Diversity (CBD, 2011), the Sustainable Development Goals of the UN Agenda 2030 (Resolution 70/1), and the establishment of the Intergovernmental Platform on biodiversity and Ecosystem Services (IPBES; Lariguaderie & Mooney, 2010) are encouraging responses to the biodiversity crisis (Ceballos *et al.*, 2017). However, for these international efforts to be successful, reliable assessments of animal populations and the ability to monitor changes in biodiversity, along with their societal impact, are critical (Burton *et al.*, 2015; Navarro *et al.*, 2017). In the effort to reach such goals, a major challenge is the quality of available biodiversity data for conservation decisions. Ideally, species information for monitoring indicators should come from primary data collected using consistent methodologies that can be deployed at a wide range of spatial and temporal scales, and made available in near-real time. Indicators using primary data that meet these criteria would be less biased and more precise than indicators derived from secondary and summary data (Pereira *et al.*, 2013; Yoccoz *et al.*, 2001). For example, this is a major issue in global studies of wildlife communities in

tropical protected areas, whose results are frequently based on aggregated secondary data and expert opinion (Geldmann *et al.*, 2013; Beaudrot *et al.*, 2016).

In this context, camera traps are an easily replicable field sampling method, well suited to standardization (Ahumada *et al.*, 2013). Camera trapping (i.e., the use of cameras that automatically take images and/or videos of animals and other subjects passing in front of them) is a powerful research method that has been used to investigate wildlife since the 1920s (O'Connell, Nichols, & Karanth, 2011). Its application expanded with the advent of commercial wildlife camera traps in the early 1990s and, more recently, with the advent of digital camera traps (Rovero *et al.*, 2013). It is considered a non-invasive method that generally causes a minimum disturbance to animals (Rovero *et al.*, 2013; Fegraus *et al.*, 2011; Sollmann *et al.*, 2013). While the presence of camera traps (CTs), the noise in the ultra-infrasonic range emitted by some models (Meek *et al.*, 2014), the smell signature of humans on the unit (Munoz *et al.*, 2014) and the flash could potentially influence the behavior of passing animals, these potential sources of disturbance are clearly not comparable to those from faunal detection methods that require trapping and handling of animals (Rovero & Zimmermann, 2016). CTs work day and night and can be left unattended in the field for several weeks and even months. Such automatism not only allows for intensive and prolonged data collection over large and potentially remote areas, but makes the traps suited to study animals that are rare, elusive and only live in remote areas (e.g. Wang & MacDonald, 2009; Silver *et al.*, 2004). CTs are low-cost and standard tools with high efficiency, including abundance of data collected (O'Brien, 2010). Technological advances have led to widespread adoption of these cost-efficient tools (O'Brien, 2010; Rowcliffe *et al.*, 2008), and their methodology now encompasses a wide range of equipment and ecological applications: CTs are now being used to survey and assess wildlife distribution, abundance, behavior and community structure (Meek *et al.*, 2014; Burton *et al.*, 2015), to study medium-to-large terrestrial mammals and birds (reviews in Rovero *et al.*, 2010; O'Connell *et al.*, 2011; Meek *et al.*, 2012; Burton *et al.*, 2015), arboreal mammals (e.g. Goldingay *et al.*, 2011), small mammals (e.g. Oliveira-Santos *et al.*, 2008) and herpetofauna (e.g. Pagnucco *et al.*, 2011).

Overall, global CT research has largely focused on mammals (Agha *et al.*, 2018), a class of vertebrate that is widely recognized as playing a key role in numerous ecological functions, including predation (Terborgh *et al.*, 2001; Sinclair *et al.*, 2003), grazing (Pringle *et al.*, 2007)

and seed dispersal (Fragoso *et al.*, 2003; Ahumada *et al.*, 2011), profoundly influencing the environment beyond direct species interactions, such as through cascading trophic effects (Côté *et al.*, 2004; Crooks & Soulé, 1999). Large mammals also are sensitive to habitat fragmentation that isolates populations (Crooks, 2002). For these reasons they are usually good indicators of ecosystem health and of environmental connectivity in anthropic habitats. Indeed, arguably because they include many charismatic species, mammals have been important flagships (i.e. species selected to act as an ambassador, icon or symbol for a defined habitat, issue, campaign or environmental cause) for conservation efforts (Leader-Williams & Dublin, 2000; Walpole & Leader-Williams, 2002; Rondinini, Rodrigues & Boitani, 2011). They also provide important human benefits such as food (Fa *et al.*, 2003), recreation (Hoyt *et al.*, 2000) and income (Archabald *et al.*, 2001). Notwithstanding their iconic appeal, the overall conservation status of the world's mammals is precarious, and their diversity and abundance have been rapidly depleted in the face of threats such as habitat loss (due mainly to expanding agriculture and logging) and overexploitation (Hoffman *et al.*, 2011; Davis *et al.*, 2018). A combination of rarity, anthropogenic impacts, and political endemism has put about a quarter of terrestrial mammal species, and a larger fraction of their populations, at risk of extinction (Ceballos *et al.*, 2005; Schipper *et al.*, 2008), with declines taking place even in protected areas (Western *et al.*, 2009, Craige *et al.*, 2010). The unrelenting decline of mammals suggests many vital ecological and socio-economic services that these species provide will be lost, potentially changing ecosystems irrevocably (Ripple *et al.*, 2016). However, knowledge of mammalian diversity is still surprisingly disparate, both regionally and taxonomically (Schipper *et al.*, 2008), and many of the drivers, patterns and consequences of this decline remain poorly understood (Ripple *et al.*, 2016).

Species distribution modelling is an important tool for biodiversity conservation, as knowledge about species distributions is vital for informing and prioritizing conservation actions and for effective conservation planning (Kery *et al.*, 2013). Spatio-temporal patterns of wild species are an expression of multiscale and multifactorial processes that act simultaneously, and estimating the distribution of a species or suite of species across the landscape provides wildlife biologists with crucial information for monitoring and conserving animal populations (Noon *et al.*, 2012). Additionally, understanding the spatial and temporal patterns in human pressures on the environment and how species richness and composition

differ as a result of management treatments, can help determine potential ecological consequences and mitigating environmental damage with effective conservation actions (Zipkin *et al.*, 2010; Venter *et al.*, 2016). Over the last few decades many species distribution modelling approaches have been proposed (Guisan & Zimmermann, 2000); however, most of them don't formally account for one of the hallmarks of ecological data: imperfect detection (Yoccoz *et al.*, 2001; Kery, 2002; Kery & Schmidt, 2008), an issue also relevant for sessile organisms such as plants (Chen *et al.*, 2013). If imperfect detection is not accounted for, bias is induced in the occupancy estimator, and this can lead to the incorrect classification of occupied sites as empty and biased community-level parameters (Guillera-Arroita & Lahoz-Monfort, 2012). Regardless of the state variable of interest, imperfect detection should be considered when working with ecological data, all the way from study design, through data collection, to analyses (Guillera-Arroita, 2017). To tackle this problem, MacKenzie *et al.* (2002) and Tyre *et al.* (2003) proposed the joint modelling of occupancy ( $\psi$ , defined as the probability that the focal taxon occupies, or uses, a sample unit) and detection probabilities based on data resulting from a sampling protocol in which discrete replicate surveys are carried out at each sampling site, a modelling framework that has become widely used by ecologists. Given their tremendous flexibility and relative ease of data collection, the rise of occupancy modelling as a method to account for imperfect detection has led to its application in CT surveys as a surrogate for abundance (MacKenzie *et al.* 2006; O'Brien *et al.* 2010; Ahumada, Hurtado & Lizcano 2013; Bailey *et al.*, 2014). The occupancy framework has also been applied to multispecies CT assessments, such as species interactions (Steinmetz, Seuaturien & Chutipong, 2013) and community dynamics (Burton *et al.* 2012), as well as other parameters, for example reproductive success (Fisher, Wheatley & Mackenzie 2014; Burton *et al.*, 2015). Additionally, the ultimate target of occupancy studies is often to detect potential occupancy differences. The interest might be in assessing differences temporally (e.g. has occupancy changed since the last survey?) or spatially (e.g. is occupancy different in these two areas or habitat types?) (Guillera-Arroita & Lahoz-Monfort, 2012). Occupancy analysis is particularly well suited for camera trapping data, because the sampling period is fractioned, during analysis, into a number of multiple, sequential sampling occasions, e.g. 1 day each, on modelling detection as a continuous process (Guillera-Arroita *et al.*, 2011).

On these grounds, this thesis addresses different ecological hypotheses in the population and community ecology field, by coupling camera-trapping data to the conceptual clarity of the hierarchical occupancy modelling framework, in most cases together with the benefits of Bayesian methods as a mode of analysis and inference. Indeed, in the past few decades ecologists have become increasingly interested in the use of Bayesian methods of data analysis (Dorazio, 2016). This is mainly because a Bayesian approach to inference often provides some benefits, by means of a flexible and coherent framework to fit even very complex hierarchical models, and by a transparent accounting for all sources of variation in estimates or predictions (Gelman & Hill, 2006). All Chapters of my thesis investigate spatio-temporal patterns of various mammal species and communities of protected mountain ecosystems. The minimum knowledge needed of effective management of mammals within protected areas includes knowing what species are present, their distribution within the area, and their relative abundances across different habitat type and in response to different biotic and abiotic factors. Well-designed monitoring programmes with standardized protocols can provide robust data to obtain such information, and also monitor the long-term populations and biodiversity trends (Pereira & Cooper, 2006). This is the case of the TEAM (Tropical Ecology and Monitoring) Network, that collects data for monitoring long-term trends in tropical biodiversity through a network of field stations in protected areas, distributed in proportion to tropical forest cover on each continent (Rovero & Ahumada, 2017). TEAM developed and implemented a standardized protocol to monitor mammal and bird communities using camera trap arrays, based on the collective experience of many field biologists (TEAM Network, 2011; Jansen *et al.*, 2014). All Chapters of my thesis focus on the analysis of datasets obtained through the TEAM Network's Vertebrate Monitoring Protocol applied to a specific TEAM site in Tanzania, or through the adaptation of this protocol to other ecological contexts.

Chapters 1 and 2 investigate spatio-temporal patterns of medium-to-large mammals in a human-modified mountainous area in the central Italian Alps. The Alps represent a priority area for conservation globally (Olson & Dinerstein, 2002), being one of the richest biodiversity hot spots of Europe and at the same time, despite the natural fragility of its ecosystem, one of the most intensively exploited mountain ecosystems in the world (Lassen & Savoia, 2005). The study area is partially inside a protected mountain area (Adamello Brenta Natural Park) of particular faunal importance for the historical presence of the last alpine population of brown

bear (*Ursus arctos*) that was recently reintroduced (as the result of the releases of 10 animals translocated from Slovenia from 1999 to 2002 (Mustoni *et al.*, 2003; Preatoni *et al.*, 2005), as well as for the current recolonization of the wolf (*Canis lupus*; Razen *et al.*, 2015). The main objective was investigate the influence of anthropogenic disturbance on the community of medium-to-large mammals, by assessing species-specific drivers in occupancy and detectability as well as daily activity patterns and their relationship with human disturbance. Chapter 2 provides a focus on the spatial (site use) and temporal (daily activity) patterns of the brown bear in relation to human disturbance across the study area, an important issue for the coexistence of bears and people in the Alps. By using images of people and vehicles to quantify human passages, I could directly relate anthropogenic presence to bears' activity.

In Chapter 3 and 4, I investigated different topics about spatio-temporal patterns and community composition of mammal species within the Udzungwa Mountains of Tanzania, an area of outstanding value for biological endemism and biodiversity conservation (Rovero *et al.*, 2014a), and TEAM Network site since 2009. These mountains of south-central Tanzania are part of the Eastern Arc Mountains, a series of ancient and isolated mountain blocks stretching from southern Kenya to south-central Tanzania. Portions of the Eastern Arc Mountains are believed to have supported moist forest for c. 30 million years (Wasser & Lovett, 1993). The age, stability, isolation and fragmented nature of these forests have combined to produce high levels of biological diversity and endemism (Burgess, Fjeldsa & Botterweg, 1998; Myers *et al.*, 2000; Dinesen *et al.*, 2001). The biodiversity importance of the Udzungwa Mountains is well reflected in the mammalian fauna (Kingdon & Howell, 1993), with five Udzungwa endemic mammals in this area and 13 of the 17 mammals that are endemic to the Eastern Arc Mountains, Southern Highlands and Mount Kilimanjaro (Burgess *et al.*, 2007; Rovero & DeLuca, 2007). The larger endemic mammal species in the Udzungwa Mountains include Abbott's duiker (*Cephalophus spadix*), the newly discovered grey-faced sengi (*Rhynchocyon udzungwensis*), and three endemic primates: Udzungwa red colobus (*Procolobus gordonorum*), Sanje mangabey (*Cercocebus sanjei*), and the kipunji (*Rungwecebus kipunji*), a newly-described genus (Topp-Jorgensen *et al.*, 2009). Chapter 3 aims to investigate the yearly occurrences of medium-to-large mammals within the Udzungwa Mountains National Park, and to evaluate the effects of habitat and proxies of human disturbance, namely illegal hunting with snares and firewood collection, on species' occurrence probabilities over an 8-year period. Chapter 4 explores the

differences between forest mammal communities in two ecologically comparable protected areas in the Udzungwa Mountains with contrasting management regimes. Using camera-trapping data, I assessed the target communities in terms of species richness, functional composition (i.e., proportions of trophic guilds) and species-specific occurrences.

I contributed to Chapter 5 as side project of my PhD programme, but perfectly in line with background and aims of this thesis. Indeed, methods, target species and analysis as carried out in this work are all broadly relevant to my PhD approach. This study investigates co-occurrence patterns among the elusive, IUCN-Vulnerable snow leopard *Panthera uncia* (McCarthy *et al.*, 2017), one of its main wild prey – the Siberian ibex *Capra sibirica* – and domestic ungulates in a National Park in the Altai Mountains of Mongolia. The aim was to assess the local compatibility of pastoralism with wildlife conservation by studying the spatial interactions among these three ‘players’, and to assess the usefulness of this approach to evaluate spatial patterns of mammals by using an occupancy model that explicitly assesses co-occurrence.

In the final chapter I draw some general conclusions stressing the main findings and common implications that join the different applications outlined in chapters 1 to 5. Supporting information for all chapters is provided in the appendices from A to E, respectively, as well as the published papers for Chapters 1, 4 and 5. Chapter 3 is currently under review (following a ‘Minor revision’ received) in *Ecology and Evolution*, while Chapter 2 has been recently submitted to *Oryx* as a ‘Short Communication’.



## **Chapter 1.**

### **The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping**

**Valentina Oberosler**, Claudio Groff, Aaron Iemma, Paolo Pedrini, Francesco Rovero, 2017. *Mammalian Biology*, 87, pp.50-61.

#### **Abstract**

As human activities increase in natural areas, so do threats to wildlife, potentially leading to immediate and long-term impacts on species' distribution, activity, reproduction and survival. This is particularly relevant for large-bodied vertebrates that are especially sensitive to human presence and human-driven habitat changes. Assessing the impact of anthropogenic disturbance requires data on species distribution and activity patterns of target species in relation to human presence and infrastructures. Here, we used camera trap data to study the influence of anthropogenic disturbance on the community of medium-to-large mammals in a mountainous area in the eastern Italian Alps, with emphasis on the local population of brown bear (*Ursus arctos*). In 2015, we sampled a study area of 220 km<sup>2</sup> with 60 camera trap locations adopting a systematic grid. Such design was inspired by the Terrestrial vertebrate Monitoring Protocol developed by the TEAM Network, a pan-tropical biodiversity programme. Camera traps run for 30 days in each site and cumulated 1,978 camera trapping days, yielding 1,514 detection events of 12 species of mammals. For the 8 most recorded species, we used detection/non-detection data to model estimated occupancy and detection probability in relation to a suite of environmental and disturbance covariates. Our analysis revealed that human disturbance plays a significant role in influencing species-specific detection probability, while we found little evidence of significant relationship between occupancy and anthropogenic

disturbance. For example, we found that brown bear's detectability was negatively correlated with capture rate of humans at sampling sites, and positively correlated with distance from settlements. We also assessed species-specific daily activity patterns and found that, for all species, the overlap with human diel pattern decreases significantly at sites with higher human presence. We also discuss the potential of our approach for building cost-efficient and long-term monitoring of mammals.

**Keywords:** Camera traps; Activity pattern; Human impact; Detectability; *Ursus arctos*

## 1.1 Introduction

In human-dominated landscapes, increased habitat fragmentation and accessibility to natural areas are bringing humans in closer contact with wild populations (Preisler *et al.*, 2006). Outdoor recreation is typically assumed to be compatible with biodiversity conservation and permitted in most protected areas worldwide, but its effect is still a relatively unknown topic in the conservation science literature (Taylor & Knight, 2003; Blumstein *et al.*, 2005; Sutherland, 2007). Human recreation and diversification of outdoor activities have become of major conservation concern as tourism expands into natural parks (Margules & Pressey, 2000). Recreation is important for maintaining public support for protected areas and connecting people with nature (Kays *et al.*, 2016), but at the same time it could also be a major disturbance to wildlife (Baker, 1992; Hobbs & Huenneke, 1992; Larson *et al.*, 2016). In addition to habitat degradation resulting from the development of recreational facilities and infrastructure, which can cause an array of impacts on the distribution, reproduction and survival of wildlife (George & Crooks, 2006; Reed & Merenlender, 2008), human disturbance can elicit costly behavioral responses such as flight (Arlettaz *et al.*, 2007; Thiel *et al.*, 2007), feeding disruption (Fernandez-Juricic & Telleria, 2000) or changes in spatial/temporal habitat use (Rogala *et al.*, 2011). Species with large spatial requirements and low population densities, typically the large carnivores, are especially sensitive to human infrastructure and activities (Crooks, 2002). Stankowich (2008) indicates that experience with humans and their recreational activities also has a significant impact on ungulate behaviour. For these reasons, larger mammals are considered a proxy of ecosystem health and habitat connectivity (Crooks *et al.*, 2011; e.g. Peters *et al.*, 2015); hence, understanding how their spatio-temporal patterns of habitat use are locally

affected by human disturbance becomes an increasingly important research question (Larson *et al.*, 2016).

Here, we examined habitat preferences and the influence of human disturbance on spatial and temporal patterns of medium-to-large terrestrial mammals in a human-disturbed mountainous area in the eastern Italian Alps. The Alps represent a priority area for conservation globally (Olson & Dinerstein, 2002), being one of the richest biodiversity hot spots of Europe and at the same time one of the most intensively exploited mountain ecosystems in the world (Lassen & Savoia, 2005). This mountain range, despite the natural fragility of its ecosystems, is the first destination for outdoor winter sports in the world, which is emblematic of the anthropogenic pressure (Elsasser & Messerli, 2001). The study area is partially inside a protected mountain area (Adamello Brenta Natural Park, PNAB) of particular faunal importance for the historical presence of the last alpine population of brown bear (*Ursus arctos*) that was recently reintroduced (Preatoni *et al.*, 2005), as well as for the current recolonization of the wolf (*Canis lupus*; Ražen *et al.*, 2015).

The on-going expansion of tourism and recreation into wildlife habitats calls for measures to mitigate the negative effects of anthropogenic disturbance (Sutherland, 2007). Mitigating such disturbance requires knowledge on how human disturbance impact wildlife occurrence and activity patterns. We aimed to study the potential influence of human disturbance on spatial (i.e. occupancy and detectability) and temporal (daily activity) patterns of wildlife in the study area, especially in relation to the elevated presence of tourism in the summer. Our specific objectives were: (1) to assess species' probability of occurrence by estimating occupancy and detection probability ( $p$ ), (*sensu* MacKenzie *et al.* (2002)), (2) to determine anthropogenic and habitat drivers of variations in these metrics, and (3) to assess daily activity patterns of the species in the study area and investigate the relationship between these and human presence.

## 1.2 Material and Methods

### 1.2.1 Study area

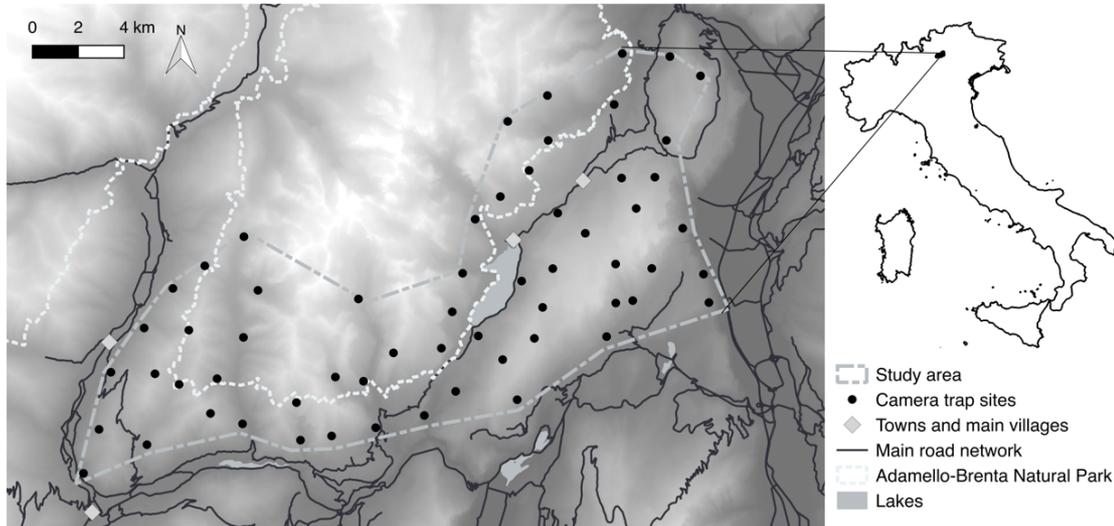
We conducted the camera trap survey between June and August 2015 in an area of about 220 km<sup>2</sup> within Trento Province, NE Italy (centred on 46°06'45"N and 10°55'50"E; Fig. 1.1). This mountainous area encompasses the southern part of Brenta, the westernmost Dolomite group,

and its adjacent valleys, which are partially included within the PNAB. While this is formally a protected area, not being a National Park its regulations allow for activities such as hunting, logging and road building, and therefore we assumed that human disturbance does not differ inside and outside the protected area. Therefore, the most relevant feature for our study aims was that some of the sampling sites within the PNAB were more distant from settlements and trafficked roads, and at relatively higher elevation. The sampling area holds part of the core area of the brown bear population (Groff *et al.*, 2015) and represents a large variation in both habitat type and altitudinal range (300-2,800 m a.s.l.), with a dominant mountainous terrain. The vegetation composition 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*). Above the treeline (at about 1,800 m) vegetation is dominated by mountain pine (*Pinus mugo*) and open habitats comprised of alpine herbaceous species. The climate of the study area varies from continental to alpine, in relation to altitude. The average resident population density is of 32.2/km<sup>2</sup> (<http://www.urbistat.it/AdminStat/it/>) and occurs along the main valleys to the west, south and east of the core study area, with intense tourism presence in the summer. Tourists contribute largely to human activity in summer across the study area.

### 1.2.2 Data collection: camera trapping

We designed our sampling protocol by adapting the one developed by the Tropical Ecology Assessment and Monitoring (TEAM) Network (TEAM Network, 2011; Jansen *et al.*, 2014), a pan-tropical biodiversity monitoring programme. We used QGIS version 2.8.2 (QGIS Development Team, 2013) to design a regular grid of 60 camera trap stations evenly spaced and initially positioned at random across the study area to cover an altitudinal gradient from 500 to 1,900 m a.s.l., i.e. with no sampling sites above the tree line. Relative to TEAM's, our protocol differed because we set one camera trap site every 4 km<sup>2</sup> instead of 2 km<sup>2</sup>. This compromised between maximizing the overall area monitored, especially given the large home range of brown bears (Preatoni *et al.*, 2005), and avoiding too large gaps between camera trap sites (Fig. 1.1). In addition, being the area diffusely covered by forestry roads and trails, which we considered suitable sites for detecting passing wildlife, sampling sites were chosen to fall equally on these categories. Hence, 30 sites were located on forestry roads and 30 on trails (of which 10 were

hiking trails and 20 other types of trails, mostly used by hunters). Field sampling was done through two sequential arrays of 30 camera traps each, for easier implementation and due to limited equipment available. Each camera trap sampled for a minimum of 30 consecutive days.



**Fig. 1.1.** Map of the study area (left) in western Trentino province, Northern Italy. The 60 camera trap locations are shown as black dots and the border of the Adamello-Brenta Natural Park is also shown. The background is a Digital Terrain Model, with brighter tones corresponding to higher elevation. The geographic location of the study area in Italy is shown in the map on the right.

We used two digital camera trap models that mount an infrared flash array, distributed randomly and in equal number across sites: (1) Reconyx HC 500 (Reconyx Inc., Holmen, WI, USA) with a 0.20 s trigger delay, and (2) UOVision UV572 IR+ (UOVision Technology, Shenzhen, China) with 1 s trigger delay. We set camera traps on suitably located trees, i.e. at a distance of 5-6 m from the target trail for the IR+ and 3-4 m for the Reconyx, based on flash intensity and trigger speed of these models, and at an average height of 50 cm, depending on terrain morphology. Cameras were fastened with locks. We cleaned the ground in front of the camera traps of debris and vegetation that could cover the animals or reflect light. We used rechargeable high-performance NiMH batteries. Date and time were stamped in each image and camera traps saved on SD memory cards (Verbatim Premium SDHC cards, 4/8 GB). Cameras were set to take photos with no delay between consecutive triggers. We checked cameras approx. 15 days after the placement, to avoid prolonged malfunctioning. We recorded the

location of the camera trap sites by using handheld GPS units (Garmin GPSMap 64s). We did not use any bait for attracting animals.

### 1.2.3 Data collection: covariates

We downloaded road network and settlement digital maps and Digital Elevation Model (DEM) raster at 10 m spatial resolution from the PAT Geoportal (<http://www.territorio.provincia.tn.it>), and used them in software GRASS 7.0 (GRASS Development Team, 2015) and QGIS 2.8.2 (QGIS Development Team, 2013). We derived elevation and slope of the sites from the DEM, and measured distance from settlements and from the main road network as potential proxies of disturbance. Thus, the covariates at the camera trap sites were: (1) elevation (in m a.s.l.); (2) slope expressed in radians; (3) distance (m) from main (paved) road network; (4) distance (m) from settlements; (5) trail type in 3 categories: hiking trails, other types of trails, mostly used by hunters, and forestry, unpaved roads; (6) capture rate of humans as computed from sampling data; (7) capture rate of vehicles as computed from sampling data; (8) camera model as resulted from the placement across sites. Elevation and slope were taken as representative of the trap sites, being the DEM accuracy diffused by the 10 m spatial resolution. For variable (7), we checked if capture rate of humans was different inside and outside the park border, and found no significant difference (Welch Two Sample t-test,  $N_1=18$ ,  $N_2=40$ ,  $P\text{-value}=0.24$ ).

### 1.2.4 Photo Processing

At sampling completion, we recovered camera traps and extracted images from the memory cards for identification (Fig. 1.2) using dedicated open-access software, Wild.ID (Fegraus & MacCarthy, 2016). After we annotated all of the images, we exported the entire data set to a comma-separated values (.csv) file used for further analyses. Species identification of clear images was straightforward with the exception of distinguishing with a sufficient degree of certainty between beech marten (*Martes foina*) and pine marten (*Martes martes*), because: (1) the only evident (i.e. potentially observable in the collected images) difference between the two species in dimensions and coat lies in the colour of the chest stain, but most of the images were recorded by night and so monochrome (due to the cameras' features) and (2) the two species are sympatric on a large part of the Italian Alps (Boitani *et al.*, 2003). Therefore, we classified all these images as *Martes spp.*



**Fig.1.2.** Selection of images taken by camera traps during the sampling in the study area, Italian Alps. From the left to the right, from up to down: roe deer, wolf, red deer and brown bear.

### 1.2.5 Data Analysis

We analysed data using a hierarchical modelling approach that allows to explicitly consider imperfect detection (MacKenzie, 2006). Thus, occupancy ( $\psi$ ) is defined as the proportion of area, patches or sites occupied by a species (MacKenzie *et al.*, 2002) and is considered a surrogate of abundance (MacKenzie and Nichols, 2004). We extracted matrices for analysis by processing the raw data in the software R (R Development Core Team, 2015), using scripts prepared by the TEAM Network and available through Rovero & Spitale (2016). We first derived standard descriptors of species and community by filtering the image records for each species to get the number of independent events. We defined the minimum time between two independent events as 15 minutes, hence mostly avoiding that images of the same individual pausing in front of the camera trap were scored as multiple events. This interval is smaller than usually found in the literature (1 h the most common; e.g. Tobler *et al.*, 2009), but Kays and Parsons (2014) and

F. Rovero (unpublished data) found that a few minutes generally suffice. We then computed a capture rate, or relative abundance index (RAI), as the number of events divided by sampling effort (camera days) and multiplied by 100 (i.e. events per 100 days of camera trapping; e.g. Rovero *et al.*, 2014b). Camera days were computed as the number of 24-h periods from deployment of camera until the camera was retrieved, or until the last image was taken in cases when the memory card filled up before camera retrieval. We also computed the naïve occupancy as the number of camera trap sites occupied on sites sampled.

We built a species accumulation curve with cumulative camera trap days to assess if survey effort was sufficient for the curve to level off, i.e. to capture the majority of species present in the community. The order in which samples (they consisted of number of events per 15 min) were included in the curve was randomized 1,000 times and results were used to derive 95% confidence intervals around the mean, using the package ‘vegan’ in R (Gotelli & Colwell, 2001). Even though this approach ignores imperfect detection of individual species, it is useful for comparison with other studies.

For species detected with >20 events, we performed occupancy analysis using the package ‘unmarked’ in R (Fiske & Chandler, 2011 and 2015). For each species, we built detection/non-detection matrices of sites by surveys using a sampling occasion of 5 days. Such occasion length compromised between losing information to estimate detectability - and hence precision in the estimates - when increasing, and incurring in convergence problems when decreasing (Rovero & Spitale, 2016). We used these matrices as the input for the single-season occupancy model (MacKenzie, 2006). We used a common set of models for all the species of interest. In addition to the null model, that assumes constant  $\psi$  and  $p$  (i.e.  $\psi(\cdot)$ ,  $p(\cdot)$ ), for other models  $p$  and  $\psi$  were allowed to vary by sub-sets of covariates, as reported in Table 1.1. Our hypothesis was that animals’ probability of detection would have been influenced by sources of anthropic disturbance, and we also wanted to test possible differences in performance among camera models. Prior to the analysis, we standardized covariates to have a mean of zero and unit SD, and we tested them for collinearity, which resulted in dropping ‘distance from paved roads’ as it was significantly correlated with ‘distance from settlements ( $r=0.7$ ). We used the Akaike Information Criterion (AIC; Burnham and Anderson, 2002; Zuur *et al.*, 2009) to rank candidate models. In the case of top-ranked models with similar AIC (with  $\Delta\text{AIC} < 2$ ), we applied a model-averaging technique to estimate occupancy from these multiple models with the function

available in the R package ‘MuMIn’ (Bartoń, 2015). The relative importance of the model parameters was calculated with the R package ‘AICmodavg’ (Mazerolle, 2012). We first determined the best species-specific models for detectability among the 31 models obtained by combination of 5 covariates of interest. A set of best models for each species was selected and from the model average the most significant variables were retained based on relative variable importance criterion ( $> 0.20$ ). Once we fixed the model part for detection, we fitted the one for occupancy.

For the same pool of species analysed in occupancy framework, we also investigated diel activity pattern and its relationship with human activity. By following the procedures described by Ridout and Linkie (2009), we subsampled the raw data for consecutive detections of a given species at each site recorded within 30 min (Zimmermann *et al.*, 2016). We considered each camera site as either having high or low human disturbance based on capture rate of humans, using the mean value as threshold, and this resulted in 41 low and 17 high disturbance camera trap sites. For each of the two disturbance levels, we then performed pairwise comparisons of activity patterns between wild mammals and humans by estimating the coefficient of overlapping  $\Delta$  (ranging from 0, no overlap, to 1, complete overlap) using the package ‘overlap’ (Meredith & Ridout, 2016) in R. We hypothesized overlap to be smaller where human disturbance was greater. To assess the significance of this difference, we generated distributions of overlap values by randomly resampling 1,000 times the data set of detections for each species and calculating each time  $\Delta$ . Then, for each species, we used the Welch Two-Sample t-test to assess if the two generated distributions of  $\Delta$  values were significantly different.

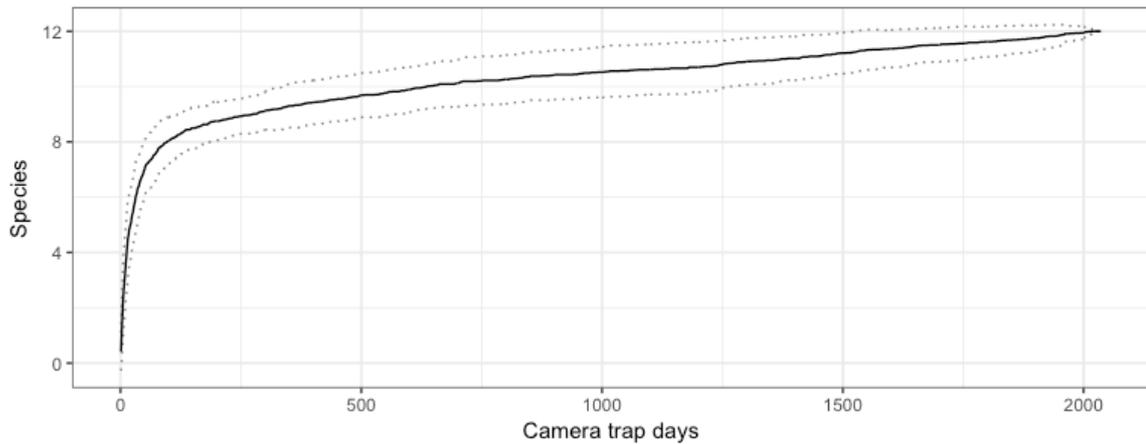
**Table 1.1.** List of environmental and disturbance covariates on detection probability ( $p$ ) and occupancy ( $\psi$ ) respectively, as used in occupancy analysis, and the assumed relationship with  $p$  and  $\psi$ .

| Covariates                      | Hypothesized relationship   |
|---------------------------------|---|
| Covariates on detection ( $p$ ) |   |
| Camera model                    | IR+ cameras have larger detection zone hence greater detectability especially for smaller species.                              |
| Trail type                      | Trails are less disturbed by the passage of vehicles, but some are intensively frequented by tourists during the summer season. |

|                                    |  |
|------------------------------------|--|
| Distance from settlements          | Noisy and disturbing human activities and presence may affect the behaviour of the species.  |
| Capture rate of humans             | The passage of people can decrease animal detection.   |
| Capture rate of vehicles           | The passage of noisy vehicles can decrease animal detection.   |
| <hr/>                              |  |
| Covariates on occupancy ( $\psi$ ) |  |
| <hr/>                              |  |
| Elevation                          | Elevation reflects habitat and forest variation, and is also correlated with distance from settlements (increase in elevation corresponds to decrease in permanent human disturbance). |
| Elevation squared                  | Quadratic term was used to test whether the relationship with elevation was linear or not.   |
| Slope                              | Species may avoid or prefer steep sites.   |
| Capture rate of humans             | Noising and disturbing human activities may affect animal behaviour and can cause avoidance and fleeing responses.   |
| Capture rate of vehicles           | The noisy passage of vehicles can cause avoidance of roads and surrounding areas.  |
| <hr/>                              |  |

### 1.3 Results

Of the 60 camera traps set two malfunctioned and did not yield enough data for analysis. The remaining 58 accumulated 1,978 camera days (mean per site 34.1). Sampling yielded 4,462 independent events overall, of which 1,514 were of wild mammals. Blank images were 16,074 (87% taken by IR+ cameras), while 1,499 had an unidentifiable subject, i.e. images where the subject appeared blurry, overexposed or outside the flash range. These were taken for 92% by the IR+ cameras. Twelve species of wild mammals were recorded (range 1-8, mean 3.8). The list of detected mammals and standard descriptors are reported in Table 1.2. The checklist matched the expectations based on knowledge of the local fauna, with no species representing new records in the area (see Discussion). We also recorded 6 bird species (11 events) and 5 domestic species (60 events), predominantly dogs. Humans were recorded both as pedestrians/bikers (1,952 events) and vehicles (925 events). The randomized species accumulation curve with sampling effort is shown in Fig. 1.3. We could fit occupancy models for the eight most recorded species. Estimated  $\psi$  ranged from 0.29 to 0.83 and  $p$  ranged from 0.13 to 0.54 (Table 1.3).



**Fig. 1.3.** Randomized species accumulation curve (solid line), with sampling effort for the community of medium-to-large mammals detected by camera trapping in the eastern Alps. Dotted lines indicate 95% confidence intervals.

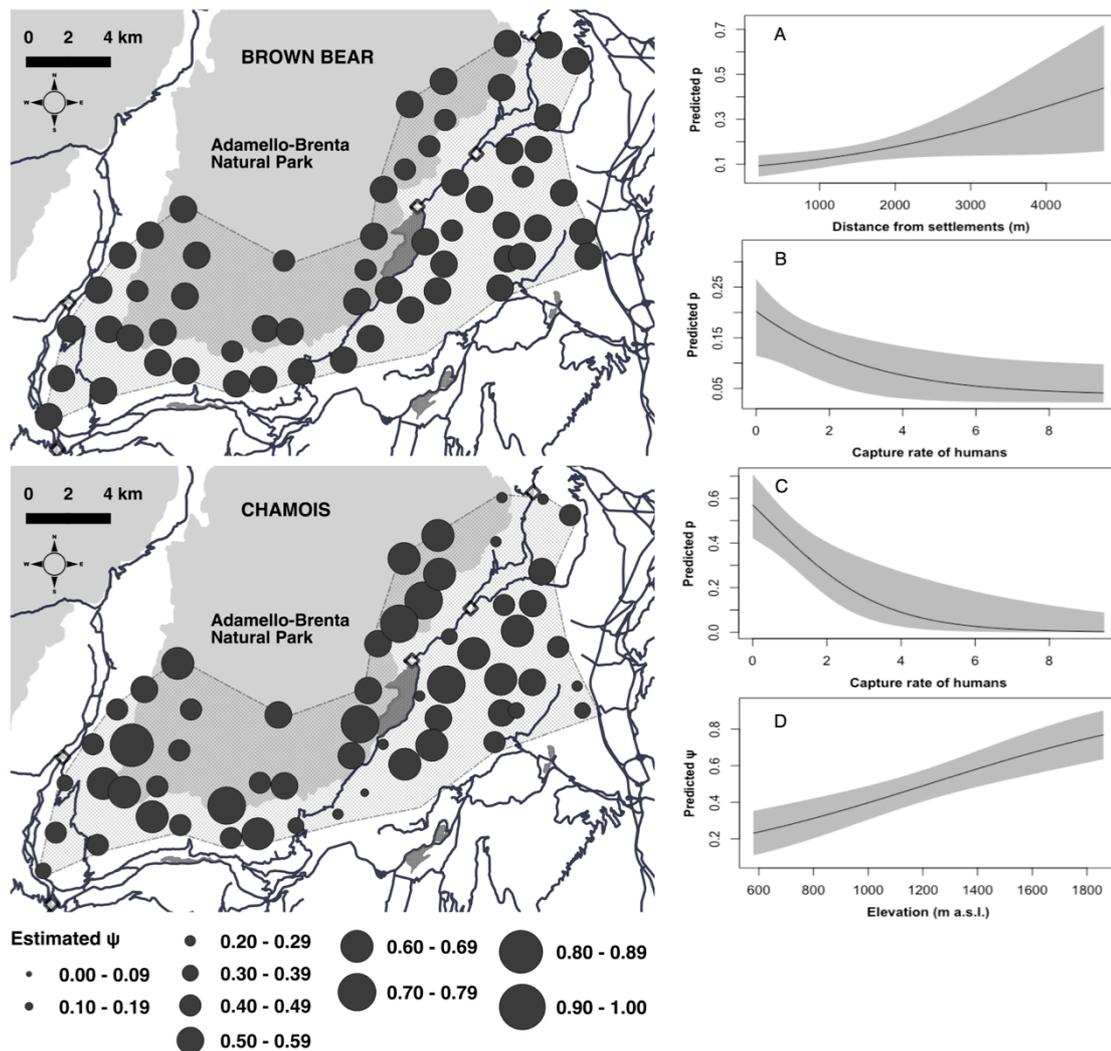
The ‘null’ model (i.e. without covariates) was among the best supported for only one species, the brown bear, while at least one of the covariates affected significantly or marginally significantly  $\psi$  or  $p$  of all the others. Model selection indicated that no single model was demonstrably better (i.e. with  $\Delta\text{AIC}$  being 2 points greater than the following in rank) for any of the species. We therefore used model averaging. For the brown bear, significant correlations were only found for its detection probability (Table 1.3; Fig. 1.4). The average model included distance from settlements (positive relationship), and capture rate of humans (negative relationship). Among ungulates, predicted  $\psi$  for the chamois (*Rupicapra rupicapra*) at the camera trap stations was highly variable (range 0.19-0.82; Fig. 1.4), and both slope and elevation positively affected  $\psi$ . Capture rate of humans negatively affected red deer’s (*Cervus elaphus*) detectability; trail type significantly affected roe deer’s (*Capreolus capreolus*) detectability, with a positive influence of trails in relation to forestry roads. The three species of mesocarnivores had similar patterns, with a positive correlation between disturbance covariates and  $\psi$ , i.e. capture rate of humans with red fox (*Vulpes vulpes*) and marten’s (*Martes* sp.) occupancy, capture rate of vehicles with badger’s (*Meles meles*). For all the eight analysed species, camera model significantly affected species’ detectability, which was positively correlated with the IR+ model. For marten and red fox the differences in detection due to camera models were too high to be properly accounted for by the analysis; hence, for these two species we excluded camera model as a covariate in model

selection. Results of model selection and of model averaging for each species are reported in Suppl. Table A1 and A2.

**Table 1.2.** Checklist of mammals detected by camera trapping in the eastern Alps, ordered by decreasing number of events. Naïve occupancy ( $\psi$ ) is computed as the number of sites the species was trapped divided by all sites sampled ( $n = 58$ ). The capture rate (or RAI, relative abundance index) was computed as the number of events divided by sampling effort and multiplied by 100 (i.e. events per 100 days of camera trapping).

| <b>Latin name</b>          | <b>Common name</b> | <b>Taxonomic order</b> | <b>Functional guild</b> | <b>Events</b> | <b>Capture rate</b> | <b>Naïve <math>\psi</math></b> |
|----------------------------|--------------------|------------------------|-------------------------|---------------|---------------------|--------------------------------|
| <i>Vulpes vulpes</i>       | Red fox            | Carnivora              | Omnivore                | 562           | 28.41               | 0.621                          |
| <i>Capreolus capreolus</i> | Roe deer           | Ungulates              | Herbivore               | 302           | 15.27               | 0.793                          |
| <i>Cervus elaphus</i>      | Red deer           | Ungulates              | Herbivore               | 208           | 10.52               | 0.638                          |
| <i>Rupicapra rupicapra</i> | Chamois            | Ungulates              | Herbivore               | 166           | 8.39                | 0.448                          |
| <i>Lepus europaeus</i>     | Brown hare         | Lagomorpha             | Herbivore               | 114           | 5.76                | 0.293                          |
| <i>Meles meles</i>         | Badger             | Carnivora              | Omnivore                | 64            | 3.24                | 0.328                          |
| <i>Martes sp.</i>          | Marten             | Carnivora              | Carnivore               | 49            | 2.48                | 0.241                          |
| <i>Ursus arctos</i>        | Brown bear         | Carnivora              | Omnivore                | 38            | 1.92                | 0.328                          |
| <i>Sciurus vulgaris</i>    | Red squirrel       | Rodentia               | Rodent                  | 8             | 0.40                | 0.086                          |
| <i>Canis lupus</i>         | Wolf               | Carnivora              | Carnivore               | 1             | 0.05                | 0.017                          |
| <i>Marmota marmota</i>     | Alpine marmot      | Rodentia               | Rodent                  | 1             | 0.05                | 0.017                          |
| <i>Mustela nivalis</i>     | Least weasel       | Carnivora              | Carnivore               | 1             | 0.05                | 0.017                          |

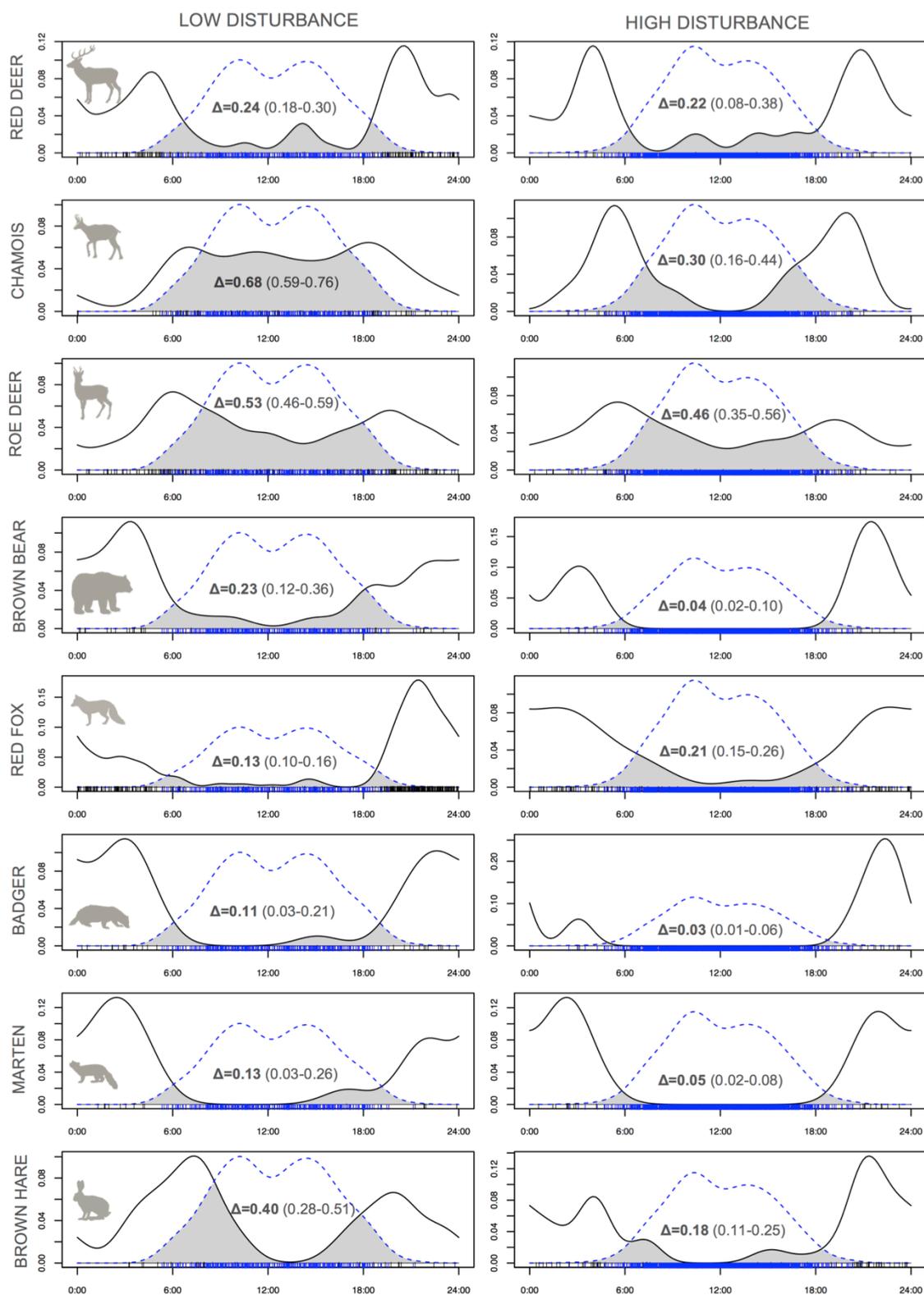
The results of the analysis of activity patterns are summarised in Figure 1.5. For the majority of the target species, the analysis of the relationship between overlap and disturbance revealed significantly smaller overlap with greater disturbance. The red fox was the only species for which the coefficient of overlap slightly increased with greater disturbance. All t-tests for differences in activity overlap between low and high disturbance had a significant outcome ( $P < 0.001$ ).



**Fig. 1.4.** Map of the distribution of the brown bear and chamois in the study area, eastern Alps, with locations of camera traps shown as dots of size proportional to their estimated occupancy. Charts show the influence of significant covariates on occupancy ( $\psi$ ) or detectability ( $p$ ).

## 1.4 Discussion

Our study revealed that human disturbance plays a significant role in influencing the detection probability of target species, indicating that in this coupled human-natural system patterns of habitat association of larger mammals are inherently dependent on human-generated disturbance, and translating into processes of avoidance or, for certain species, tolerance. This also applies to the activity pattern, as for all species it resulted significantly influenced by human activity, supporting our hypothesis that the coefficient of overlap in diel activity between human and wildlife is smaller where disturbance is greater (Fig. 1.5).



**Fig. 1.5.** Diel activity patterns for the eight most detected species in the study area, eastern Italian Alps. The overlap with human activity is shown for low and high disturbance levels. The activity pattern of people is shown as dotted lines. The coefficients of overlap ( $\Delta$ ) are also reported, along with their confidence intervals.

**Table 1.3.** Summary of species-specific occupancy ( $\psi$ ) and detection probability ( $p$ ) estimates for the eight most detected species by camera trapping in the eastern Alps, ordered by decreasing estimated occupancy. Parameters are average values of predicted  $\psi$  and  $p$  from the final models at the 58 camera trap stations. Significant outcomes of the relationships between  $\psi$  or  $p$  and covariates are also indicated with their directionality (positive/negative relationship), shown in parenthesis when the significance is marginal ( $0.05 < P < 0.1$ ). Only the variables with at least one significant outcome are shown. Naïve occupancy values are also shown.

For the brown bear population, that is of remarkable conservation attention (Peters *et al.*, 2015), our results provide novel information on habitat associations as well as patterns in the responses of bears to disturbance. That no covariate of occupancy was retained in more than one model among the best ones suggests the lack of a marked preference for any particular habitat as well as tolerance to human presence. However, the capture rate of humans was negatively correlated with bears' detectability, indicating that the presence of people, which is intense in the summer, may induce a behavioural response of increased shyness of bears at these sites. This is concordant with the comparable pattern of increased detectability with increasing distance from settlements, which may reflect bears' elusiveness in proximity of a

| Species            | Naïve $\psi$ | $\psi$ | SE ( $\psi$ ) | $p$  | SE ( $p$ ) | $\psi$ (elevation) | $\psi$ (capture rate of humans) | $p$ (camera model[model]) | $p$ (trail type[type]) | $p$ (distance from settlements) | $p$ (capture rate of humans) | $p$ (capture rate of vehicles) |
|--------------------|--------------|--------|---------------|------|------------|--------------------|---------------------------------|---------------------------|------------------------|---------------------------------|------------------------------|--------------------------------|
| Roe deer           | 0.79         | 0.83   | 0.09          | 0.42 | 0.06       |                    |                                 | - [Reconyx]               | + [trail/trailS]       |                                 |                              |                                |
| Red deer           | 0.64         | 0.74   | 0.11          | 0.34 | 0.05       |                    |                                 | - [Reconyx]               |                        | (+)                             | -                            | +                              |
| Red fox            | 0.62         | 0.62   | 0.11          | 0.54 | 0.04       | (-)                | +                               | Not used                  |                        | (-)                             |                              | +                              |
| Badger             | 0.33         | 0.54   | 0.14          | 0.18 | 0.05       | -                  |                                 | - [Reconyx]               |                        |                                 |                              |                                |
| Brown bear         | 0.33         | 0.52   | 0.15          | 0.13 | 0.06       |                    |                                 | (-)[Reconyx]              |                        | (+)                             | (-)                          |                                |
| Chamois            | 0.45         | 0.51   | 0.13          | 0.36 | 0.06       | (+)                |                                 | (-)[Reconyx]              |                        |                                 | -                            |                                |
| Brown hare         | 0.29         | 0.45   | 0.12          | 0.21 | 0.07       |                    | +                               | - [Reconyx]               |                        |                                 |                              |                                |
| <i>Martes</i> spp. | 0.24         | 0.29   | 0.10          | 0.25 | 0.06       |                    |                                 | Not used                  |                        | -                               | +                            |                                |

direct and permanent source of disturbance. Both results matched an earlier study in the same areas on detections of bears at rub trees (Tattoni *et al.*, 2015) and other studies in Europe, where bears are known to avoid people (Swenson, 1999; Zedrosser *et al.*, 2001). Interestingly, the brown bear had the lowest average detection probability, and this in turn resulted into a proportionally higher estimated occupancy relative to the naïve occupancy (i.e. from 0.33 to 0.52). The analysis of activity pattern of bears and people revealed clear temporal segregation overall; in addition, analysis of overlap in activity as computed for different disturbance levels showed a significant temporal shift in bear activity at the sites with greater human passage, indicating that bears adjust their movement patterns in time as well as in space to decrease chances of encountering humans. This matches findings of an earlier study (Tattoni *et al.*, 2015) as well as studies from both North America and Europe reporting that in areas with low intensity of human utilization bears are largely diurnal, whereas in areas with high intensity of human utilization or during periods of frequent human access bears shift to nocturnal behaviour (Gibeau *et al.*, 2002; Kaczensky *et al.*, 2006; Moe *et al.*, 2007). Our results support the assumption that the nocturnal activity pattern observed in European brown bears is more likely an effect of individual learning than a genetically fixed trait (Kaczensky *et al.*, 2006). These findings suggest both spatial and temporal displacement in response to human presence, an important prerequisite for the coexistence of brown bears and people in the study area and the Alps in general. This is especially relevant in the current context of increasing human-bear conflicts.

Occupancy analysis revealed co-occurrence of the three ungulates across the study area. Although the red deer is known as superior competitor to smaller ungulates with similar diets (e.g. roe deer and alpine chamois) and this competition is even higher during the summer season (Lovari *et al.*, 2014), habitat heterogeneity can promote coexistence between herbivores (Anderwald *et al.*, 2016). The most distinct patterns among the ungulates are related to the chamois, as indeed for this species the estimated occupancy varied markedly among the 58 sites (Suppl. Table A3). Results of increasing occupancy with increasing elevation and slope are of straightforward interpretation, reflecting how well adapted is this species to rugged and rocky terrain (Corlatti *et al.*, 2011). At the same time, the negative influence of elevation and slope on both deer's occupancy may be evidence of spatial, i.e. altitudinal, segregation with the chamois, whose results included the same spatial drivers, but with converse relationships, as already

documented in the Alps (Anderwald *et al.*, 2016). That capture rate of humans was included in model average as negatively affecting roe deer's probability of occurrence is consistent with the fact that this species proved to be rather active during the day as well as people, even if with crepuscular peaks of activity, with a pattern that seemed to be relatively unaffected by different levels of human passage. The roe deer was the only species for which the trail type was retained as significantly affecting detectability, showing that the passage of vehicles decreases detections. A negative relationship of capture rate of humans with red deer's detection probability and a positive relationship with distance from settlements suggest a certain level of shyness of this species towards human activities and avoidance of permanent sources of human disturbance. For this species, daily activity pattern showed a low coefficient of overlap with humans, with little difference between levels of disturbance. For the chamois, the activity pattern analysis in the sites with low disturbance revealed a typical diurnal behaviour, and the coefficient of overlap with human activity was the highest among all species. In contrast, the daily pattern in the sites with higher disturbance was predominantly crepuscular, suggesting a clear shift in diel activity related to human disturbance.

Results for the red fox and marten are similar in suggesting a high level of tolerance to human presence, which could depend on the availability of human-driven food resources and shelters, and a high heterogeneity of potential ecological niches (Červinka *et al.*, 2014). Their occupancy was positively correlated to the capture rate of both humans and vehicles. Such apparent spatial association with proxies of human disturbance is, however, counterbalanced by an evident temporal segregation between mesocarnivores and people. Indeed, they all showed a typical nocturnal behaviour. Results for the badger suggest secretive habits and higher shyness of this species in response to human disturbance as compared to red fox and marten.

Overall, the checklist of 12 species matched the expectations based on previous accounts (Boitani *et al.*, 2003), indicating that sampling effort was sufficient to detect the great majority of the mammal community, including species that are known to be very rare or localised. Indeed, the record of a wolf as species of conservation concern is of interest and confirms the current, natural recolonization this species in the eastern Alps (Groff *et al.*, 2015). No lynx (*Lynx lynx*) has been recorded, according to the fact that today the only animal known to be present in Trento province is a male that originally dispersed from Switzerland and has recently moved its home range to the SW part of the province (Groff *et al.*, 2015). On the contrary, we did not

record the mouflon (*Ovis musimon*), though it is known to be present over some of the focal part of the study area (data from Servizio Foreste e Fauna of Trento Province). Lastly, that we did not record the alpine ibex (*Capra ibex*) is not surprising as this species occurs only in the western part of the PNAB (data from Servizio Foreste e Fauna of Trento Province); furthermore, it is not a forest-dweller and in the summer season it occupies areas at higher altitudes than the area sampled in our study (Aublet *et al.*, 2009).

As general considerations, an important aspect related to the main goal of assessing human disturbance is that the area we sampled is a complex matrix of intermingled disturbance sources in space and time (settlements, infrastructures, road networks, touristic facilities, hikers, etc.). The lack of a clear and unidirectional disturbance gradient, from outside the protected area to its interior, complicates the analysis and interpretation of results. A similar assessment in a national park with stricter regulations and a stronger gradient of disturbance may therefore reveal clearer patterns of human-wildlife interactions. However, we believe that the context we studied may be more representative of the general environmental settings in the Alps. From a methodological perspective, we inspired our design to a systematic protocol developed by the TEAM Network to monitor medium-to-large mammal communities in the tropics. We introduced differences that should be considered for multi-year monitoring, the most limiting being the use of different camera trap models. Indeed the performances of the two models caused clear differences in estimated detection probability. Seemingly, Reconyx cameras had lower sensitivity than the IR+, with increasing significance for the smaller-sized species. The difference was likely due to the much wider detection angle of the IR+ model (100°, as compared to 33° of the Reconyx), resulting in higher detectability of target species. However, the IR+ yielded a much higher rate of blank/unidentifiable images and two camera malfunctioned, hence overall performing less well. The two models were set on a nearly equal number of trails and roads, suggesting that the difference in detection efficiency are indeed to be attributed to differences in camera performance and not to differences in species' occurrence between trails and forestry roads.

In conclusion, while we found little evidence for a direct impact of human presence on mammals' occurrence in the study area, we found an effect on their detectability, and, interestingly, on their activity pattern. Our results are relevant for protected area managers to assess the degree at which biodiversity conservation is compatible with infrastructural

development, and overall human presence in the Alps. Key recommendations for replicating the study towards setting-up a long-term monitoring include consistency in camera model, camera sites and field routines over the years. These in turn require a solid and collaborative institutional set-up. Sampling is cost-efficient as it requires relatively modest field work (human effort deployed amounts to approximately 60 man/days per year). Data from multiple years can eventually be used to derive globally-set indicators for assessing biodiversity change, such as the Wildlife Picture Index (O'Brien *et al.*, 2010).



**Chapter 2.****Spatial-temporal patterns of human avoidance by brown bears in a reintroduced population**

**Valentina Oberosler**, Simone Tenan, Francesco Rovero. *Oryx (Submitted)*.

**Abstract**

The preservation of large carnivores is a formidable challenge for biodiversity conservation in Europe, where few areas can be considered wilderness. Today, brown bears in Europe coexist with people in densely settled, multi-use landscapes and hence have to cope with diffuse human activities. This calls for an improvement of our knowledge on the effects that these have on brown bear distribution and behaviour. Here, sampling a study area of 220 km<sup>2</sup> with 60 camera trap locations, we investigated the effect of human recreation and settlements on brown bear spatial and temporal patterns across the core area of the small Alpine population in the central Italian Alps. By using images of people and vehicles to quantify human passages, we could directly study how anthropogenic presence affects bears' activity. We assessed bear's daily patterns and found a predominantly crepuscular and nocturnal behaviour, with peaks of activity before dawn and after dusk. We also modelled bear's site use and detection probability in hours when likelihood of encounters with humans was highest. We found a negative effect of the number of people passages on bear occurrence probability, and a significant positive effect of the distance from settlements on its detection probability. Our results suggest that human presence impact brown bears in the central Italian Alps through inducing temporal and spatial displacement. These findings confirm earlier evidence that bears living in human-modified landscapes adapt their spatio-temporal patterns to avoid humans, an important prerequisite for the coexistence of bears and people in the Alps.

**Keywords:** recreation, activity pattern, human disturbance, site use, hierarchical modelling, camera trapping, spatio-temporal displacement

## 2.1 Introduction

The preservation of large carnivores is a formidable challenge for biodiversity conservation (Chapron *et al.*, 2014; Dorresteijn *et al.*, 2014). This is especially true in Europe where, due to higher human population densities and increased habitat fragmentation and alteration (Chapron *et al.*, 2014; Zedrosser *et al.*, 2011), few areas can be considered wilderness (Linnell *et al.*, 2001; Zedrosser *et al.*, 2011). Despite this challenge, in recent decades carnivores have been making a comeback, largely due to re-colonization of historical ranges following the decline of traditional agricultural activities, abandonment of mountain areas by humans, forest restoration, ungulate recolonization and change of conservation policy (Breitenmoser, 1998; Peters *et al.*, 2015). That is the case for the brown bear (*Ursus arctos*) that, although being historically persecuted, is now the most abundant large carnivore in Europe, with all population ranges being relatively stable or slightly expanding (Chapron *et al.*, 2014). However, success in carnivore recovery also increases conflict with humans (Linnell & Boitani, 2011). This calls for an improvement of our knowledge on the effects that human activity has on brown bear distribution and behavior, especially in areas where wild populations are still vulnerable.

Anthropogenic activities, predominantly for recreation, are particularly common in bear habitats across Europe (Fortin *et al.*, 2016), where forests are heavily managed by foresters and hunters and are used by the general public mainly for hiking, camping and mountain biking (Kaczensky *et al.*, 2006). Despite the potential impacts on wildlife and the need to identify mitigating management, the literature on disturbance caused by recreational activities is relatively limited (Fortin *et al.*, 2016). Previous studies in Europe suggest that the primary mechanism by which recreation may impact brown bears is through temporal and spatial displacement (Kaczensky *et al.*, 2006; Fortin *et al.*, 2016). The small Alpine population is the result of a reintroduction project in the central Italian Alps (Tosi *et al.*, 2015), a landscape where human presence is widespread, due to dense settlements and intense tourism presence that largely contributes to human activity across the core area of the local bear population (Oberosler *et al.*, 2017). This represents a suitable model system to investigate the effect of human disturbance on wildlife. We used camera trapping coupled to activity pattern and occupancy

analysis to investigate the effect of human activity on brown bear spatial (site use) and temporal (daily activity) patterns across the Alpine core area in western Trentino, Italy (Groff *et al.*, 2015). We hypothesized (1) temporal displacement between brown bears and people, with a shift to crepuscular/nocturnal activity by bears, as already documented by a previous study across the same study area (Oberosler *et al.*, 2017) and other studies across Europe (Kaczensky *et al.*, 2006; Klinka & Reimchen, 2002). We also hypothesized (2) that in the time slots when both bears and humans are active, bears would spatially avoid sites of higher human passage and activity.

## 2.2 Methods

### 2.2.1 Study area and data collection

We conducted our study in an area of about 220 km<sup>2</sup> in the central Italian Alps (centred on 46°06'45"N and 10°55'50"E). This mountainous area encompasses the southern part of the Brenta group, the westernmost Dolomite group, and its adjacent valleys, which are partially included within the Adamello-Brenta Natural Park (PNAB). The sampling area holds part of the core area of the brown bear population (Groff *et al.*, 2015) and represents a large variation in both habitat type and altitudinal range (300–2800 m a.s.l.), with a dominant mountainous terrain. Tourists contribute largely to human activity in the summer across the study area. Camera trapping data were collected yearly during 2015–2018. Every summer season (June–September), Reconyx HC500 (Reconyx Inc., Holmen, WI, USA) camera traps were distributed over two consecutive arrays of 30 cameras, for a total amount of 60 sampling sites. Cameras were placed at a density of one camera per 4 km<sup>2</sup>, and locations were selected to be representative of the habitat and elevation gradient of the forest. Every sampling season, each camera was deployed for a minimum of 30 days (generally 30–35 days) and placed on a tree to record a trail segment approximately 2–4 m away (Fig. 2.1). For other details about the study area and data collection see Oberosler *et al.* (2017).

### 2.2.2 Data analysis

We investigated daily activity patterns for brown bears and people across the study area over the 4-year period. By following the same procedure applied in Oberosler *et al.* (2017), we estimated the coefficient of overlapping between bear and people activity, and also assessed the

significance of the difference between daily patterns (Meredith & Ridout, 2014; Ridout & Linkie, 2009). To assess site use of bears in relation to human passage, we extracted from the total dataset all images obtained in time intervals 05:00-10:00 am and pm, respectively (hereafter referred to as ‘crepuscular’ hours). These were defined based on the results of the activity pattern analysis (this study and Oberosler *et al.*, 2017). Crepuscular detections of the brown bear during the entire sampling period were summarized in an array,  $Y$ , with elements  $y_{i,t}$ , which denoted the total number of detections for the brown bear at site  $i$ , during year  $t$ . We used a sampling occasion of 5 days, which led to a median of 8 total sampling occasions  $K_{i,t}$  among different sites and years. We carried out single-species occupancy analysis using a hierarchical modelling framework (MacKenzie *et al.*, 2002). True occurrence was modelled as a Bernoulli random variable,  $z_{i,k} \sim \text{Bern}(\psi_{i,t})$  with probability  $\psi_{i,t}$ , where  $z=1$  when the species was present at site  $i$  during year  $t$ , and zero otherwise. We modelled occurrence probability as a function of the number of independent passages of people (both pedestrians and vehicles, discretized using 15 min as interval between consecutive events), as detected by camera traps during each sampling season in crepuscular hours (denoted PEOPLE). We also included a fixed year effect to the linear predictor for occupancy to account for variability across years (YEAR\_PSI), where year 1 is the reference year. We defined the *logit* transformation of the occurrence probability as follows:

$$\text{logit}(\psi_{i,t}) = \alpha_0 + \text{YEAR\_PSI}_t + \alpha_1 * \text{PEOPLE}_{i,t}$$

We also specified the detection model for the observational data,  $y_{i,t}$  for the brown bear at site  $i$  in year  $t$  as  $y_{i,t} \sim \text{Bin}(p_{i,t} * z_{i,t}, K_{i,t})$ , where  $p$  is the detection probability of bears at site  $i$  in year  $t$ , conditional on species presence ( $z=1$ ), and  $K_{i,t}$  is the number of sampling occasions at site  $i$  in year  $t$ . We expected detection probability  $p_{i,t}$  to vary based on distance from settlements (m, denoted VILLAGE). Our hypothesis was that animals would be more elusive near settlements because of greater disturbance (Oberosler *et al.*, 2017). In addition, we added a fixed year effect to account for variability across years (YEAR\_P):

$$\text{logit}(p_{i,t}) = \beta_0 + \text{YEAR\_P}_t + \beta_1 * \text{VILLAGE}_i$$

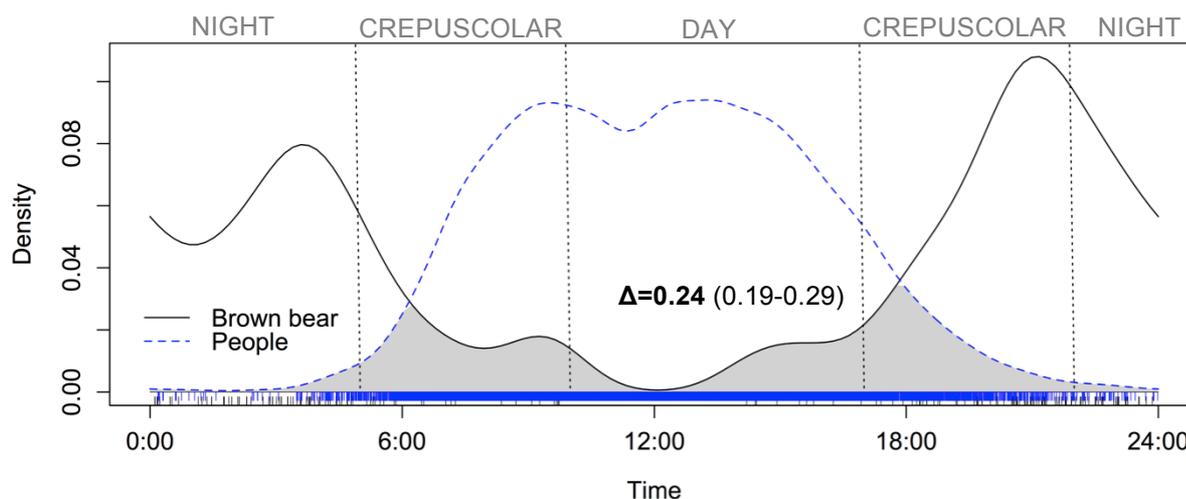


**Fig.2.1.** A selection of brown bear images taken by camera traps during the sampling seasons 2015-2018 in the study area, central Italian Alps.

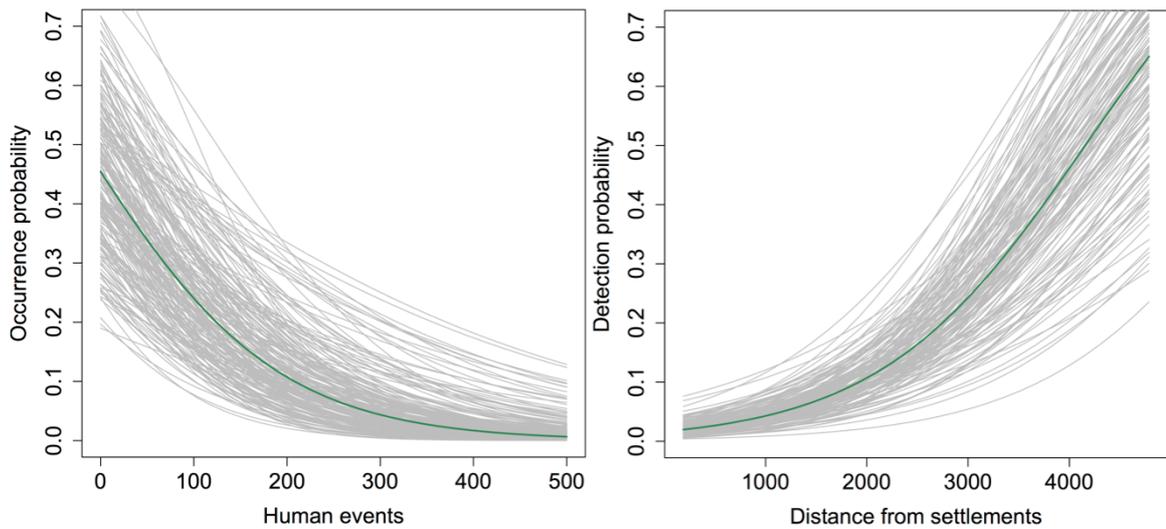
We ran 3 chains of length 150,000, discarded the first 10,000 iterations as burn-in, and thinned the remaining results by taking each 20<sup>th</sup> value from the chains, yielding 21,000 total samples from the joint posterior. Covariates were standardized to have mean zero and unit variance. We verified convergence through visual inspection of the chains and with the Gelman-Rubin diagnostic (Brooks & Gelman, 1998). For information about prior distributions we refer to the model code (Suppl. Material B1).

### 2.3 Results

Result of the activity patterns analysis showed a predominantly crepuscular and nocturnal behaviour for the brown bear across the study area over the 4-year sampling seasons. Activity peaked before dawn (04:00 am) and after dusk (09:00 pm). Brown bear activity curve was significantly different from that of humans, with a coefficient of overlap of  $\Delta=0.24$  (0.19-0.29,  $p<0.00001$ ) (Fig. 2.2). Results for the site use model showed a significant negative effect of the number of people events on bear occurrence probability ( $\alpha_1 = -0.94$ , 95% Bayesian Credible Interval [BCI] -1.64 – -0.37) (Fig. 2.3). Additionally, we found a significant positive effect of the distance from settlements on bear detection probability ( $\beta_1 = 0.91$ , 95% BCI 0.59 – 1.25; Fig. 2.3 and Suppl. Table B2).



**Fig. 2.2.** Diel activity patterns (kernel density curve) for the brown bear over the 4-year period in the study area, central Italian Alps, and its overlap with human activity (dashed line). The dotted vertical lines delimit the crepuscular window of time considered in the occupancy analysis. The coefficient of overlap ( $\Delta$ ) and relative confidence interval are also reported.



**Fig. 2.3.** Significant effects of covariates on occurrence and detection probability for the brown bear across the study area (Trentino, Italian Alps), as assessed within the crepuscular hours (05:00-10:00 am and 05:00-10:00 pm).

## 2.4 Discussion

Our results suggest that human activity (motorised and non-motorised, predominantly for recreation) and settlements affect brown bears in the central Italian Alps through temporal and spatial displacement. Analysis of activity patterns showed temporal displacement between bears and people, with bears being active mostly during the night and in crepuscular hours, and human activity typically being high during daylight. Spatial site-use analysis carried out for crepuscular hours, i.e. when bears and people are both active, revealed spatial displacement, with bears avoiding sites with high people passage, and being less detectable close to settlements.

These results are partially consistent with preliminary findings from the same study area on the baseline year of data collection (Oberosler *et al.*, 2017). In particular, the coefficient of overlap between daily activity of bears and peoples for the 4-year period was consistent with the one computed on the 2015 dataset for sites with lower human disturbance. This is likely because the majority of bear detections are from sites where human pressure is relatively low. Interestingly, however, results of bear spatial site-use analysis from the preliminary study, which took into account the dataset of the whole 24-h period (i.e., that did not consider the

temporal displacement of bears and people), showed no significant effects of human disturbance on bear's site use (Oberosler *et al.*, 2017). The pattern of increased detectability with increasing distance from settlements we detected may reflect bears' elusiveness in proximity of a direct and foreseeable source of disturbance. This result matches previous studies in the same area (Tattoni *et al.*, 2015; Oberosler *et al.*, 2017).

Brown bear switching from diurnal to crepuscular or nocturnal activity to avoid encounters with people has already been documented for other bear populations across Europe (Fortin *et al.*, 2016; Kaczensky *et al.*, 2006; Klinka & Reimchen, 2002; Olson, Squibb & Gilber, 1998), as well as spatial avoidance, which primarily includes bears avoiding areas close to humans and leaving areas in response to humans (Fortin *et al.*, 2016). However, our study offers new insights into the only Alpine bear population and provides for a unique data collection, whereby we could quantify bear and human activity simultaneously and at the same scale. Furthermore, this extensive sampling with camera traps, consistent over the 4-year period, allowed us to investigate with the same dataset both spatial and temporal patterns of human avoidance by bears.

This predominantly 'shy' behaviour is typical of carnivores, which show diurnal activity in remote areas and often become more nocturnal when in human-dominated landscapes (Ordiz *et al.*, 2017). In North America, for example, where areas inhabited by bears are generally characterized by low intensity of human utilization, brown bears seem largely diurnal (Klinka & Reimchen, 2002) and more aggressive than their European counterparts (Swenson *et al.*, 1999). However, patterns of spatial avoidance of roads and trails with high human passages, especially motorised recreational traffic, have also been documented for grizzly bears (Northrup *et al.*, 2012; Ladle *et al.*, 2019).

The area inhabited by the study population has one of the highest human population densities among those occupied by brown bears (De Barba *et al.* 2010; Chapron *et al.* 2014). In this context, this small brown bear population of the central Italian Alps is of remarkable importance for conservation: it is subject to high rates of anthropogenic mortality (Tenan *et al.*, 2016), has no immigration, and its density steadily decreases from the point where founders were released, indicating their limited dispersal ability (Tenan *et al.*, 2017). Indeed, its core range in Trentino is a key requisite for the purpose of facilitating the establishment of the larger Alpine population in the future (Groff *et al.*, 2015; Peters *et al.*, 2015; Mustoni *et al.*, 2003;

Linnell *et al.*, 2008). Yet, connectivity of this population remains a concern at multiple spatial scales (Peters *et al.*, 2015). Overall, our results deliver a reassuring message for forest users and managers and provide more evidence that bears living in human-modified landscapes have developed a solid pattern of human avoidance. This is an important prerequisite for the coexistence of brown bears and people in the study area and the Alps in general, and is especially relevant in the current context of increasing human-bear conflicts.



### **Chapter 3.**

## **When parks work: effect of anthropogenic disturbance on occupancy of tropical forest mammals**

**Valentina Oberosler**, Simone Tenan, Elise F. Zipkin, Francesco Rovero, 2019. *Ecology and Evolution* (In review).

### **Abstract**

Protected areas (PAs) in the tropics are vulnerable to human encroachment and, despite formal protection, they do not fully mitigate anthropogenic threats to habitats and biodiversity. However, attempts to quantify the effectiveness of PAs and to understand the status and changes of wildlife populations in relation to protection efficiency remain limited. Here, we used camera-trapping data collected over 8 consecutive years (2009-2016) to investigate the yearly occurrences of medium-to-large mammals within the Udzungwa Mountains National Park (Tanzania), an area of outstanding importance for biological endemism and conservation. Specifically, we evaluated the effects of habitat and proxies of human disturbance, namely illegal hunting with snares and firewood collection (a practice that was banned in 2011 in the park), on species occurrence probabilities. Our results showed variability in species' responses to disturbance: the only species that showed a negative effect of the number of snares found on occurrence probability was the Harvey's duiker, a relatively widespread forest antelope. Similarly, we found a moderate, positive effect of the firewood collection ban on only the suni, another common antelope, and a negative effect on a large opportunistic rodent, the giant-pouched rat. Importantly, we found evidence of temporal stability in occurrence probability for all species over the 8-year study period. Our findings suggest that well managed PAs can sustain mammal populations in tropical forests. However, variability among species in their responses

to anthropogenic disturbance necessitates consideration in the design of conservation action plans.

**Keywords:** camera trapping, bushmeat hunting, Udzungwa, hierarchical modelling, snares, Tanzania

### 3.1 Introduction

Tropical forests are the most biologically rich ecosystems on earth (Myers *et al.*, 2000) and their rapid disruption imperils global biodiversity more than any other contemporary phenomenon (Gibson *et al.*, 2011). With deforestation advancing quickly, protected areas (PAs) are becoming critical refuges for threatened species, and growing concern about the impacts of anthropogenic activities on tropical biodiversity has led to increases in their number and extent (Jenkins & Joppa, 2009). However, many PAs in the tropics are vulnerable to human encroachment (Bruner *et al.*, 2001) and do not fully mitigate threats to habitat and biodiversity. This is due to multiple reasons including chronic under-staffing, inadequate funding and political instability hampering adequate law enforcement (Bruner *et al.*, 2001; Naughton-Treves *et al.*, 2005; Laurance *et al.*, 2012; Tranquilli *et al.*, 2014). For these reasons, PAs are not always effective to prevent wildlife declines, and local extirpations have increased (Craigie *et al.*, 2010). Yet, efforts to quantify the effectiveness of PAs and understand whether they can sustain biodiversity remain limited (Leverington *et al.*, 2008; Geldmann *et al.*, 2013).

Here, we used camera-trapping data collected over 8 consecutive years (2009-2016) to investigate the temporal occurrences of mammals within the Udzungwa Mountains National Park (UMNP, Tanzania), an area of outstanding importance for biological endemism and biodiversity conservation (Rovero *et al.*, 2014a). Thanks to efficient law enforcement, this park is relatively well protected from extractive uses. Yet, instances of human disturbance, specifically hunting and logging, have been regularly reported (Rovero *et al.*, 2012). Our main objective was to investigate the effect of habitat variables and different sources of human disturbance on occurrence probabilities of target forest mammal species over the 8-year period. Wire snares are the most used hunting method in African forests because they are inexpensive, effective, and easy to obtain, set and conceal (Noss, 1998). Snaring is difficult to control by management authorities (Jones *et al.*, 2019) and being non-selective it confers by-catch

mortality on a variety of species (Lindsey *et al.*, 2011). Another potential source of disturbance in the UMNP was firewood collection by adjacent villagers, permitted until 2011. Firewood collection is widespread and increasing across Africa, where woodfuels are the dominant energy source, both as primary energy supply and number of people relying on them (Bailis *et al.*, 2005). Selective firewood harvesting may change forest composition and ecosystem functioning, with cascading effects on the structure of wildlife populations and communities (Naughton-Treves *et al.*, 2007).

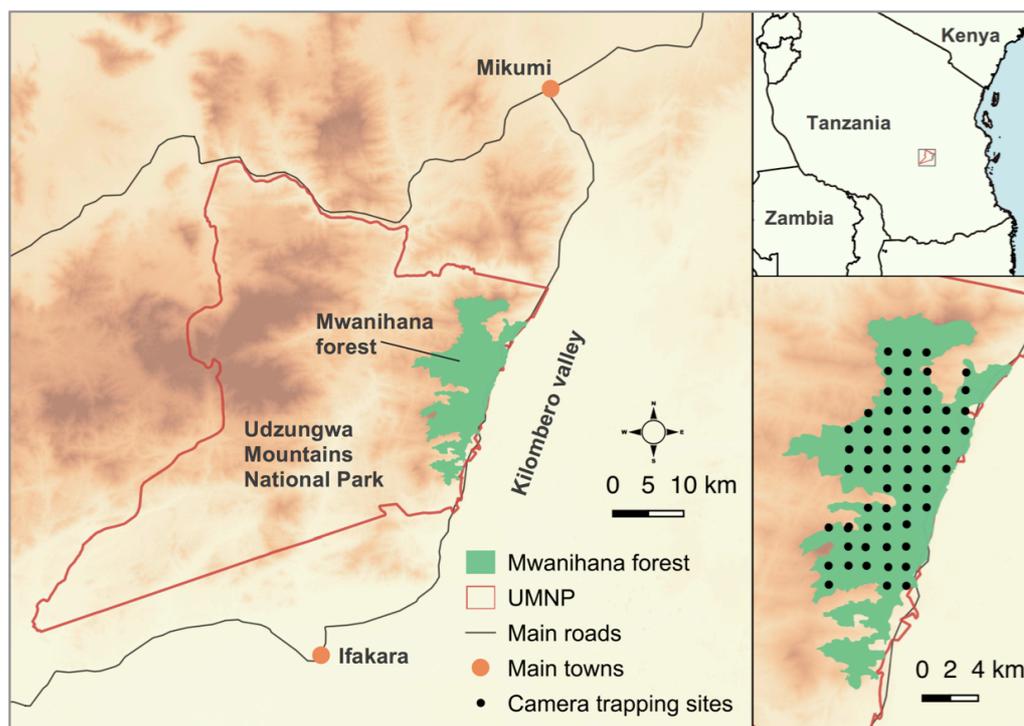
We focused on terrestrial, ground-dwelling, medium-to-large mammals that are relatively easily detected by camera traps and particularly sensitive to ground-occurring human disturbance (e.g. Ahumada *et al.*, 2011). Mammals are key components of tropical ecosystems as they perform critical functions such as predation, grazing, and seed dispersal, and provide important human benefits such as food, recreation, and income (Hoffmann *et al.*, 2011). Furthermore, mammals include many charismatic species that are important flagships for conservation efforts (Leader-Williams & Dublin, 2000; Rondinini *et al.*, 2011). We used occupancy (i.e. the estimated probability of a species occurrence at a collection of sites; MacKenzie *et al.*, 2002) as the metric of choice to address our objectives. Given its documented correlation with abundance (MacKenzie *et al.*, 2003), occupancy provides information on both density and extinction likelihood (MacKenzie *et al.*, 2005). Furthermore, this metric accounts for imperfect detection (MacKenzie, 2005) and thus can adequately address the problem that species may go undetected where present. Issues of imperfect detection are ubiquitous in ecological field data and if unaddressed can bias inferences on habitat relationships and ‘true’ species occurrence (Kéry, 2011). We expected a positive effect of the firewood collection ban on species-specific occurrence probabilities, and a negative effect of the number of snares. We also predicted average species-specific occurrence probability to be stable over the 8-year period, due to overall effective protection in the park.

## 3.2 Methods

### 3.2.1 Study area

We conducted our study in Mwanihana forest (MW, centred on 36°46'E, 7°47' S), located in the UMNP, which was established in 1992 (Fig. 3.1). The UMNP (1990 km<sup>2</sup>) contains large areas of mountain forest and grassland and is the only national park that support significant Eastern Arc

habitat in Tanzania (Burgess *et al.*, 2007). It is managed by the Tanzania National Parks Authority (TANAPA), a well-resourced national agency (Rovero *et al.*, 2014b). MW is an east-facing escarpment slope, characterized by a unique continuous vegetation cover from lowland, sub-montane deciduous forest to evergreen moist montane forest (Lovett, 2008). The forest extends over 177 km<sup>2</sup>, with elevation ranging between 290–2300 m a.s.l. The anthropogenic pressure in MW comes mainly from villages located along the eastern side of the forest. Earlier assessments showed that active law enforcement in MW resulted in virtually no disturbance (DeFries *et al.*, 2010), even though evidence of illegal hunting, mainly from snares set to catch ungulates, have been repeatedly reported (Rovero *et al.*, 2012; this study). Another potential source of disturbance was firewood collection by adjacent villagers; this practice was allowed weekly only within 1 km off the PA boundary, and was banned in June 2011.



**Fig. 3.1.** Map of the study area, Mwanihana forest, in the Udzungwa Mountains of Tanzania. This forest represents the interface between the densely settled Kilombero valley and the Udzungwa Mountains National Park (UMNP). Camera traps locations in the forests are shown as black dots. The geographic location of the study area in Tanzania is shown in the map on the upper right.

### 3.2.2 Target species

We conducted our analysis on eight ground-dwelling forest species that were recorded every year between 2009 and 2016 in MW with sufficient independent events to ensure identifiability of model parameters (see Suppl. Table C1). These species are characterized by different conservation status, trophic position and relative abundance, overall representing the variability within the larger community. We included the (1) Harvey's duiker (*Cephalophus harveyi*), a medium-bodied forest antelope that is common but declining across its range, and the (2) suni (*Nesotragus moschatus*), which is a small antelope that remains common through parts of its range but locally threatened. The IUCN-vulnerable (3) grey-faced sengi (*Rhynchocyon udzungwensis*) is a recently discovered insectivore whose total range is confined to two forests in the Udzungwa Mountains (Rovero *et al.*, 2014b; IUCN, 2016). Two other species included in the analyses, listed as IUCN-endangered (IUCN 2016), are the Udzungwa's endemic and iconic monkey (4) Sanje mangabey (*Cercocebus sanjei*), and the poorly known, large-bodied (5) Abbott's duiker (*Cephalophus spadix*), endemic of highland forests of Tanzania. The widespread (6) giant-pouched rat (*Cricetomys gambianus*) is a strictly nocturnal, large omnivore. Targeted mesocarnivores included the (7) bushy-tailed mongoose (*Bdeogale crassicauda*), widely distributed in eastern Africa, and the (8) Lowe's servaline genet (*Genetta servalina lowei*), a poorly known subspecies endemic of the Eastern Arc Mountains.

### 3.2.3 Data Collection

Camera trapping data were collected yearly during 2009-2016 in MW as part of the Tropical Ecology Assessment and Monitoring (TEAM) Network programme (Rovero & Ahumada, 2017). Every dry season (July-November), Reconyx RC45 and HC500 (Reconyx Inc., Holmen, WI, USA) camera traps were distributed over three consecutive arrays of 20 cameras according to a standardized protocol for monitoring terrestrial vertebrates (TEAM Network, 2011), for a total of 60 sampling sites (Fig. 3.1). Cameras were placed at a density of one camera per 2 km<sup>2</sup>, and locations were selected to be representative of the habitat and elevation gradient of the forest. Every sampling season, each camera was placed on a tree to record a trail segment approximately 2-3 m away and deployed for a minimum of 30 days (generally 30-35 days). The area within the sensor field of the camera was cleared of ground vegetation for better visibility. Functioning camera traps (58-60 per year, mean=59.3) accumulated 14,743 camera days (31.1

mean per camera, 1842.9 mean per year). Sampling yielded 141,541 images of 31 wild mammal species (see Suppl. Table C1 for detection events per year).

### 3.2.4 Data Analysis

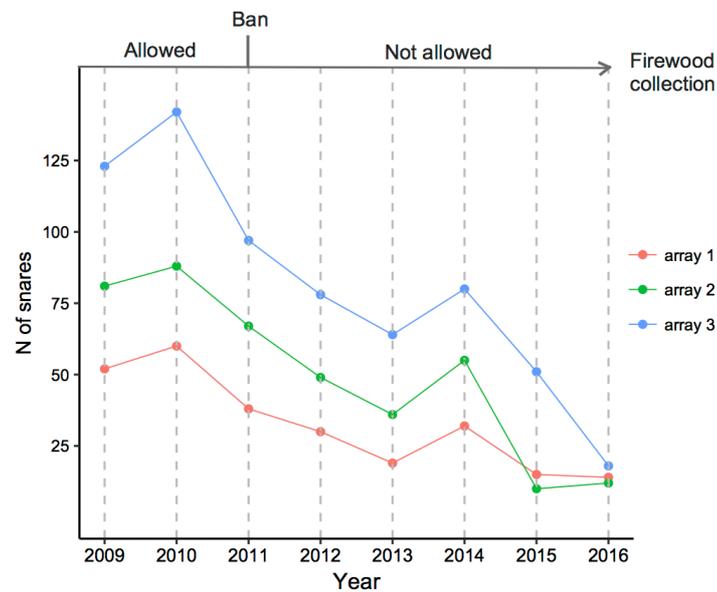
We summarized species-specific detection/non-detection data at each site  $i$ , sampling occasion  $j$ , during year  $k$ , in 3-d arrays  $Y_{i,j,k}$ , using a sampling occasion of 5 days. Such resolution was small enough to yield stable parameter estimates, and large enough to ensure the model was computationally tractable. We carried out single-species occupancy analyses using a hierarchical modelling framework (MacKenzie *et al.*, 2002). The observational data,  $y_{i,j,k}$ , denoted detections ( $y=1$ ) or non-detection ( $y=0$ ) for each species at site  $i$ , sampling occasion  $j$ , during year  $k$ . True occurrence was only partially observable and was modelled as a Bernoulli random variable,  $z_{i,k} \sim \text{Bern}(\psi_{i,k})$  with probability  $\psi_{i,k}$ , where  $z=1$  when the species was present at site  $i$  during year  $k$ , and zero otherwise. We modelled occurrence probability as a function of elevation (m a.s.l., denoted ELEV), which we considered a proxy for variation in forest composition over the study area and hence a proxy for habitat type (Lovett, 2008). We also included a square term for the effects of elevation, to account for potential mid-altitude peaks in species-specific distribution (ELEV<sup>2</sup>). The number of snares (SNARES) for illegal hunting collected by the field team during the deployment of each array of camera traps in every sampling season was used as a yearly-site continuous covariate and a proxy for the amount of illegal hunting at sites. We also included a binary (0-1) year-specific covariate to describe the management status of the forest regarding the firewood collection activity (BAN), to test for potential effects of its ban on species-specific occurrence probabilities (Fig. 3.2). We developed an auto-logistic model, such that the intercept term in the occurrence model was dependent on whether or not the species was present at site  $j$  in the previous year (Zipkin *et al.*, 2012). Compared to the full colonization/extinction model, this is considered to be a more convenient parameterization when covariates are thought to influence occupancy, rather than its components colonization and persistence (Royle & Dorazio, 2008). Furthermore, in such cases the auto-logistic formulation appears to yield a more efficient Bayesian implementation. So, we assumed that the *logit* transformation of the occurrence probability is a linear combination of the auto-logistic component and the effects of covariates as follows:

$$\text{logit}(\psi_{i,k}) = \alpha_0 + \alpha_1 * z_{i,k-1} + \alpha_S * \text{SNARES}_{i,k} + \alpha_E * \text{ELEV}_i + \alpha_{E2} * \text{ELEV}^2_i + \alpha_B * \text{BAN}_k$$

Here,  $(\alpha_0 + \alpha_1 * z_{i,k-1})$  is the intercept term, where  $\text{inverse-logit}(\alpha_0)$  is the species' colonization probability and  $\text{inverse-logit}(\alpha_0 + \alpha_1)$  the persistence probability, while  $\alpha_S$ ,  $\alpha_E$ ,  $\alpha_{E2}$  and  $\alpha_B$  are the effect of covariates on occupancy. The linear predictor of occurrence probability in the first year was similarly formulated as:

$$\text{logit}(\psi_{i,1}) = \alpha_2 + \alpha_S * \text{SNARES}_{i,1} + \alpha_E * \text{ELEV}_i + \alpha_{E2} * \text{ELEV2}_i$$

We did not include the SNARE covariate in the occupancy model for the grey-faced sengi because, given its small size, this species is not affected by hunting with snares (F.R., unpubl. data).



**Fig. 3.2.** Summary of the year-dependent covariates used in the species-specific occupancy models of eight mammal species in the Udzungwa Mountains of Tanzania. At the top, the management status of the forest in terms of firewood collection (used as binary 0-1 year-specific covariate). Below, the number of snares for illegal hunting collected by the field team during the deployment of each array of camera traps across years

Occurrence is imperfectly observed, which confounds the estimation of  $\psi_{i,k}$ . We therefore specified the detection model for the observational data as  $y_{i,j,k} \sim \text{Bern}(p_i * z_{i,k})$ , a Bernoulli random variable dependent on the occupancy state, where  $p$  is the detection probability at site  $i$ , given that the species is present. We expected detection  $p_i$  to vary based on

the shortest linear distance to the park border (BORDER), a continuous site-covariate. We hypothesized that animals would be more elusive near the border because of greater disturbance and, possibly, denser forest floor vegetation, both limiting detection by camera traps (Rovero *et al.*, 2014a). The detection model for each species at site  $i$  was specified as:

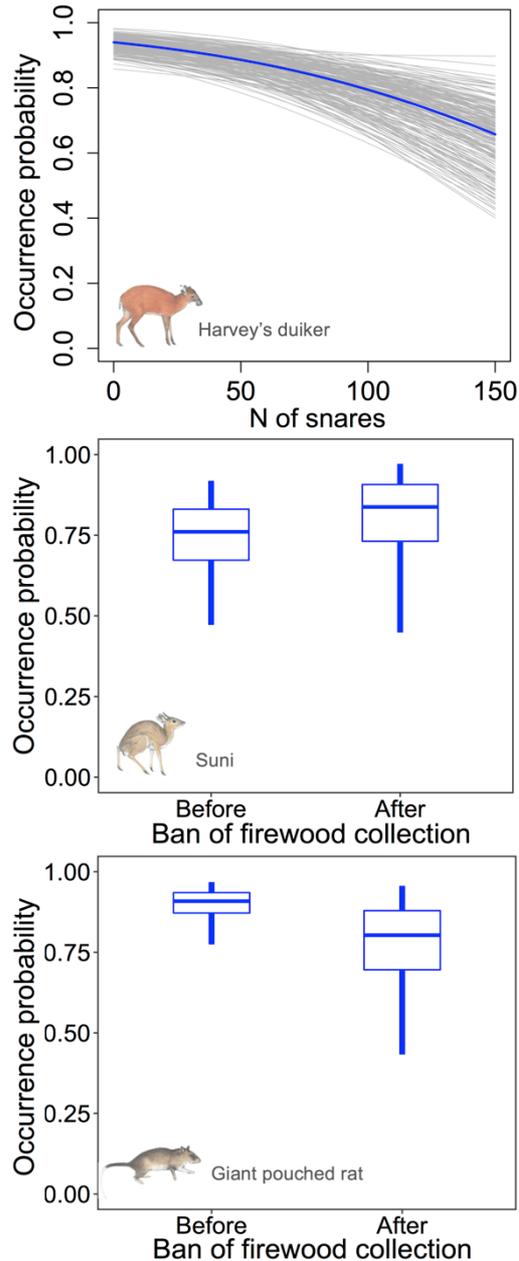
$$\text{logit}(p_i) = \beta_0 + \beta_B * \text{BORDER}_i$$

We fit the model using a Bayesian formulation and Markov chain Monte Carlo using JAGS (Plummer, 2003), called from R (R Development Core Team, 2016) through the package ‘jagsUI’ (Kellner, 2016). For each model, we ran 3 chains of length 100 000, discarded the first 5000 iterations as burn-in, and thinned the remaining results by taking each 20<sup>th</sup> value from the chains. Continuous covariates were derived using geo-processing tools available in QGIS 2.18.0 (QGIS Development Team, 2017), and standardized to have mean zero and unit variance. Elevation and distance from border were collinear (Pearson’s  $r=0.7$ ), but this did not affect the analysis since their effects were included on different parts of the model. Finally, we did not include a year effect on occupancy probability because it was inversely correlated with snares (Pearson’s  $r=0.7$ ; see Fig. 3.2). We used uninformative priors (see Suppl. Table C4) and verified convergence through visual inspection of the chains and with the Gelman-Rubin diagnostic (Brooks & Gelman, 1998).

### 3.3 Results

The effects of covariates on occupancy varied among species (Fig. 3.3, Suppl. Table C2). The only species for which the number of snares collected had a significant effect on occupancy was the Harvey’s duiker, showing a negative effect ( $\alpha_S$ : mean -0.49, 95% Bayesian credible interval [BCI] -0.76 – -0.21). Firewood collection ban had a positive, but marginally non-significant effect (i.e. BCI overlapped 0) on the occurrence probability of the suni ( $\alpha_B$ : mean 0.49, 95% BCI -0.09 – 1.09). On the contrary, the ban had a negative effect on the giant-pouched rat ( $\alpha_B$ : mean -0.90, 95%BCI -1.50 – -0.32; Fig. 3.3). Model results also showed that occurrence at a site in one year had a strong influence on species occurrence probabilities in the following year, revealing temporal consistency in occupancy for most species across sites. Specifically, persistence ( $\alpha_0 + \alpha_1$ ) was significantly higher than colonization ( $\alpha_0$ ) for all species, except for the bushy-tailed mongoose and the Abbott’s duiker (Table 3.1). Furthermore, the derived species-

specific average occurrence probability showed stability for all species (Fig. 3.4). Elevation ( $\alpha_E + \alpha_{E2}$ ) had variable effects on species-specific occurrence probabilities, which were significant and strong for most species (see Suppl. Table C2). Contrary to patterns in occupancy, detectability varied more consistently among species and there was an effect of distance to park border for all species except the Sanje mangabey and suni.



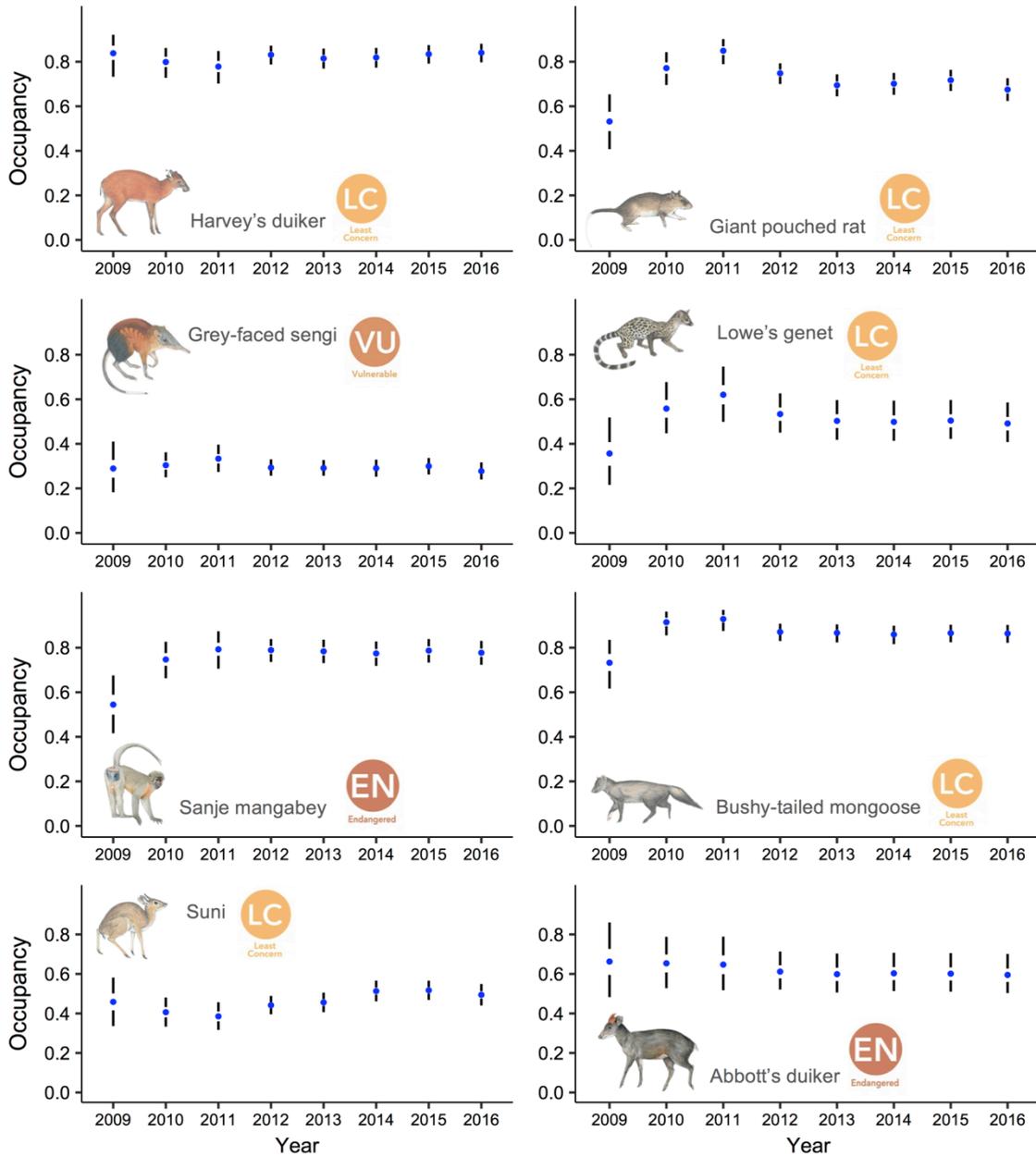
**Fig. 3.3.** Significant effects of disturbance covariates on occurrence probability for eight mammal species detected with camera traps in the Udzungwa Mountains, Tanzania. Drawings by J. Kingdon reproduced with permission.

**Table 3.1.** Parameter estimates from autologistic models of occurrence probability of eight species of mammals monitored by camera trapping in the Udzungwa Mountains of Tanzania. Values are means with 95% Bayesian credible intervals (BCI) of colonization ( $\alpha_0$ ) and persistence ( $\alpha_0 + \alpha_1$ ) probabilities for each species. Asterisks denote no overlap between 95% BCIs.

| <b>Species</b>        | <b>Colonization</b> | <b>Persistence</b> |   |
|-----------------------|---------------------|--------------------|---|
| Harvey's duiker       | 0.71 (0.55-0.84)    | 0.88 (0.80-0.93)   |   |
| Grey-faced sengi      | 0.08 (0.04-0.17)    | 0.84 (0.68-0.93)   | * |
| Sanje mangabey        | 0.75 (0.60-0.87)    | 0.93 (0.85-0.97)   |   |
| Suni                  | 0.19 (0.11-0.30)    | 0.76 (0.63-0.86)   | * |
| Bushy-tailed mongoose | 0.89 (0.76-0.96)    | 0.95 (0.90-0.98)   |   |
| Abbott's duiker       | 0.60 (0.35-0.84)    | 0.78 (0.59-0.92)   |   |
| Lowe's genet          | 0.44 (0.30-0.59)    | 0.75 (0.59-0.87)   | * |
| Giant pouched rat     | 0.59 (0.45-0.72)    | 0.91 (0.84-0.95)   | * |

### 3.4 Discussion

Using systematic camera-trapping data and hierarchical modeling, we studied the occurrences of forest mammals over 8 consecutive years (2009-2016) within the Udzungwa Mountains National Park (Tanzania). We found that target species' occurrence probability over the study period was stable in spite of illegal hunting, and firewood collection until 2011, by adjacent villagers. The responses of the target species to these sources of disturbance were variable. The Harvey's duiker was the only species negatively affected by snares. Although wire snares can potentially catch a pool of similar size species, this common antelope may be particularly vulnerable, and hunters probably place snares along trails that duikers routinely use. In addition, the Harvey's duiker is among the most abundant species in our dataset, hence the one where the effect of illegal hunting may have greater magnitude. Notably, we observed a forest-wide decline in poaching over the 8-year period as the number of snares collected across the study area decreased (Fig. 3.2). Since the number of snares was inversely correlated with the sampling year, the result for the Harvey's duiker may mirror an increase in occurrence probability for this species.



**Fig. 3.4.** Estimated mean occupancy in the 8-year period for eight mammal species camera-trapped in the Udzungwa Mountains, Tanzania. Drawings by J. Kingdon reproduced with permission.

Furthermore, although this metric may not measure accurately the actual poaching pressure across the forest, given that hunters may change their target areas periodically, this reduction, coupled with firewood collection ban in 2011, suggests a gradual decrease of human pressure in the PA and/or an improvement of management effectiveness. Firewood collection was permitted only within the lower elevation portion of the forest (Hegerl *et al.*, 2015), hence of

potentially negligible impact on species of interior forest/higher elevations. Hence, we expected a positive effect of the ban on occupancy trends mainly for edge-dwelling species (such as the Harvey's duiker and the suni). Interestingly, results showed a small positive effect of the ban only for the suni, suggesting that the impact of this practice on other species may have been minor. This result, however, could also have been contributed by the limited data available before the ban. Moreover, we found an opposite effect on occupancy for a relatively common species, the giant-pouched rat. This opportunistic species is reported to fare well in highly disturbed habitats and thus the result is not surprising (Engeman *et al.*, 2006; Roemer, Gompper & Van Valkenburgh, 2009; Hegerl *et al.*, 2015).

Our findings suggest that law enforcement in the target PA is effective in sustaining the target populations, and supports evidence from previous studies that the national park is more effective as compared to other reserves in the area where ground protection appears inadequate (Rovero *et al.*, 2012; Jones *et al.*, 2019). This is also consistent with results from a previous study over the same study area (Rovero *et al.*, 2015), which reported that estimated group abundance of arboreal primate species appeared stable over an 11-year period (2002-2012). In contrast, most species declined severely in a nearby nature reserve, due to high levels of uncontrolled illegal hunting (Rovero *et al.*, 2015; Hegerl *et al.*, 2015). These authors report a marked difference between this nature reserve and MW also in terms of PA management indicators, i.e., the annual budget allocated for forest management (USD c. 1,000 versus 400,000, respectively), and the number of permanent staff units (1 versus 78, respectively, with the latter number, related to the whole national park, including 60 rangers that are regularly involved in patrols). Our species-specific results on population trends are also consistent with the community-level stability detected by Beaudrot *et al.* (2016) in a previous study using a shorter time series of data from across the TEAM network. Thus, our findings are generally in line with global assessments suggesting less extreme deterioration in tropical forest protected areas than reports based on data lacking of standardized monitoring infrastructures (Laurance *et al.*, 2012; Beaudrot *et al.*, 2016).

Elevation was a significant effect on occupancy for five of the eight species examined. We considered elevation a proxy for preference of moist evergreen forest interior (which occurs at higher elevation) and it likely also reflects decreasing human disturbance, with human settlements bordering the eastern edge of the low elevation forest. Results showed a strong and

positive effect of elevation on occurrence probability for the grey-faced sengi. This matches earlier findings (Rovero *et al.*, 2014b) and also suggests that this species is relatively little affected by human disturbance over the study area. Accordingly, we found no significant effect of the ban of firewood collection on occupancy for the grey-faced sengi. This recently-discovered insectivore, assessed as vulnerable by the IUCN (IUCN, 2016), is endemic of only two forests across the Udzungwa Mountains (Rovero *et al.*, 2008) and our results are encouraging about its conservation. Results for the Harvey's duiker and the bushy-tailed mongoose showed a negative effect of elevation on occupancy. Results for the suni antelope showed a mid-altitude peak in its distribution with the highest occupancy probability estimates below 1,000 m a.s.l. and so close to human disturbance sources, suggesting a higher sensitivity of this species to anthropogenic disturbance and higher potential risk of extinction than other species of the interior forest and high elevations. This is consistent with the abovementioned positive effect of the firewood collection ban on occupancy showed for this species.

Given the high investment that has been made worldwide in PAs (Balmford *et al.*, 2003) and their importance for long-term conservation, it is crucial to document how effectively they are performing (Naughton-Treves *et al.*, 2005). In this context, a key information challenge in conservation practice is the quality of available biodiversity data in the tropics (Beaudrot *et al.*, 2016). In particular, there is a lack of primary in situ data on populations in tropical PAs, which results in conclusions based on aggregated secondary data and expert opinion (Geldmann *et al.*, 2013). In this regard our study highlights the effectiveness of systematic camera trapping coupled with hierarchical models to investigate the status of mammal communities, and to assess species-specific responses to anthropogenic variables (Pettorelli *et al.*, 2010; Zipkin *et al.*, 2010). This approach is particularly effective when applied to standardized and long-term data series, which are needed for long-lived animals. In conclusions, our standardized dataset provides evidence that effective ground protection is associated with stability over time in the occurrence probability of a pool of commonly camera trapped species of forest mammals, and therefore we support the notion that legal protection backed up by on-ground protection can maintain diverse mammal communities in tropical forests. This is especially relevant in Tanzania, arguably mainland Africa's most important nation for conservation, which is losing habitat and natural resources rapidly (Caro & Davenport, 2016).



## **Chapter 4.**

### **Poor management in protected areas is associated with lowered tropical mammal diversity**

**Valentina Oberosler**, Simone Tenan, Elise F. Zipkin, Francesco Rovero, 2019. *Animal Conservation*.

#### **Abstract**

Numerous protected areas (PAs) have been created worldwide to safeguard wildlife and other natural resources from anthropogenic threats such as habitat destruction and bushmeat hunting. However, conservation efforts in many tropical PAs are still inadequate, revealing deficiencies in management effectiveness. It is therefore important to quantify how different protection regimes impact wildlife within PAs. We investigated the differences between forest mammal communities in two ecologically comparable PAs in the Udzungwa Mountains (Tanzania) with contrasting management regimes. One is a well-protected national park with efficient law enforcement; the other has suffered decades of inadequate protection, mainly resulting in high levels of illegal hunting. Using camera-trapping data, we assessed the target communities in terms of species richness, functional composition (i.e., proportions of trophic guilds) and species-specific occurrences, all while accounting for imperfect detection. We found striking differences between the two mammal communities: lower species richness, alteration in the trophic structure, and reduced occurrence probabilities for most species in the forest with high disturbance. The difference in occurrence probability between the two PAs tended to be highest for larger-bodied species. Our results show that strictly-enforced legal protection is required to maintain diverse mammal communities in tropical forests under ever-increasing anthropogenic threats. While PAs are the cornerstone of efforts to conserve tropical biodiversity, the future of biodiversity within them is closely tied to the effectiveness of enforcement.

**Keywords:** camera trapping, bushmeat hunting, species richness, hierarchical modeling, community occupancy, Tanzania

#### 4.1 Introduction

Tropical rainforests are the richest terrestrial ecosystems on the planet (Myers *et al.*, 2000), harboring unparalleled diversity that provides important ecosystem services at local, regional, and global levels (Kremen *et al.*, 2000). Mammals are key components within tropical ecosystems, playing integral roles as consumers, dispersers of seeds and spores, predators, and prey (Ahumada *et al.*, 2011). Changes in the richness and structure of mammalian communities are therefore likely to have consequences for ecosystem stability (Derhé *et al.*, 2018). Mammals also tend to be charismatic species and are thus important flagships for conservation efforts (Rondinini *et al.*, 2011). Bushmeat hunting is the most widespread form of resource extraction in tropical forests (Fa *et al.*, 2002; Ripple *et al.*, 2016), and represents one of the main anthropogenic threats to wild mammals (Laurance *et al.*, 2012; Tilman *et al.*, 2017). The global bushmeat hunting crisis is difficult to address because it is intimately tied to human development challenges such as food insecurity, emergent disease risks, and land-use change (Ripple *et al.*, 2016). To face this threat, numerous protected areas (PAs) have been created worldwide to safeguard wildlife and other natural resources. However, conservation efforts in most tropical PAs are still inadequate, as management is not always effective (Laurance *et al.*, 2012; Tranquilli *et al.*, 2014). With wildlife populations declining outside PAs, poaching pressure is also increasing in many parks and reserves (Ripple *et al.*, 2016), hence the notion of “paper parks”, i.e. PAs that only exist on paper, where ground conservation is minimal or non-existent (Bruner *et al.*, 2001; Joppa *et al.*, 2008). It is therefore critical to document and quantify how different protection regimes of PAs impact wildlife communities to develop effective conservation strategies.

Here, we investigate the differences between forest mammal communities in two ecologically comparable PAs with contrasting management regimes in the Udzungwa Mountains of Tanzania: Mwanihana and Uzungwa Scarp forests. The Udzungwa Mountains are of outstanding value for biological endemism and biodiversity conservation (Rovero *et al.*, 2014a). The main difference between the two PAs is the degree to which management and protective measures are enforced. The first one, Mwanihana, is a well-protected national park where active

law enforcement is ensured and disturbance is virtually absent (DeFries *et al.*, 2010). In contrast, the other one, Uzungwa Scarp, has suffered decades of inadequate protection, mainly resulting in much higher levels of illegal hunting (Rovero *et al.*, 2012). For example, Rovero *et al.* (2010) showed an increase in disturbance in this reserve of 19% in just 10 years (1998-2008), including numerous snares for poaching, forest fires, gunshots, and tree harvesting. Notably, snare density in Uzungwa Scarp was among the highest in African tropical forests (Topp-Jorgensen *et al.* 2009). Although logging and firewood collection may also partially affect mammal abundance (Rovero *et al.*, 2012), evidence suggests that the level of poaching is the main difference between these PAs and the main threat to wildlife (Topp-Jorgensen *et al.*, 2009; Rovero *et al.*, 2010, 2012; Hegerl *et al.*, 2015). The two target PAs share several ecological and climatic characteristics, making them an excellent model system to address our study objectives. They have similar extent and altitudinal range of forest cover, and remarkably comparable mean annual rainfall and temperature range (Hegerl *et al.*, 2015). This results in a high degree of overlap in tree species composition (Lovett, 2008) and, until the last century, comparable mammal richness and diversity, with the exception of a few species with very limited range that do not occur in both PAs (Dinesen *et al.*, 2001).

We compared mammal communities using the same sampling design over the two study areas. We evaluated the target communities in terms of species richness, functional composition (i.e., richness and proportions of trophic guilds) and species-specific occurrence probabilities, which together provide critical information for conservation. While species richness represents the canonical, most direct and mainly used measurement of biodiversity (Gotelli & Colwell, 2001), functional composition (Petchey & Gaston, 2002), which links diversity to ecological processes, has been shown to be a good descriptor of ecosystem function, with growing applications in ecology and conservation science (Mouillot *et al.*, 2013; Derhé *et al.*, 2016). In addition, as many threatened mammal species remain poorly studied (Ripple *et al.*, 2016), species-specific metrics of occurrence are greatly valuable, particularly if communities hold rare and endemic species. We focused on terrestrial (i.e., predominantly ground-dwelling), medium- to large-bodied mammals that are relatively easily detected by camera traps. We modeled the data using a multi-species hierarchical occupancy approach (Dorazio *et al.*, 2006), which allowed us to investigate the two communities while accounting for multiple sources of uncertainty including imperfect detection (Zipkin *et al.*, 2010; Rich *et al.*, 2016). Our analysis

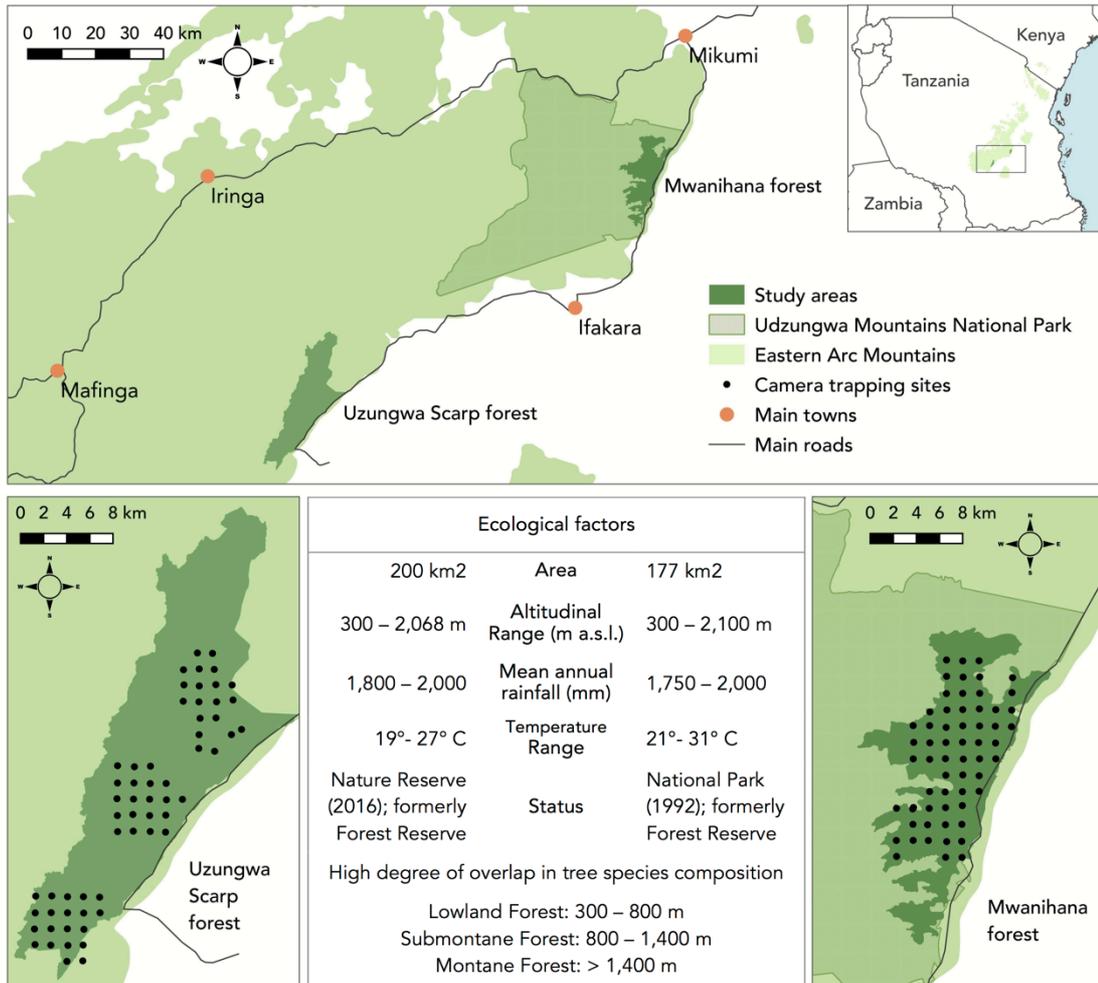
uses a recently proposed multi-region model that incorporates all species observed during sampling, regardless of sample sizes, and allows for hypothesis testing on guild- and community-specific species richness as well as estimation of species-specific occurrence probabilities (Tenan *et al.*, 2017). Our objective was to compare the target mammal communities in view of the different hunting and protection levels. Furthermore, given that vulnerability to disturbance may disproportionately impact larger-bodied species (Cardillo *et al.*, 2005; Ripple *et al.*, 2016), we also tested the correlation between average species-specific body mass and differences in estimated average occurrence probability in the two PAs. We hypothesized that (1) species richness and species-specific occurrence probabilities are inversely related to human disturbance, with large-bodied species showing the strongest correlation; and (2) the functional composition of the mammal community is modified in the disturbed forest in relation to the well-protected one as a result of changes in richness of the trophic guilds most sensitive to disturbance.

## 4.2 Methods

### 4.2.1 Study area

The highland forests of Tanzania are among the most important areas in the world for biodiversity conservation due to the exceptional density of threatened and endemic species (Rovero *et al.*, 2014a). In particular, the Udzungwa Mountains are a stronghold for many rare species, including mammals (Rovero & DeLuca, 2007), such as the recently discovered endemic grey-faced sengi (*Rhynchocyon udzungwensis*), the IUCN-endangered Abbott's duiker (*Cephalophus spadix*, a large-bodied forest antelope which is endemic of Tanzania and threatened by hunting and habitat loss; Bowkett *et al.* 2014), and the ground-dwelling, IUCN-endangered (and Udzungwa's iconic monkey) Sanje mangabey (*Cercocebus sanjei*; Rovero *et al.*, 2014a; IUCN, 2016). Mwanihana (177 km<sup>2</sup>) is a forest within the Udzungwa Mountains National Park, while Uzungwa Scarp (200 km<sup>2</sup>) is a nature reserve (Fig. 4.1). Both forests are east-facing escarpment slopes, characterized by a unique continuous vegetation cover from lowland (300-800 m), sub-montane deciduous forest (800-1400 m) to evergreen moist montane forest (>1400 m; Lovett, 2008). In both areas the forest at lower elevation zones was historically degraded and hence has large portions of secondary, regenerating vegetation. The interior forest is comparatively undisturbed with large chunks of pristine, closed-canopy moist

forest, although in Uzungwa Scarp these zones are generally more degraded than Mwanihana (Rovero *et al.*, 2014b). Shared ecological and climatic characteristics are reported in Fig. 4.1. Active law enforcement has taken place in Mwanihana since establishment of the area as a national park in 1992 (Rovero *et al.*, 2012). On the contrary, Uzungwa Scarp has not received adequate protection over the same time period (Rovero *et al.*, 2010, 2012).



**Fig. 4.1.** Map of the study area, Udzungwa Mountains of Tanzania. Camera traps locations in the two forests (Mwanihana and Uzungwa Scarp) are shown as black dots. The geographic location of the study area in Tanzania is shown in the map on the upper right, and a summary of the main ecological factors of the two forests is also reported

Thus, anthropogenic disturbance in Uzungwa Scarp is much higher, primarily from illegal hunting through snares, but also because of habitat destruction and logging (Nielsen, 2006;

Hegerl *et al.*, 2015). In addition, the anthropogenic pressure in Mwanihana comes from villages located only along the eastern side of the forest, with the other sides bordering drier but protected habitats within the national park. On the contrary, Uzungwa Scarp is an isolated forest completely surrounded by villages and hence with no protected natural habitat buffering the reserve. As an indication of poaching incidence, during the setting of camera traps in Uzungwa Scarp we found nearly 300 snares, while only 50 were found in Mwanihana. Additionally, Hegerl *et al.* (2015) report a marked difference between Mwanihana and Uzungwa Scarp both in the annual budget allocated for forest management, (USD c. 400,000 versus 1,000, respectively), and in the number of permanent staff units (78 versus 1, respectively).

#### 4.2.2 Data collection

We sampled both forests simultaneously during the dry season 2016 (July-November) according to a standardized protocol for monitoring terrestrial vertebrates (TEAM Network, 2011). We employed three arrays of 20 cameras in both forests for a total of 60 sampling locations in each PA (Fig. 4.1). Cameras were placed at a density of one camera per 2 km<sup>2</sup>. Locations were selected to be representative of the habitat and elevation gradient of each forest. Each camera was placed on a tree to record a trail segment approximately 2-3 m away and was deployed for 30-35 days. The area within the sensor field of the camera was cleared of ground vegetation for better visibility. In Mwanihana, data were collected through the Tropical Ecology Assessment and Monitoring (TEAM) Network project (Rovero & Ahumada, 2017) by deploying Reconyx HC500 camera traps (Reconyx Inc., Holmen, WI, USA). In Uzungwa Scarp, two different camera trap types were used according to availability and randomly placed across the sites: (1) Reconyx HC500 and (2) Cuddeback Ambush IR flash camera traps (Ambush IR, Cuddeback, De Pere, Wisconsin, USA). The realized sampling effort was 1,922 (mean per camera 32.03) camera days in Mwanihana and 1,816 (33.63) in Uzungwa Scarp, respectively (Fig. 4.2).

#### 4.2.3 Statistical analysis

Total number of detections of each species during the entire sampling period were summarized in an array,  $Y$ , with elements  $y_{i,j,r}$ , for the  $i$ th species, in site  $j$  of region  $r$ . We used a sampling occasion of 5 days, which led to a median of 7 total sampling occasions  $K_{j,r}$  among different sites and regions. Sampling at each point  $j$  with  $K > 1$  sampling occasions over a short period (such

that the community remained closed for the duration of the survey) allowed us to formally distinguish between species absence and non-detection.



**Fig. 4.2.** Images taken by camera traps in the study areas, Udzungwa Mountains of Tanzania. From the left to the right, from up to down: bushbuck, bushpig, Abbott's duiker, Sanje mangabey, suni, African palm civet.

We analyzed the data using a multi-region community occupancy model (Tenan *et al.*, 2017). We structured our model to compare species richness and community composition of the sampled mammal communities between the two regions (Mwanihana and Uzungwa Scarp,  $r=2$ ) based on four trophic guilds ( $g=4$ ), with the underlying model assumption that each species  $i=1,2, \dots, n_r$  (where  $n_r$  is the number of observed species in each region) can be assigned to only one guild. Each detected species was assigned to one of the following guilds (diet data sourced from Wilman *et al.*, 2014): (1) carnivore (>50% of diet based on vertebrates), (2) herbivore (include grazers, browsers, granivores and frugivores, with >50% plant material), (3) insectivore

(>50% invertebrates), (4) omnivore (generally both plant and animal material; Robinson & Redford, 1986). Guild was thus known for all observed species but not for unobserved ones. We augmented the detection and guild data for both regions such that the total number of possible species in the community was  $M=100$ , i.e. by  $M - n_r$  number of ‘all-zero’ encounter histories for each region, a proportion  $\Omega_r$  of which are the estimated unobserved species that exist in the community but that were never detected (Dorazio *et al.*, 2006). We chose  $M$  so that it was much larger than the total number of species in either community and equal across regions (Sutherland *et al.*, 2016). The latent binary variable  $\omega_{i,r} \sim \text{Bern}(\Omega_r)$  denotes whether species  $i$  truly exists in community  $r$  ( $\omega_{i,r}=1$ ) or not ( $\omega_{i,r}=0$ ). For species that were observed in a region,  $\omega_{i,r}=1$ . Variation across regions in guild-specific richness is assumed to be a Poisson process where  $N_{g,r} \sim \text{Poiss}(\lambda_{g,r})$  and  $\lambda_{g,r}$  is the expected guild- and region-specific richness. Following the model formulation of Tenan *et al.* (2017), we marginalized over a binomial prior distribution (assuming  $M$  trials each having probability  $\Omega_r$  of occurring) to estimate the total number of species in each community,  $N_r$ . We specified  $\Omega_r = (\sum_g \lambda_{g,r})/M$  and assumed a guild indicator variable  $g_{i,r} \sim \text{Cat}(\pi_r)$  that allowed the model to estimate guild membership for the augmented species, with  $\pi_r = (\pi_{1,r}, \dots, \pi_{G,r})$  and  $\pi_{g,r} = \lambda_{g,r}/\sum_g \lambda_{g,r}$ . Thus,  $\pi_{g,r}$  represented the derived probability that species  $i$ , in region  $r$ , belongs to guild  $g$ .

We define species-, site- and region-specific occurrence,  $z_{i,j,r}$ , as a binary variable in which  $z_{i,j,r}=1$  if species  $i$  is present at camera trap site  $j$  in region  $r$ . The occurrence state is defined as the outcome of a Bernoulli process in which  $z_{i,j,r} \sim \text{Bern}(\psi_{i,j,r} * \omega_{i,r})$ , where  $\psi_{i,j,r}$  is the probability that species  $i$  occurred at site  $j$  in region  $r$ . We model occurrence as a function of elevation (ELEV), which in turn is a proxy for habitat type because elevation is the strongest driver of variation in forest composition over the study regions (Lovett, 2008). We also included a square term on the effects of elevation (ELEV<sup>2</sup>) to account for potential mid-altitude peaks in species-specific distributions. We assume that the *logit* transformation of the occurrence probability (Kéry & Royle, 2008) is a linear combination of a species- and region-specific effect (intercept), and species-specific quadratic effects of elevation as follows:

$$\text{logit}(\psi_{i,j,r}) = \alpha_{0,i,r} + \alpha_{1,i,r} * \text{ELEV}_{j,r} + \alpha_{2,i,r} * \text{ELEV}_{j,r}^2.$$

Thus, the inverse-logit of  $\alpha_{0,i,r}$  is the occurrence probability for species  $i$  in region  $r$  in sites with average elevation. Occurrence is imperfectly observed, which confounds the estimation of  $\psi_{i,j,r}$ .

We therefore specify the detection model for the observational data,  $y_{i,j,r}$  for species  $i$  at site  $j$  in region  $r$  as  $y_{i,j,r} \sim \text{Bin}(p_{i,j,r} * z_{i,j,r}, K_{j,r})$ , where  $p$  is the detection probability of species  $i$  at site  $j$  in region  $r$ , conditional on species presence ( $z=1$ ), and  $K_{j,r}$  is the number of sampling occasions at site  $j$  in region  $r$ . We expected detection probability  $p_{i,j,r}$  to vary based on distance from  $j$  to the park/reserve border (m, denoted BORDER). Our hypothesis was that animals would be more elusive near the border because of greater disturbance and, possibly, denser forest floor vegetation, both limiting detection by camera traps (Rovero *et al.*, 2014b). In addition, we also incorporated a binary covariate (0-1) corresponding to the camera type used at each  $j$  site in region  $r$  (CAM\_TYPE) to account for potential differences in performance:

$$\text{logit}(p_{i,j,r}) = \beta_{0i,r} + \beta_{1i,r} * \text{BORDER}_{j,r} + \beta_{2i,r} * \text{CAM\_TYPE}_{j,r}.$$

We assume that the species-level parameters  $\alpha_0$ ,  $\alpha_1$ ,  $\alpha_2$ ,  $\beta_0$  and  $\beta_1$  are random effects, each governed by community-level hyper-parameters. For example, we assume that  $\alpha_{1i,r} \sim N(\mu_{\alpha_1,r}, \sigma_{\alpha_1,r})$ , where  $\mu_{\alpha_1,r}$  is the mean community intercept (across species) and  $\sigma_{\alpha_1,r}$  is the standard deviation (among species). To account for the fact that rare species may be more difficult to detect, we included a correlation structure between occupancy and detection probability with region-specific correlation parameters  $\rho_r$  (Dorazio & Royle, 2005; see Appendix S1 in Tenan *et al.*, 2017).

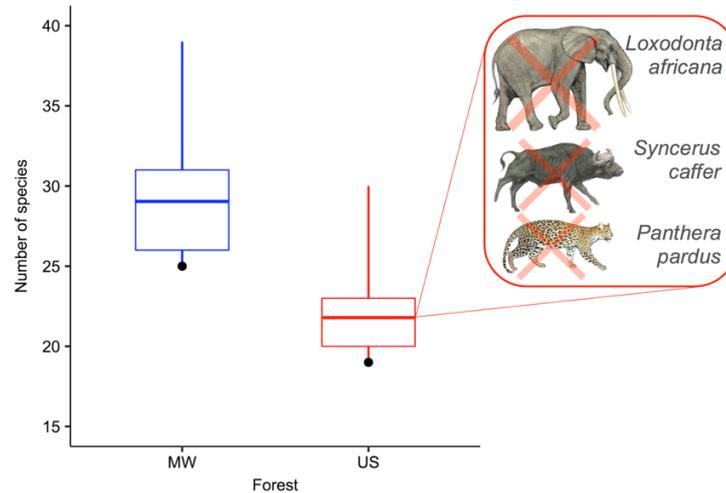
We fit the model with a Bayesian formulation and Markov chain Monte Carlo using JAGS (Plummer, 2003), called from R (R Development Core Team, 2016) through the package 'jagsUI' (Kellner, 2016). We ran three chains of length 150,000, discarded the first 15,000 iterations as burn-in, and thinned the remaining chains by taking each 20<sup>th</sup> value. Continuous covariates were derived using geo-processing tools available in QGIS 2.18.0 (QGIS Development Team, 2017), and standardized to have mean zero and unit variance. Elevation and distance from border were collinear, but this did not affect the analysis since their effect was tested on different parameters. We used uninformative priors (see Suppl. Material D1) and verified convergence through visual inspection of the chains and with the Gelman-Rubin diagnostic (Brooks & Gelman, 1998). We considered an effect significant if the 95% Bayesian credible interval (BCI) for the related posterior distribution did not encompass zero. Finally, to test the relationship between species-specific body mass and related occurrence probability ( $\psi$ ), we calculated the Pearson's coefficient ( $r$ ) in a post-hoc correlation analysis, using the posterior

distributions of the species-specific differences in estimated  $\psi$  between the two areas as a function of species-specific body mass (average values taken from Smith *et al.*, 2003). We then derived the 95% BCI for the correlation coefficient and the probability of a positive correlation, i.e.  $\Pr(r>0)$ .

### 4.3 Results

The number of detected species was 25 in Mwanihana and 19 in Uzungwa Scarp (see Suppl. Table D2). Species detected in Uzungwa Scarp were a subset of the species detected in Mwanihana, except for two, the greater cane rat (*Thrynomys swinderianus*) and the blue duiker (*Philantomba monticola*). Thus, seventeen species were shared by the two PAs. Estimated species richness differed substantially between the two forests, with a median of 28 (mean 29.0, 95% BCI 25-39) in Mwanihana and 21 (mean 21.8, 95% BCI 19-30) in Uzungwa Scarp (Fig. 4.3). Insectivore richness was significantly lower in Uzungwa Scarp compared to Mwanihana (median 2 [95% BCI 2-4] as compared to 5 [95% BCI 5-9] in Mwanihana), and also comprised a lower proportion of the community (10%, vs. 20% in Mwanihana). Carnivores showed a similar gap, with a median of 5 species (95% BCI 5-6, proportion of the community 20%) in Mwanihana and only 3 (95% BCI 3-6, 16%) in Uzungwa Scarp. The estimated number of herbivore and omnivore species was similar between forests (herbivores: median 12 [95% BCI 11-18] in Mwanihana and 11 [95% BCI 10-16] in Uzungwa Scarp; omnivores: 4 [95% BCI 4-7] in Mwanihana and 4 [95% BCI 4-7] in Uzungwa Scarp), while the proportions in the community increased in Uzungwa Scarp, since the total number of species decreased (Fig. 4.4). For species detected in both forests, estimated occurrence probabilities were generally significantly lower in Uzungwa Scarp relative to Mwanihana (Fig. 4.5). For example, estimated median occupancy for the Uzungwa-endemic and flagship Sanje mangabey was 0.71 (95% BCI 0.58-0.81) in Mwanihana and 0.27 (95% BCI 0.16-0.40) in Uzungwa Scarp, and for the Tanzania-endemic and rare Abbott's duiker was 0.52 (95% BCI 0.37-0.66) in Mwanihana and only 0.08 (95% BCI 0.03-0.17) in Uzungwa Scarp. The opposite pattern, among species native to both regions, was found for only two species, the giant pouched rat (*Cricetomys gambianus*) and the checkered giant sengi (*Rhynchocyon cirnei*). We also found a positive association between body mass and species-specific differences in average occurrence probabilities (Pearson's coefficient of  $r=0.22$  [95% BCI 0.11-0.33], with  $\Pr(r>0) = 0.999$ ; Fig. 4.6). At the species-specific level, the effects of

elevation (both linear and squared term) on  $\psi$  were variable. We found no significant effect of distance to PA border on detection probability for any of the species, in either forest. The use of different camera types had a significant effect on species detectability, with greater detection using the Ambush IR camera, which was used at some sites in Uzungwa Scarp (see Suppl. Table D3).



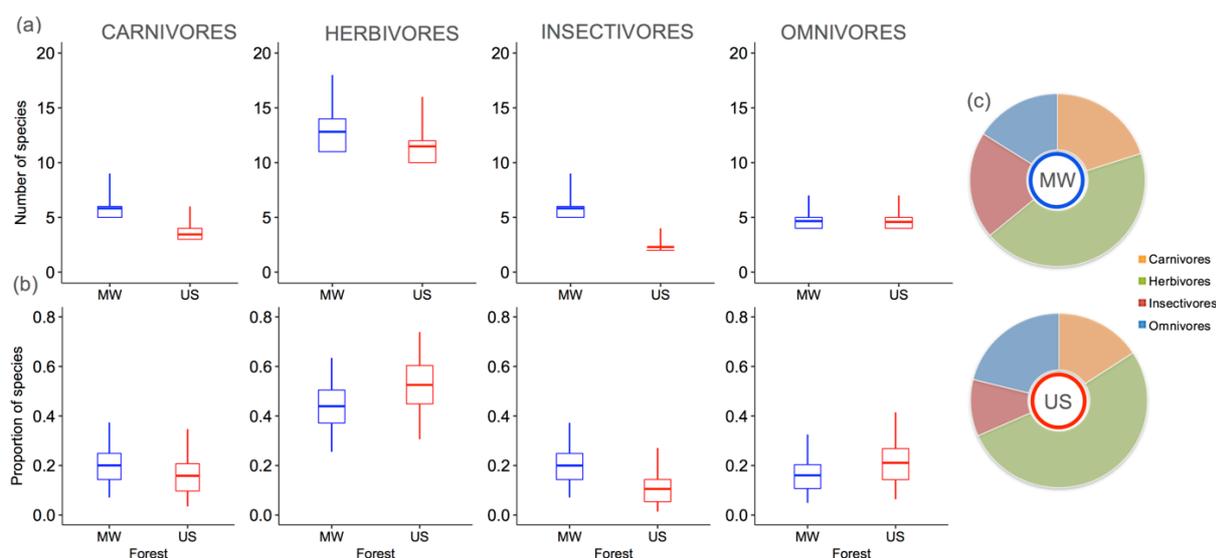
**Fig. 4.3.** Estimated species richness in Mwanihana (MW) and Uzungwa Scarp (US) forests (mean, 50% BCI and 95% BCI). Black dots are the number of observed species. Large-bodied mammals that were extirpated from Uzungwa Scarp by the early 1970s are shown in the red box. Drawings by J. Kingdon reproduced with permission.

#### 4.4 Discussion

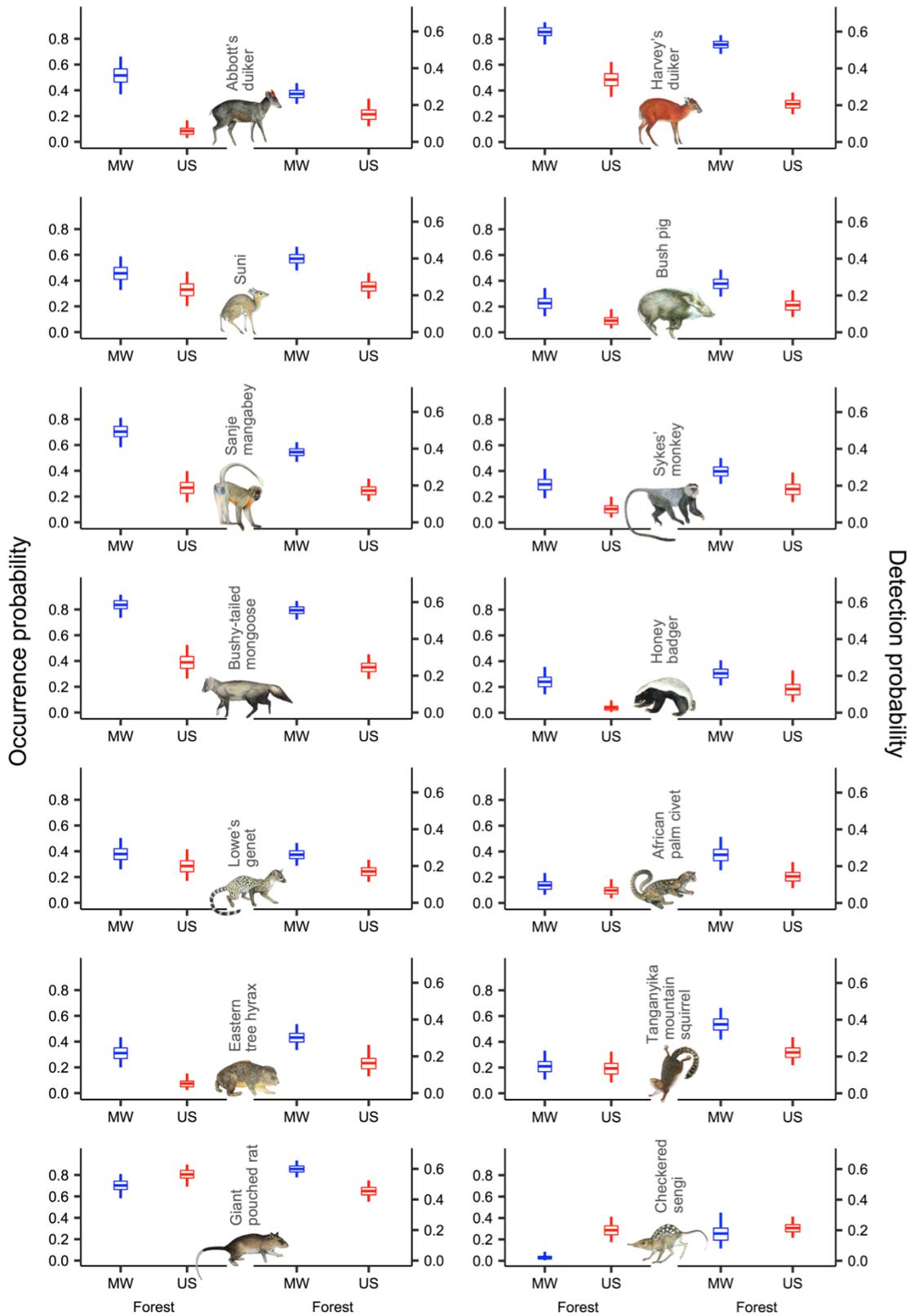
Our analyses revealed clear differences between target mammal communities under contrasting protection regimes. In line with our hypotheses, we found lower species richness and reduced occurrence probabilities for most mammal species in the forest with high disturbance (Uzungwa Scarp), with a tendency of greater decrease in occurrence probability by the larger-bodied species. We also found that the composition of trophic guilds varied between the two PAs. The significant loss of species in Uzungwa Scarp, as compared to Mwanihana, is alarming given the outstanding biological value of the area (Burgess *et al.*, 2007; Rovero *et al.*, 2014a). Furthermore, such loss can have profound repercussions on tropical forest dynamics, including the composition, structure, regeneration and carbon storage potential of vegetation (Kurten, 2013; Osuri *et al.*, 2016). Our results confirm the absence of large-bodied mammals, including elephant (*Loxodonta africana*) and leopard (*Panthera pardus*) in Uzungwa Scarp, likely a result of intensive hunting for bushmeat trade since the 1970s (Rovero *et al.*, 2012). This

supports the notion that larger mammals face higher extinction risk (Cardillo *et al.*, 2005; Ripple *et al.*, 2016). Much of the conservation effort in the tropics is focused on extending the area under official protection rather than on improving the enforcement of existing reserves (Harrison, 2011; e.g., Brooks *et al.*, 2004; Joppa *et al.*, 2008). Hunting is now the biggest threat to tropical biodiversity in many parts of the tropics (Harrison, 2011), yet many of the mammal species threatened by hunting remain poorly studied and are in great need of basic biological and ecological research, including abundance estimations (Ripple *et al.*, 2016). Studies on the consequences of defaunation have also consistently indicated that the ecology of heavily hunted forests is severely disrupted (Fa & Brown, 2009; Harrison, 2011). Worldwide, Africa is considered one of the regions with the most species facing this threat (Ripple *et al.*, 2016). Tanzania is arguably mainland Africa's most important nation for conservation, as the country is losing habitat and natural resources rapidly (Caro & Davenport, 2016).

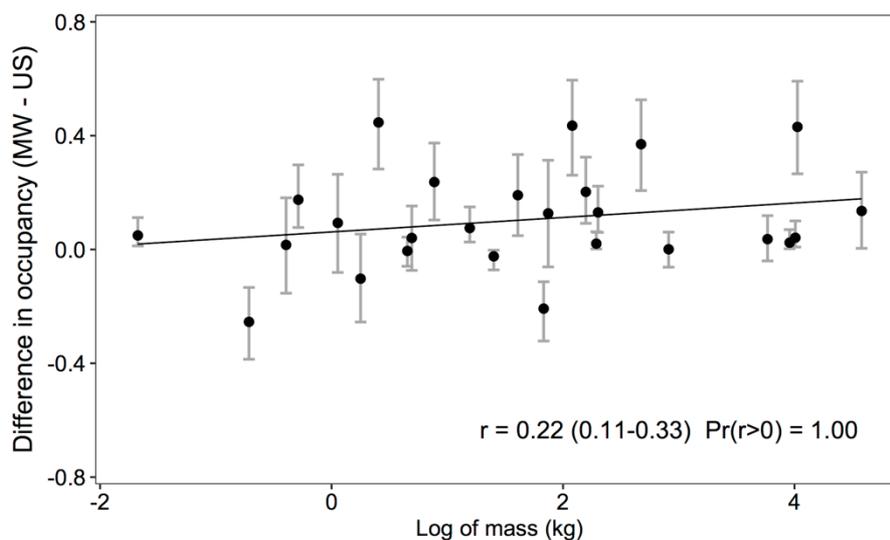
We documented a decrease in insectivores and carnivores in Uzungwa Scarp, the highly disturbed PA, as compared to Mwanihana, the PA with higher levels of protection. Carnivores are experiencing massive declines in their populations and geographic ranges globally (Ripple *et al.*, 2014); our results for mammal insectivores match findings on birds, as insectivorous birds have also shown a disproportionate sensitivity to disturbance (Gray *et al.*, 2007).



**Fig. 4.4.** Estimated number of species for each functional guild (a) in Mwanihana (MW) and Uzungwa Scarp (US) forests, respectively (mean, 50% BCI and 95% BCI), and their proportions (b) in each community (mean, 50% BCI and 95% BCI), also shown with pie charts (c)



**Fig. 4.5.** Species-specific mean occurrence and detection probabilities, in Mwanihana (MW) and Uzungwa Scarp (US) forests, respectively, for 14 forest-dwelling mammals that were detected in both areas (mean, 50% BCI and 95% BCI). Drawings by J. Kingdon reproduced with permission.



**Fig. 4.6.** Species-specific differences in estimated occurrence probabilities between Mwanihana (MW) and Uzungwa Scarp (US) forests (MW – US; mean and 95% BCI), for species detected in at least one forest, as a function of the log of average body mass (kg). The elephant was considered an outlier and excluded from this analysis. The estimated correlation coefficient, along with the probability of a positive correlation ( $Pr(r>0)$ ) is reported.

Global declines in insect abundance could also have been affecting insectivores (Sánchez-Bayo & Wyckhuys, 2019). The less pronounced differences we found for herbivores and omnivores may mirror their greater resilience and/or reflect compensatory dynamics within the community, with some species able to fill the ecological niche(s) of others (Wright *et al.*, 2003). Medium-sized omnivores include many opportunistic species that have the ability to use a wide array of habitats and resources, thriving even after extensive human modification (Roemer, Gompper & Van Valkenburgh, 2009). However, this result is somewhat surprising for herbivores, given that they face unprecedented extinction rates at the global scale (Ripple *et al.*, 2015).

Our results at the species-specific level indicate that estimated occurrence probabilities were significantly lower in Uzungwa Scarp relative to Mwanihana for most species detected in both PAs. These differences are of particular conservation concern for endemic species, or species with narrow ranges, such as the Abbott’s duiker and the Sanje mangabey. Yet, we found decreased occurrence probabilities in the disturbed forest even for generalist and widespread species, suggesting that failure to enforce protection is associated with changes in the whole mammal community (Robinson & Bennett, 2000). Occurrence estimates were higher in

Uzungwa scarp only for the giant pouched rat and the checkered sengi, matching the results of a previous study (Hegerl *et al.*, 2015). However, this previous study lacked a standardized sampling design and temporal consistency in sampling effort between forests. Furthermore, the community composition analysis was based on raw detection rates. The giant pouched rat seems to be relatively unaffected by the level of human disturbance, potentially because this medium-sized omnivore is a generalist, adaptable species with a high reproductive rate (Engeman *et al.*, 2006). This can also be the result of low predation and reduced interspecific competition from depleted populations of other species, or even an effect of potential benefits to habitat created by disturbance. The much higher estimated occurrence probability for the checkered sengi in Uzungwa Scarp as compared to Mwanihana may be related to reduced interspecific competition with the endemic and narrow-ranged grey-faced sengi that is found in Mwanihana but not in Uzungwa Scarp (Rovero *et al.*, 2013). Similar biogeographic reason explains the non-detection of the blue duiker in Mwanihana. Our results also show marked differences in species-specific detection probabilities between forests, with a general trend of lower detection in Uzungwa Scarp as compared to Mwanihana. This may be an effect of the correlation structure between occurrence and detection in the model, suggesting that abundance for species may be lower in Uzungwa Scarp. However, it may also reflect different behaviors, as individuals may become more elusive with increasing disturbance (Rovero *et al.*, 2014b). To explore this result, we reran the model without the correlation structure. We found that the differences in species-specific detection probabilities between forests were still marked and significant, suggesting a behavioral response due to higher levels of anthropogenic disturbance in Uzungwa Scarp. Our results also provide evidence that hunting in Uzungwa Scarp is associated with a decrease in larger-bodied species, consistent with other research that has documented higher sensitivity of larger species to human disturbance (Cardillo *et al.*, 2005).

Across the study area hunting mainly targets duikers and other medium-sized forest mammals (Rovero *et al.*, 2010; Jones *et al.*, 2019). These include the relatively common Harvey's duiker (*Cephalophus harveyi*) and the poorly-known, endemic and IUCN-Endangered Abbott's duiker (IUCN, 2016). Indeed both species have striking and significant differences in occurrence probability between Mwanihana and Uzungwa Scarp. Yet, being non-selective, snares used for hunting cause significant by-catch mortality on a variety of species (Lindsey *et al.*, 2011). Moreover, as the larger ungulates and bushpigs have decreased in Uzungwa Scarp,

snaring tends to target smaller species. Detrimental effects of hunting on the abundance of arboreal primates, particularly the colobines, have also been documented (Rovero *et al.*, 2015; Cavada *et al.*, 2018).

The study design and analytical framework we used allowed us to simultaneously assess species richness, functional composition, and species-specific occurrence across two different communities. Based on our results, differences in mammal communities strongly associate with the disproportionately greater hunting pressure in Uzungwa Scarp than Mwanihana. Logging and firewood collection may also affect mammal diversity and abundance and eventually lead to local extinction of some species through changes in the forest structure (Laurance *et al.*, 2006; Arroyo-Rodríguez & Dias, 2010; Rovero *et al.*, 2012). Nevertheless, in the disturbed forest there is little spatial overlap between such activities: logging and firewood collection occur mainly towards the lower edge of the reserve (Hegerl *et al.*, 2015), whereas hunting occurs across the forest and especially in the interior zones. Since we placed camera traps evenly across both PAs, hunting is likely to be a more significant factor (Rovero *et al.*, 2012).

The upgrading of Uzungwa Scarp from forest reserve to nature reserve status in 2017 (the year right after our data collection) is a valuable step towards more efficient management, as it should bring boosted law enforcement to the PA. Protection should especially target areas adjacent to settlements, where direct disturbance is higher, and include the creation of buffer zones (Cavada *et al.*, 2018). Restoration of connectivity to reverse habitat isolation of Uzungwa Scarp will also help to address the long-term conservation of mammal communities, with wildlife corridors that maintain viability of isolated populations while ensuring ecosystem functionality (Ruiz-Lopez *et al.*, 2016; Rovero & Jones, 2012). Our study suggests that legal protection backed up by on ground protection plays a determinant role in maintaining diverse mammal communities in tropical forests. Protected areas are the cornerstone of efforts to conserve tropical biodiversity and final refuges for threatened species across the globe, but the future of biodiversity within them is closely tied to actual enforcement efficacy. This, in turn, is linked to adequate funding and capacity of PA management (Bruner *et al.*, 2001; Laurance *et al.*, 2012; Tranquilli *et al.*, 2014). Robust assessments on the status of wildlife populations remain fundamental to determine how effectively PAs are performing (Naughton-Treves *et al.*, 2005) and to design efficient and long-term conservation plans.

## Chapter 5.

### **Co-occurrence of snow leopard *Panthera uncia*, Siberian ibex *Capra sibirica* and livestock: potential relationships and effects**

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#### **Abstract**

Understanding how livestock impacts native wildlife is of increasing conservation relevance. For the endangered snow leopard *Panthera uncia*, wild prey reduction, intensifying human-wildlife conflicts and retaliatory killings are severe threats determined by livestock presence. Therefore, elucidating patterns of co-occurrence among snow leopard, wild ungulates as their main prey, and livestock, is relevant to assess the compatibility of pastoralism with conservation. We used camera trapping to study the occurrence interactions among livestock, Siberian ibex *Capra sibirica* and snow leopard in a National Park in the Altai mountains. We obtained 494 detections of wild mammals and 912 of domestic ungulates, dogs and humans. Snow leopards yielded 14 detections and Siberian ibex 33. We used co-occurrence modeling and found that livestock had higher estimated occupancy (0.65) than ibex, whose occupancy was lower in presence of livestock (0.11) than in its absence (0.34-0.35 depending on scenarios modelled). In contrast, snow leopard occupancy did not appear to be affected by presence of livestock nor by presence of ibex, however the robustness of such inference was limited by uncertainty around the estimates. Although our sampling at presumed snow leopard passing sites may have biased ibex detections, results indicate that livestock may displace wild ungulates, while they may not directly affect the occurrence of snow leopard. This may not imply that snow leopards are not threatened by livestock, as overstocking may trigger human-carnivore conflicts and eventually hamper enduring conservation of large carnivores. Further research will be required to assess the generality and strength of our results.

**Keywords:** Altai mountains; camera trapping; Mongolia; occupancy; occurrence interactions; human-wildlife conflicts

## 5.1 Introduction

The impact of livestock on native wildlife is a global conservation issue (Prins, 1992; Fleischner, 1994; Berger *et al.*, 2013) but also one that despite much debate remains poorly understood (e.g. Ekernas *et al.*, 2017). A number of studies have established how high densities of livestock induce competitive exclusion, resulting in wild herbivore decline (Bagchi *et al.*, 2004; Madhusudan, 2004). Some studies have addressed the impacts of pastoralism on large carnivores (e.g. Ogutu *et al.*, 2005; Ripple *et al.*, 2014). Yet, in areas such as Central Asia where wild-ranging livestock have increased exponentially over the last decades (Berger *et al.*, 2013), including within protected areas (Bagchi *et al.*, 2004), the cascading threats on large carnivores such as snow leopard *Panthera uncia* and wolf *Canis lupus* are of concern. These span from the intensification of human-carnivore conflicts due to depredation, with retaliatory killing of carnivores, to the negative effects due to reduction of wild herbivores as main prey (Treves & Karanth, 2003; Mishra *et al.*, 2010; Sharma *et al.*, 2015). A recent study in Mongolia's Gobi steppe shows how complex the cascading effects of pastoralism might be (Ekernas *et al.*, 2017). Therefore, understanding spatial interactions among large carnivores, wild herbivores and livestock is of conservation relevance, representing baseline knowledge for planning sustainable livestock grazing regimes.

We focussed on co-occurrence patterns among snow leopard, one of its main wild prey - the Siberian ibex *Capra sibirica* - and domestic ungulates in a protected area in North-western Mongolia. Snow leopard has a vast but fragmented distribution across central Asia's mountain landscape, and its survival depends primarily on wild ungulates (Jackson *et al.*, 2008; Snow Leopard Network, 2014). Globalization of cashmere wool trade in recent decades has increased livestock numbers across the snow leopard range (particularly in China and Mongolia), exposing this cat to intensified threats (Berger *et al.*, 2013; Sharma *et al.*, 2015). Prey reduction, human-wildlife conflicts and direct killing are primary threats determined by livestock (Snow Leopard Network, 2014). Conflicts generated by depredation of livestock have been assessed (e.g. Chen *et al.*, 2016; Li *et al.*, 2013), along with patterns of predation on livestock versus wild prey (Johansson *et al.*, 2015). The impact of livestock on snow leopard prey has also been established

(e.g. Bagchi *et al.*, 2004), however how livestock impact snow leopards remains less understood. Sharma *et al.* (2015) report evidence of increased intensity in snow leopard site use with increasing livestock numbers, with a possible decrease beyond a threshold of livestock densities. Bagchi & Mishra (2006) found greater predation on livestock by snow leopards in areas with lower prey abundance, although the proportion of wild ungulates does not seem to influence the presence of livestock in the diet of the snow leopard (see Lovari *et al.*, 2013, for a review).

We used camera trapping data and an occupancy framework (*sensu* MacKenzie *et al.*, 2002) to study the spatial interactions among the three ‘players’ of our study system. The efficiency of camera trapping to detect snow leopards has been widely tested (e.g., Janečka *et al.*, 2011). Moreover, recent studies show the potential of site occupancy modelling to study patterns in distribution and predictors (Alexander *et al.*, 2016a; Alexander *et al.*, 2016b). We aimed to assess the usefulness of this approach to evaluate co-occurrence patterns of Siberian ibex, snow leopard and livestock by using an occupancy model that explicitly assesses co-occurrence (Waddle *et al.*, 2010).

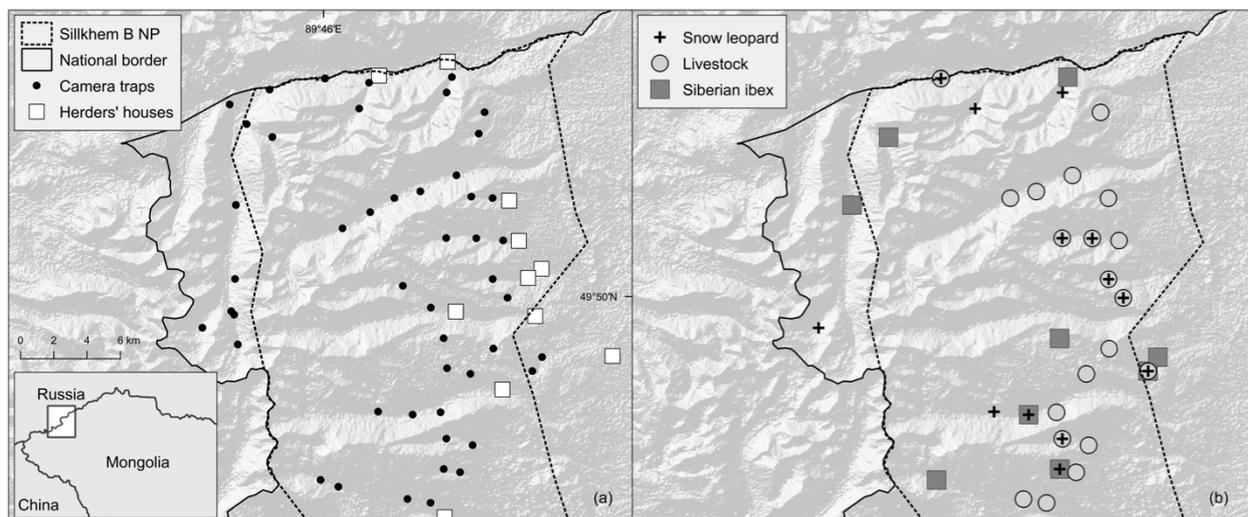
## 5.2 Methods

### 5.2.1 Study area

We conducted the study in the ‘Siilkhem B’ National Park (centred on 49°49’21.42” N, 89°44’56.84”E; 1,400 km<sup>2</sup>) in the Altai Mountains, North-western Mongolia (Fig. 5.1). The area is steep, rocky and dry mountain habitat reaching 3,965 m a.s.l. The slopes are mainly covered in grassland with sparse shrubs, with valley bottoms sparsely covered by larch *Larix sibirica*. The local community is represented by pastoralists, with traditional livestock husbandry allowed in the limited use zones of National Parks (1994 Mongolian law on special protected area; <http://extwprlegs1.fao.org/docs/pdf/mon77268E.pdf>). However, we detected livestock in large numbers (see Results): shepherds with dogs herding during daytime along valleys and accessible slopes and housing livestock in corrals at night. In the study district goats increased from 21,937 in 1970 to 105,376 in 2015, with similar increases in other domestic animals (Mongolian Statistical Information Centre; <http://www.1212.mn/en/>).

### 5.2.2 Data collection

From March to June 2015, we sampled 49 camera trap sites across an area of 513 km<sup>2</sup> (minimum convex polygon around sites). We originally designed a regular grid of camera trap sites, with cells of 2 km<sup>2</sup> in size, laid over the entire central-to-northern portion of the park, considered suitable to snow leopard presence based on preliminary information. Such spacing ensured that at least three sites sampled the home-range of snow leopards based on the lower end of published estimates (11-142 km<sup>2</sup>: Jackson, 1996; MacCarthy *et al.*, 2005). Based on topography and presumed snow cover, we then reduced the extent of the grid so to sample reachable valleys and slopes to 3,200 m a.s.l. We placed camera traps in each cell of this resulting grid, on the nearest site suitable to snow leopard passage based on signs. In the absence of these, we placed camera traps along presumed passing sites such as narrow valley bottoms and saddles along ridges. This site selection criterion was motivated by the fact that snow leopard is likely the rarest and most elusive species. While opportunistic sightings of ibex and livestock indicated that sites may also be suitable to capture their presence, we acknowledge that this design may have under-sampled ibex and livestock relative to snow leopard. Sites selected had an elevation range of 2,219-3,126 m and locations as in Fig. 5.1.



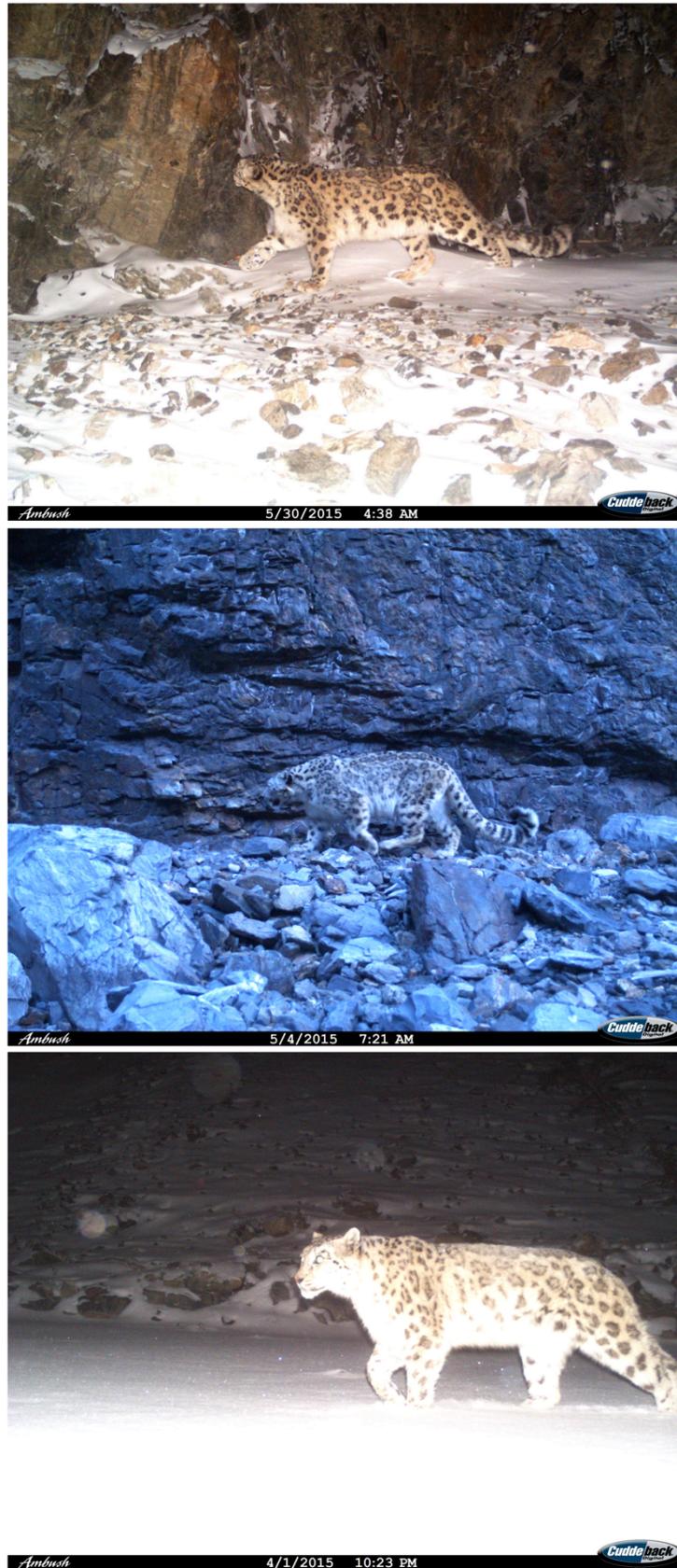
**Fig. 5.1.** The study area within Siilkhem National Park, Part B, north-western Mongolia: (a) locations of the 49 camera traps and herders' houses and camps; (b) sites where we detected livestock, Siberian ibex and snow leopards.

For easier logistics we split the sampling into two grids, the first (26 sites) sampled from 17 March to 4 May and the second (23) from 5 May to 29 June. We used Xenon white flash digital camera traps (Cuddeback Ambush, Non Typical Inc. Green Bay, WI, USA), which take colour images in night and day with trigger time of 0.25 sec. We set camera traps to work in continuous mode, and fitted them in ad-hoc made wood bases on small rock piles at approximately 50 cm from the ground (Fig. 5.2).

### 5.2.3 Statistical analysis

We processed data in R (R Development Core TEAM, 2015), and first derived species' raw descriptors of captures: independent events (using a 15 min interval to separate subsequent images of the same species), relative abundance index (RAI, i.e. the ratio of events on sampling effort) and naïve occupancy (e.g. Rovero *et al.*, 2014b). For snow leopard, ibex and domestic ungulates we built matrices of detection/non-detection on daily occasions and used a model for estimating co-occurrence of interacting species developed by Waddle *et al.* (2010). Occurrence and detectability were modelled in order to have a single dominant species and one or more subordinate species, where probabilities referred to subordinate species are conditional on presence of the dominant one. Given the limited amount of snow leopard and ibex detections, we fitted models by contrasting two scenarios where livestock occurrence was assumed independent of that of the other two species: (scenario 1) livestock presence conditions the occurrence of both snow leopard and ibex; (scenario 2) livestock presence conditions the occurrence of ibex and, in turn, ibex occurrence conditions snow leopard occurrence. Sample sizes also constrained the number of environmental and human disturbance factors that we could use as model covariates. Thus, we considered (1) elevation at the camera trap site ('elev'), derived from a Digital Elevation Model, as a proxy of the variation in habitat that we observed within the elevation range sampled, and (2) distance of camera trap sites to occupied herders' houses and camps ('dist'; see Fig. 5.1), as a proxy of anthropogenic disturbance.

Detailed model formulation and parameter constraints as well as model fitting procedures are reported in Suppl. Material E1. Livestock occurrence probability was modelled as a function of elevation and distance to herders' houses. We assumed ibex occurrence to depend on the occurrence of livestock, with an additional effect of distance to herders' houses.



**Fig. 5.2.** Images of snow leopards taken by camera traps in the study area, north-western Mongolia.

Livestock encounter probability was assumed to be constant and independent of occurrence of other species. Ibex encounter probability was tested for an effect of distance to herders' houses and camps. Snow leopard encounter probability was a function of distance to herders' houses and camps, as we assumed these places may influence the elusiveness of snow leopards. Models were fitted using the Markov chain Monte Carlo (MCMC) framework, implemented in program JAGS (Plummer, 2003), that we executed from R (see Suppl. Material E2 for model code and Figure E3-E4 for the Bayesian learning plots of the posterior distributions).

### 5.3 Results

We realized a sampling effort of 2,225 camera days (average  $\pm$  SD per camera  $45.4 \pm 6.6$ ) from the 49 camera traps set, yielding 494 events of 12 species of mammals, 105 of people and 367 of livestock, primarily goats and sheep (188) and cattle/yaks (163). Livestock was detected at 21 locations (naïve occupancy = 0.43) (Suppl. Table E5), with herds of sheep and goats that numbered in the order of hundreds. We obtained 17 images of snow leopard representing 14 events at 13 locations (naïve occupancy = 0.27). By comparing animals' coat patterns across events, we concluded that three individual leopards were detected. The sex of these individuals could not be determined from the photographs. We also recorded 33 events of Siberian ibex at 9 locations (naïve occupancy = 0.18) (Fig. 5.1). The minimum group size of ibex, as we determined from both images and opportunistic sightings, ranged from 1 to 31 animals. Detections did not show any marked pattern of daily temporal segregation among species: livestock and ibex were predominantly diurnal although ibex was sporadically detected also in the first hours after dusk; snow leopard was active from 5 am to 12 pm and the few detections did not reveal any peak of activity.

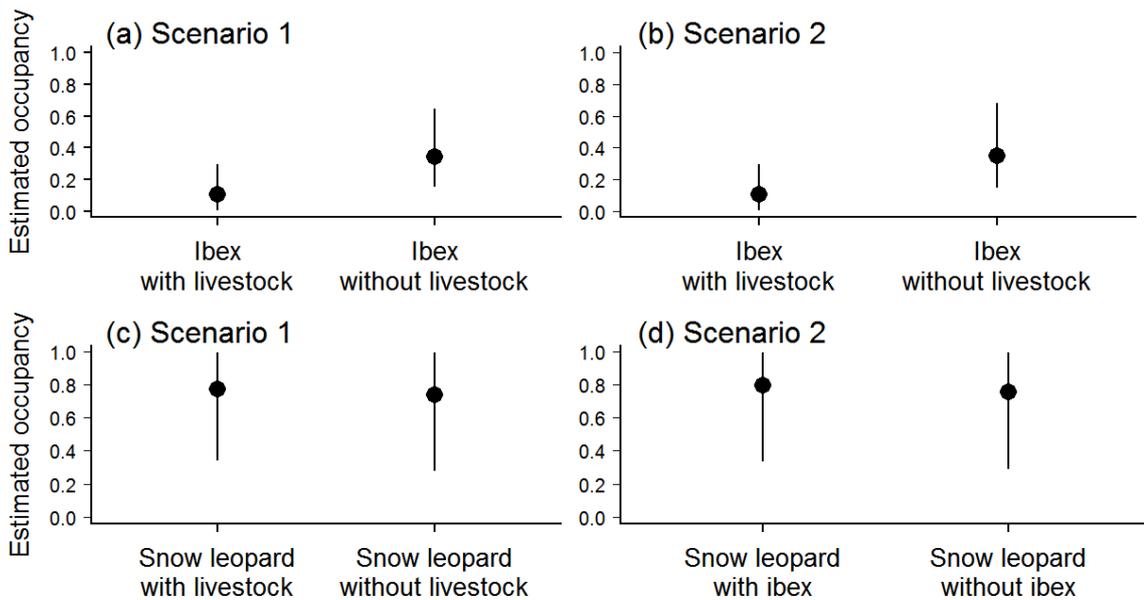
Occupancy modelling showed that for both scenarios livestock had higher mean estimated occupancy (mean and 95% credible interval = 0.65, 0.44 – 0.83; Table 5.1) relative to ibex, and ibex occupancy was negatively affected by the presence of livestock. The drop in mean point estimate of ibex occupancy varied from 0.34 to 0.11 and from 0.35 to 0.11 in the absence and presence of livestock, for scenarios 1 and 2, respectively (Fig. 5.3, Table 5.1). In the first scenario, in contrast, the mean point estimate of snow leopard occupancy was not affected by the presence of livestock (0.77 and 0.74 with and without livestock, respectively; Fig. 5.3), and

the same held for detectability, which was estimated on average at 0.01 in the presence (0.004 – 0.022, 95% CRI) and absence (0.003 – 0.021) of livestock (Table 5.1). Similarly, in the second scenario, the occupancy of snow leopard was not affected by the presence of ibex (0.80, 0.340 – 0.996, and 0.76, 0.295 – 0.994, in the presence and absence of ibex). The only relationship with covariates that resulted significant (i.e. 95% credible interval did not encompass zero) was that site elevation had a negative effect on the estimated occupancy of livestock, in both scenarios (Table 5.1).

**Table 5.1.** Posterior parameter estimates (mean, SD, and 95% credible interval quantiles) for occupancy ( $\psi$ ) and detection probability ( $p$ ) in the two scenarios of co-occurrence relationship among livestock (LI), Siberian ibex (IB) and snow leopard (SL) in north-western Mongolia. The apex notation refers to the co-occurrence relationship modelled (e.g.  $\bar{\psi}^{\text{IB|LI}}$  is the intercept of ibex occupancy in the presence of livestock, and  $\bar{\psi}^{\text{IB|\bar{LI}}}$  is the intercept of ibex occupancy in the absence of livestock; see Appendix E for more details). Coefficients  $\beta$  and  $\alpha$  quantify the effect of distance from human disturbance (dist) and elevation (elev) on the occurrence and detection probability, respectively. Estimates of the occurrence and detectability intercepts are given in the probability scale; coefficients  $\alpha$  and  $\beta$  are in the logit scale.

| Parameter                         | Scenario 1    |                 | Scenario 2    |                 |
|-----------------------------------|---------------|-----------------|---------------|-----------------|
|                                   | Mean (SD)     | CRI (2.5-97.5%) | Mean (SD)     | CRI (2.5-97.5%) |
| Occurrence                        |               |                 |               |                 |
| $\bar{\psi}^{\text{LI}}$          | 0.649 (0.100) | 0.443 – 0.830   | 0.648 (0.100) | 0.445 – 0.830   |
| $\bar{\psi}^{\text{IB LI}}$       | 0.105 (0.074) | 0.013 – 0.292   | 0.106 (0.074) | 0.013 – 0.292   |
| $\bar{\psi}^{\text{IB \bar{LI}}}$ | 0.341 (0.123) | 0.156 – 0.646   | 0.346 (0.128) | 0.155 – 0.679   |
| $\bar{\psi}^{\text{SL LI}}$       | 0.771 (0.184) | 0.345 – 0.995   | -             | -               |
| $\bar{\psi}^{\text{SL \bar{LI}}}$ | 0.736 (0.203) | 0.281 – 0.992   | -             | -               |
| $\bar{\psi}^{\text{SL IB}}$       | -             | -               | 0.796 (0.183) | 0.340 – 0.996   |
| $\bar{\psi}^{\text{SL \bar{IB}}}$ | -             | -               | 0.758 (0.197) | 0.295 – 0.994   |
| Detectability                     |               |                 |               |                 |
| $\bar{p}^{\text{LI}}$             | 0.165 (0.012) | 0.142 – 0.189   | 0.165 (0.012) | 0.142 – 0.188   |
| $\bar{p}^{\text{IB}}$             | 0.057 (0.013) | 0.034 – 0.084   | 0.057 (0.013) | 0.004 – 0.016   |
| $\bar{p}^{\text{SL}}$             | -             | -               | 0.009 (0.003) | 0.004 – 0.016   |
| $\bar{p}^{\text{SL LI}}$          | 0.010 (0.005) | 0.004 – 0.022   | -             | -               |

|                      |                |                 |                |                 |
|----------------------|----------------|-----------------|----------------|-----------------|
| $\bar{p}^{SL LI}$    | 0.010 (0.005)  | 0.003 – 0.021   | -              | -               |
| Effect of covariates |                |                 |                |                 |
| $\beta_{elev}^{LI}$  | -2.189 (0.721) | -3.777 – -0.943 | -1.190 (0.718) | -3.768 – -0.965 |
| $\beta_{dist}^{LI}$  | -0.850 (0.715) | -2.291 – 0.529  | -0.858 (0.711) | -2.311 – 0.510  |
| $\beta_{elev}^{SL}$  | -0.214 (1.670) | -3.258 – 3.553  | -0.311 (1.702) | -3.307 – 3.475  |
| $\beta_{dist}^{SL}$  | -0.279 (1.552) | -3.191 – 3.186  | -0.280 (1.630) | -3.288 – 3.157  |
| $\alpha_{dist}^{SL}$ | -0.273 (0.448) | -1.174 – 0.578  | -0.350 (0.449) | -1.283 – 0.493  |
| $\beta_{dist}^{IB}$  | 0.569 (0.780)  | -0.427 – 2.729  | 0.618 (0.840)  | -0.408 – 2.953  |
| $\alpha_{dist}^{IB}$ | -0.158 (0.265) | -0.697 – 0.336  | -0.174 (0.269) | -0.711 – 0.328  |



**Fig. 5.3.** Occupancy probability (mean and 95% credible interval) estimated from the modelling of co-occurrence patterns of (a) ibex depending on livestock, scenario 1; (b) ibex depending on livestock, scenario 2; (c) snow leopard depending on livestock, scenario 1; and (d) snow leopard depending on ibex, scenario 2.

### 5.4 Discussion

Our analysis suggests three patterns: (1) the estimated occurrence of livestock may have a negative effect on the occurrence of ibex, with a difference in the mean point estimates despite

some overlap in credible intervals; (2) livestock presence did not appear to affect the occurrence of snow leopards; (3) snow leopard occurrence did not seem to be affected by the presence of ibex. The small number of snow leopard and ibex detections limited the precision of our estimates, imposing caution about the generality of results. We also acknowledge that the study design we used, primarily targeted at sampling the snow leopard, may have resulted in under-sampling bias for ibex and livestock. Moreover, additional data on herd numbers and movement patterns for livestock and ibex would be required to further assess these interactions.

Despite the study area being a national park, camera trap detections of livestock exceeded by over 10-fold those of the only wild ungulate recorded, the Siberian ibex. Indeed our model estimated livestock to occur at over two thirds of sites. Data on temporal trends in the abundance of the ibex population will be required to assess whether the co-occurrence pattern we found might reflect declining abundance of wild herbivores with increasing livestock densities, as suggested by studies in the Trans-Himalaya (Mishra *et al.*, 2002; Bagchi *et al.*, 2004).

The 14 detection events of snow leopard were located across the sampled area at remote sites and larger valleys heavily used by livestock, with several sites where we detected both snow leopard and livestock (Fig. 5.1). Sharma *et al.* (2015) provide evidence that beyond a threshold of livestock density, reduced wild prey populations and associated human disturbance may negatively influence the intensity of snow leopard habitat use. In the Tost mountains, southern Mongolia, the snow leopard diet included more wild prey (73%) than livestock (27%; Johansson *et al.*, 2015), despite livestock abundance being one order of magnitude higher. Data on retaliatory killings and predation pattern will be necessary to further assess the question as to how livestock affects snow leopard. Our discussions with local herders indicate that predation of free-ranging livestock occurred regularly, but they were attributed primarily to wolves. Predations in corrals were reported to occur sporadically, matching results from the Tost mountains (Johansson *et al.*, 2015). Shepherds appeared very aware that unlike wolves, snow leopards are protected, and their overall attitude towards snow leopard seemed more positive. Indeed we found skins of wolves in a number of herders' houses, but no evidence of snow leopard poaching. These observations indicate that while in 'Siilkhem B' National Park livestock is widespread and might negatively impact the occurrence of ibex, it may not have a significant

impact on the occurrence of snow leopard, nor intense conflicts with local herders seem to have arisen.

At large scale, studies generally found a positive association between wild prey presence and site use by snow leopards (McCarthy *et al.*, 2005; Alexander *et al.*, 2016b). However, at the local scale, this pattern may not hold. Alexander *et al.* (2016a) used camera trapping in China and found that site use by snow leopard was not strongly associated with the presence of bharal *Pseudois nayaur*. Authors suggest this pattern might be a result of the lack of spatial heterogeneity in bharal, which were detected at all sites. We also did not find a pattern of association, as the estimated occurrence of snow leopard did not vary in presence or absence of ibex. This result is compatible with the hypothesis that predator-prey occurrences may be decoupled (Ekernas *et al.*, 2017), although we acknowledge that our primarily targeting snow leopard might have masked the pattern of association.

#### 5.4.1 Conclusions and conservation implications

Our results generally support the good potential of the occupancy framework to analyse snow leopard detection/non-detection data from camera traps (Alexander *et al.*, 2016a). A more conclusive evaluation of its application to model co-occurrence patterns will require sampling yielding greater sample sizes. Moreover, site selection ideally should not bias a particular species, else sampling wild prey with alternative methods should be required. The added advantage of the model we used is that interactions among species are modelled explicitly, along with the effect of environmental covariates. The main constraint was the small number of detections we obtained of snow leopard and ibex. This limited the number of parameters, hence the co-occurrence interactions and covariate effects that we could simultaneously model.

Despite our sampling design may have induced under-sampling of ibex, the indication that livestock may negatively impact wild ungulates deserves further research, as does the result that livestock may not directly affect the occurrence of snow leopard. Yet, the negative effects that depletion of wild prey may have on large carnivores are well known, in addition to the potential escalation of human-wildlife conflicts (e.g. Berger *et al.*, 2013; Ekernas *et al.*, 2017). Given the study area is national park, we suggest that enduring protection of Siberian ibex and snow leopard in 'Siilkhem B' requires a revision of the livestock grazing zone, as well as increased law enforcement, with emphasis on the creation and protection of livestock-free areas.

Conservation efforts should concomitantly target livestock practices by engaging herders in the process of developing new grazing plans, as elaborated in the Snow Leopard Survival Strategy (Snow Leopard Network, 2014).

## General conclusions

This thesis shows how camera trap data using a combination of consistent field methodology and appropriate statistical models that account and correct for possible detection bias - and that explicitly incorporate ecological and anthropogenic factors (MacKenzie *et al.*, 2003; Royle & Kery, 2007) - can yield useful indicators for species and community assessments. It also offers new insights on the spatial-temporal distribution patterns of the analysed species and communities, especially in relation to different sources of human disturbance. This is a unifying topic in all the analysed contexts. It is especially relevant in the Italian Alps where, due to higher human population densities and increased habitat fragmentation and alteration, few wilderness areas remain. On the other hand, the existing and increasing anthropogenic pressures on species and communities are severe across the tropics, and particularly in the analysed highland forests of Tanzania, given their fragility and outstanding importance for biodiversity and endemism. Finally, this is equally relevant in studies on threatened species, such as the flagship snow leopard, main target of the study in Chapter 5.

In Chapter 1, I investigated the effect of human disturbance on occurrence probability and daily activity pattern of a set of medium-to-large mammal species in the central Italian Alps. While I found little evidence for a direct impact of human presence on mammals' occurrence in the study area, I found an effect on their detectability, and, interestingly, on their activity pattern. An important aspect related to the main goal of assessing human disturbance is that the sampled area is a complex matrix of intermingled disturbance sources in space and time. The lack of a clear and unidirectional disturbance gradient, from outside the protected area to its interior, complicated the interpretation of results. However, I believe that the context I studied is representative of the general environmental settings in the Alps. These results are relevant for protected area managers to assess the degree at which biodiversity conservation is compatible with infrastructural development, and overall human presence in the Alps.

The small brown bear population of the central Italian Alps analysed in Chapter 2 is of remarkable importance for conservation. Indeed, its current core area results from the recent reintroduction, with the aim of establishing a viable larger Alpine population (Groff *et al.*, 2015; Peters *et al.*, 2015; Mustoni *et al.*, 2003; Linnell *et al.*, 2008). Yet, connectivity of this population remains a concern at multiple spatial scales (Peters *et al.*, 2015). Results suggest that human activity (predominantly for recreation) and settlements affect brown bears through temporal and spatial displacement. Analysis of activity patterns showed temporal displacement between bears and people, with bears being active mostly during the night and in crepuscular hours, and human activity typically being high during daylight. Spatial site-use analysis carried out for crepuscular hours, i.e. when bears and people are both active, revealed spatial displacement, with bears avoiding sites with high people passage, and being less detectable close to settlements. Notably, the area inhabited by the study population has one of the highest human population densities among regions occupied by brown bears (De Barba *et al.* 2010; Chapron *et al.* 2014). Overall, our results deliver a reassuring message for forest users and managers and provide more evidence that bears living in human-modified landscapes have developed a solid pattern of human avoidance. This is an important prerequisite for the coexistence of brown bears and people in the study area and the Alps in general, and is especially relevant in the current context of increasing human-bear conflicts.

Given the high investment that has been made worldwide in protected areas (Balmford *et al.*, 2003) and their importance for long-term conservation, it is crucial to document how effectively they are performing (Naughton-Treves *et al.*, 2005). The standardized dataset in Chapter 3 provides evidence that effective ground protection is associated with stability over time in the occurrence probability of a pool of commonly camera-trapped species of forest mammals. Furthermore, we found that target species' occurrence probability over the study period was stable in spite of some moderate sources of human disturbance (illegal hunting and firewood collection) by adjacent villagers. Notably, we observed a forest-wide decline in human disturbance over the 8-year period. This reduction suggests a gradual decrease of human pressure in the protected area and/or an improvement of management effectiveness, and supports the notion that the national park is more effective as compared to other reserves in the area where ground protection appears inadequate. Overall, these results support the notion that legal protection backed up by on-ground protection can maintain diverse mammal communities

in tropical forests. This is especially relevant in Tanzania, arguably mainland Africa's most important nation for conservation, which is losing habitat and natural resources rapidly (Caro & Davenport 2016).

The analyses carried out in Chapter 4 revealed clear differences between target mammal communities under contrasting protection regimes. In line with our hypotheses, we found lower species richness and reduced occurrence probabilities for most mammal species in the forest with high disturbance, with a tendency of greater decrease in occurrence probability by the larger-bodied species. We also found that the composition of trophic guilds varied between the two protected areas. This study suggests that legal protection needs to be backed up by on ground protection to play a determinant role in maintaining diverse mammal communities in tropical forests. Protected areas are the cornerstone of efforts to conserve tropical biodiversity and final refuges for threatened species across the globe, but the future of biodiversity within them is closely tied to actual enforcement efficacy. This, in turn, is linked to adequate funding and capacity of protected area management (Bruner *et al.*, 2001; Laurance *et al.*, 2012; Tranquilli *et al.*, 2014). Robust assessments on the status of wildlife populations remain fundamental to determine how effectively protected areas are performing (Naughton-Treves, Holland & Brandon, 2005) and to design efficient and long-term conservation plans.

Results of Chapter 5 support the potential of the occupancy framework for analysing snow leopard detection/ non-detection data from camera traps. Since the main constraint was the small number of detections of snow leopards and ibex, an improved evaluation of its application to model co-occurrence patterns will require greater sample sizes. The added advantage of the model used is that interactions among species are modelled explicitly, along with the effect of environmental covariates. The indication that livestock may negatively impact wild ungulates merits further research, as does the result that livestock may not directly affect the occurrence of the snow leopard. The negative effects that depletion of wild prey may have on large carnivores are well known, as is the potential resulting escalation of human-wildlife conflicts (Berger *et al.*, 2013; Ekernas *et al.*, 2017). Given that the study area is a national park, we suggest that ensuring protection of Siberian ibex and snow leopards in the Park requires a revision of the livestock grazing zone, and increased law enforcement, with emphasis on the creation and protection of livestock-free areas. Conservation efforts should concomitantly target livestock practices by engaging herders in the process of developing new grazing plans, as

elaborated in the Snow Leopard Survival Strategy (Snow Leopard Network, 2014).

Overall, these studies are methodologically unified by the hierarchical formulation of models applied to various ecological systems. The case studies analysed in all Chapters demonstrate how hierarchical models are ideally suited to accommodate in a single framework multiple sources of spatio-temporal variability, as well as multiple scales of measurement, while rigorously propagating uncertainty into every estimand of the model (Cressie & Wikle, 2015; Hobbs & Hooten, 2015). Indeed, occupancy models account for observation error, thus having the possibility of separating process variance from observation variance (Kery & Royle, 2015). Although both classical and Bayesian inference paradigms were useful for analysis of hierarchical models, I generally preferred the clarity and flexibility of the Bayesian formulation, also because classical inference based on maximum likelihood estimators was in some cases not practically feasible (e.g. for the community occupancy model).

This thesis also shows the value of occupancy as a metric in modelling habitat associations (Chapter 1), testing the effect of anthropogenic drivers (Chapter 2), assessing the impact of management actions (Chapter 4), multispecies relationships (Chapter 5) and, critically, monitoring temporal changes of populations (Chapter 3) and communities (reviews in MacKenzie *et al.*, 2017; O'Connell & Bailey, 2011; Bailey *et al.*, 2014). Although studies on populations are most often interested in measuring abundance, estimation of this requires substantial efforts because it normally implies repeated counts of individuals (while avoiding double counts of the same individual within a single observation period), or individual identification for capture-recapture models. This may be unfeasible, too resource demanding, or even not necessary. In addition, accounting for both stochasticity and environmental factors in modelling spatio-temporal variation in abundance can be more difficult than mere occupancy (Kery & Royle, 2015). Indeed, in most cases, an unbiased metric, which can be used as a proxy of abundance, has been shown to be equally useful for investigating population trends over time, or spatial variation of population in relation to covariates, so that scientific hypotheses can be tested (e.g. Chapter 1 and 2; Rovero & Zimmermann, 2016). Furthermore, the application of the recently-proposed multi-region community occupancy model (Tenan *et al.*, 2017), applied in Chapter 4, allowed me to investigate two mammal communities simultaneously in terms of species richness, functional composition (i.e., richness and proportions of trophic guilds) and

species-specific occurrences. On the other hand, the single-species approach of Chapter 3 was feasible and effective because applied to a standardized and relatively long-term data series, a requirement for investigating temporal patterns of long-lived animals. In this regard, this PhD project was also instrumental to adapt the TEAM protocol to the set up of a long-term monitoring of mammals across the study area in the central Italian Alps (see Chapter 1 and 2), which will allow for temporal analyses of the local medium-to-large mammal community (with a specific focus on the brown bear), and hence a quantitative assessment of biodiversity changes over time.

In conclusion, human pressures on the environment are changing spatially and temporally, with profound implications for the planet's biodiversity. Indeed, threats to species and ecosystems have never been so disruptive as today (Tilman *et al.*, 2017). This era of catastrophic biodiversity loss calls for robust indicators produced from standardized monitoring infrastructure, as critical means to accurately assess population outcomes and identify conservation strategies that can avert biodiversity collapse. The presented approach aims at contributing to this goal, and promotes the adoption of standardized monitoring for conservation. Finally, it can be generalized and applied to other species or ecological contexts, also as a way to inform decision-making processes.



## Appendices

### Appendix A. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping

**Table A.1** Top-ranked models for each species in the study area, eastern Alps (the null model ( $\psi(\cdot)$   $\rho(\cdot)$ ) is also shown). Change in Akaike information criterion ( $\Delta$ AIC) is the difference in AIC values between each model with the lowest AIC model, *nPars* is the number of parameters in the model and *wi* is the AIC model weight.

| Species  | Models  | AIC    | $\Delta$ AIC | nPars | wi   |
|----------|---|--------|--------------|-------|------|
| Red deer | $\psi(\sim\text{ve}) \rho(\sim\text{mod}+\text{cab}+\text{homo}+\text{ve})$             | 459.51 | 0.00         | 7     | 0.13 |
|          | $\psi(\cdot) \rho(\sim\text{mod}+\text{cab}+\text{homo}+\text{ve})$                     | 459.60 | 0.09         | 6     | 0.12 |
|          | $\psi(\sim\text{el}) \rho(\sim\text{mod}+\text{cab}+\text{homo}+\text{ve})$             | 460.50 | 0.99         | 7     | 0.08 |
|          | $\psi(\sim\text{homo}+\text{ve}) \rho(\sim\text{mod}+\text{cab}+\text{homo}+\text{ve})$ | 460.58 | 1.07         | 8     | 0.07 |
|          | $\psi(\sim\text{el}+\text{ve}) \rho(\sim\text{mod}+\text{cab}+\text{homo}+\text{ve})$   | 460.93 | 1.42         | 8     | 0.06 |
|          | $\psi(\sim\text{sl}+\text{ve}) \rho(\sim\text{mod}+\text{cab}+\text{homo}+\text{ve})$   | 460.94 | 1.43         | 8     | 0.06 |
|          | $\psi(\sim\text{sl}) \rho(\sim\text{mod}+\text{cab}+\text{homo}+\text{ve})$             | 461.03 | 1.52         | 7     | 0.05 |
|          | $\psi(\cdot) \rho(\cdot)$   | 475.33 | 15.82        |       |      |
| Roe deer | $\psi(\sim\text{sl}) \rho(\sim\text{mod}+\text{tr}+\text{cab})$                         | 557.37 | 0.00         | 7     | 0.16 |
|          | $\psi(\cdot) \rho(\sim\text{mod}+\text{tr}+\text{cab})$                                 | 558.24 | 0.87         | 6     | 0.09 |
|          | $\psi(\sim\text{sl}+\text{homo}) \rho(\sim\text{mod}+\text{tr}+\text{cab})$             | 559.08 | 1.71         | 8     | 0.07 |
|          | $\psi(\sim\text{sl}+\text{el}) \rho(\sim\text{mod}+\text{tr}+\text{cab})$               | 559.10 | 1.73         | 8     | 0.07 |

|            |   |        |       |   |      |
|------------|---|--------|-------|---|------|
|            | $\psi (\sim\text{sl}+\text{ve}) \rho (\sim\text{mod}+\text{tr}+\text{cab})$               | 559.24 | 1.87  | 8 | 0.06 |
|            | $\psi (.) \rho (.)$   | 564.85 | 7.48  |   |      |
| Chamois    | $\psi (\sim\text{sl}+\text{el}) \rho (\sim\text{mod}+\text{homo})$                        | 339.91 | 0.00  | 6 | 0.16 |
|            | $\psi (\sim\text{el}) \rho (\sim\text{mod}+\text{homo})$                                  | 340.59 | 0.69  | 5 | 0.12 |
|            | $\psi (\sim\text{sl}+\text{el}+\text{homo}) \rho (\sim\text{mod}+\text{homo})$            | 341.56 | 1.65  | 7 | 0.07 |
|            | $\psi (\sim\text{sl}+\text{el}+\text{el}2) \rho (\sim\text{mod}+\text{homo})$             | 341.66 | 1.75  | 7 | 0.07 |
|            | $\psi (\sim\text{sl}+\text{el}+\text{ve}) \rho (\sim\text{mod}+\text{homo})$              | 341.89 | 1.98  | 7 | 0.06 |
|            | $\psi (.) \rho (.)$   | 348.99 | 9.08  |   |      |
| Brown bear | $\psi (.) \rho (\sim\text{mod}+\text{cab}+\text{homo})$                                   | 221.15 | 0.00  | 5 | 0.16 |
|            | $\psi (.) \rho (.)$   | 221.27 | 0.12  | 2 | 0.14 |
|            | $\psi (\sim\text{el}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$                       | 222.21 | 1.06  | 6 | 0.10 |
|            | $\psi (\sim\text{sl}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$                       | 222.43 | 1.28  | 6 | 0.08 |
|            | $\psi (\sim\text{homo}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$                     | 223.04 | 1.89  | 6 | 0.06 |
|            | $\psi (\sim\text{ve}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$                       | 223.07 | 1.92  | 6 | 0.06 |
| Marten     | $\psi (\sim\text{homo}) \rho (\sim\text{cab}+\text{homo})$                                | 198.47 | 0.00  | 5 | 0.17 |
|            | $\psi (.) \rho (\sim\text{cab}+\text{homo})$  | 199.14 | 0.67  | 4 | 0.11 |
|            | $\psi (\sim\text{ve}) \rho (\sim\text{cab}+\text{homo})$                                  | 199.48 | 1.02  | 5 | 0.10 |
|            | $\psi (\sim\text{homo}+\text{ve}) \rho (\sim\text{cab}+\text{homo})$                      | 199.90 | 1.43  | 6 | 0.08 |
|            | $\psi (\sim\text{el}+\text{homo}) \rho (\sim\text{cab}+\text{homo})$                      | 200.17 | 1.71  | 6 | 0.07 |
|            | $\psi (\sim\text{sl}+\text{homo}) \rho (\sim\text{cab}+\text{homo})$                      | 200.26 | 1.80  | 6 | 0.07 |
|            | $\psi (.) \rho (.)$   | 204.08 | 5.61  |   |      |
| Red fox    | $\psi (\sim\text{el}+\text{homo}) \rho (\sim\text{cab}+\text{ve})$                        | 454.24 | 0.00  | 6 | 0.26 |
|            | $\psi (\sim\text{el}+\text{el}2+\text{homo}) \rho (\sim\text{cab}+\text{ve})$             | 455.94 | 1.70  | 7 | 0.11 |
|            | $\psi (\sim\text{el}+\text{homo}+\text{ve}) \rho (\sim\text{cab}+\text{ve})$              | 455.97 | 1.74  | 7 | 0.10 |
|            | $\psi (\sim\text{homo}) \rho (\sim\text{cab}+\text{ve})$                                  | 455.98 | 1.74  | 5 | 0.10 |
|            | $\psi (\sim\text{sl}+\text{el}+\text{homo}) \rho (\sim\text{cab}+\text{ve})$              | 456.15 | 1.91  | 7 | 0.10 |
|            | $\psi (.) \rho (.)$   | 467.70 | 13.46 |   |      |
| Badger     | $\psi (\sim\text{el}+\text{ve}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$             | 232.11 | 0.00  | 7 | 0.27 |
|            | $\psi (\sim\text{sl}+\text{el}+\text{ve}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$   | 233.56 | 1.45  | 8 | 0.13 |
|            | $\psi (\sim\text{el}+\text{el}2+\text{ve}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$  | 234.00 | 1.89  | 8 | 0.11 |
|            | $\psi (\sim\text{el}+\text{homo}+\text{ve}) \rho (\sim\text{mod}+\text{cab}+\text{homo})$ | 234.07 | 1.96  | 8 | 0.10 |

|            |   |        |       |   |      |
|------------|---|--------|-------|---|------|
|            | $\psi$ (.) $\rho$ (.)                       | 259.11 | 27.00 |   |      |
| Brown hare | $\psi$ (~homo) $\rho$ (~mod+tr+cab+homo)    | 224.48 | 0.00  | 8 | 0.27 |
|            | $\psi$ (~homo+ve) $\rho$ (~mod+tr+cab+homo) | 225.37 | 0.89  | 9 | 0.17 |
|            | $\psi$ (~sl+homo) $\rho$ (~mod+tr+cab+homo) | 226.46 | 1.98  | 9 | 0.10 |
|            | $\psi$ (~el+homo) $\rho$ (~mod+tr+cab+homo) | 226.47 | 1.99  | 9 | 0.10 |
|            | $\psi$ (.) $\rho$ (.)                       | 248.43 | 23.95 |   |      |

Mod=camera model; tr=trail type; cab=distance from settlements; homo=capture rate of humans; ve=capture rate of vehicles; el=elevation; el2=elevation squared; sl=slope

**Table A.2** Summaries of model average for each species. NMod is the number of models that include each covariate;  $\psi$  and  $p$  are the mean occupancy and detectability, respectively, predicted by the average model at the camera trap sites.

| Species    | Covariates | Estimate (SE)  | P value      | Rel. Imp. | N Mod | $\psi$ (SE) | $p$ (SE)    |
|------------|------------|----------------|--------------|-----------|-------|-------------|-------------|
| Brown bear | p(modRec)  | -0.858 (0.510) | 0.0924 .     | 0.62      | 5     | 0.52 (0.15) | 0.13 (0.06) |
|            | p(cab)     | 0.544 (0.290)  | 0.0613 .     | 0.62      | 5     |             |             |
|            | p(homo)    | -0.673 (0.390) | 0.0845 .     | 0.62      | 5     |             |             |
|            | psi(el)    | -0.464 (0.497) | 0.3511       | 0.12      | 1     |             |             |
|            | psi(sl)    | -0.365 (0.465) | 0.4320       | 0.10      | 1     |             |             |
|            | psi(homo)  | -0.272 (0.704) | 0.6988       | 0.08      | 1     |             |             |
|            | psi(ve)    | -0.115 (0.394) | 0.7694       | 0.08      | 1     |             |             |
| Red deer   | p(modRec)  | -0.589 (0.274) | 0.03146 *    | 1.00      | 7     | 0.74 (0.11) | 0.34 (0.05) |
|            | p(cab)     | 0.254 (0.143)  | 0.07573 .    | 1.00      | 7     |             |             |
|            | p(homo)    | -1.509 (0.381) | 7.42e-05 *** | 1.00      | 7     |             |             |
|            | p(ve)      | 0.721 (0.309)  | 0.01946 *    | 1.00      | 7     |             |             |
|            | psi(ve)    | -0.482 (0.412) | 0.24146      | 0.47      | 4     |             |             |
|            | psi(el)    | -0.346 (0.371) | 0.35156      | 0.21      | 2     |             |             |
|            | psi(sl)    | -0.263 (0.349) | 0.45076      | 0.18      | 2     |             |             |
|            | psi(homo)  | 1.068 (1.260)  | 0.39643      | 0.09      | 1     |             |             |

|          |             |                |             |      |   |             |             |
|----------|-------------|----------------|-------------|------|---|-------------|-------------|
| Roe deer | psi(sl)     | -0.755 (0.523) | 0.149372    | 0.68 | 4 | 0.83 (0.09) | 0.42 (0.06) |
|          | p(modRec)   | -0.699 (0.234) | 0.002764 ** | 1.00 | 5 |             |             |
|          | p(trtrail)  | 0.549 (0.254)  | 0.031109 *  | 1.00 | 5 |             |             |
|          | p(trtrailS) | 0.849 (0.344)  | 0.013579 *  | 1.00 | 5 |             |             |
|          | p(cab)      | -0.129 (0.114) | 0.257554    | 1.00 | 5 |             |             |
|          | psi(homo)   | -0.196 (0.340) | 0.565100    | 0.11 | 1 |             |             |
|          | psi(el)     | -0.230 (0.448) | 0.608631    | 0.11 | 1 |             |             |
|          | psi(ve)     | 0.160 (0.477)  | 0.736725    | 0.10 | 1 |             |             |
| Chamois  | psi(sl)     | 0.568 (0.396)  | 0.15110     | 0.68 | 4 | 0.51 (0.13) | 0.36 (0.06) |
|          | psi(el)     | 0.661 (0.349)  | 0.05838 .   | 1.00 | 5 |             |             |
|          | p(modRec)   | -0.632 (0.361) | 0.07998 .   | 1.00 | 5 |             |             |
|          | p(homo)     | -1.074 (0.344) | 0.00181 **  | 1.00 | 5 |             |             |
|          | psi(homo)   | -0.359 (0.582) | 0.53699     | 0.12 | 1 |             |             |
|          | psi(el2)    | 0.162 (0.330)  | 0.62338     | 0.11 | 1 |             |             |
|          | psi(ve)     | 0.037 (0.294)  | 0.90009     | 0.10 | 1 |             |             |
| Red fox  | psi(el)     | -0.630 (0.336) | 0.06114 .   | 0.78 | 4 | 0.62 (0.11) | 0.54 (0.04) |
|          | psi(homo)   | 1.420 (0.698)  | 0.04177 *   | 1.00 | 5 |             |             |
|          | p(cab)      | -0.201 (0.121) | 0.08269 .   | 1.00 | 5 |             |             |
|          | p(ve)       | 0.389 (0.146)  | 0.00768 **  | 1.00 | 5 |             |             |
|          | psi(el2)    | -0.176 (0.322) | 0.58378     | 0.13 | 1 |             |             |
|          | psi(ve)     | 0.186 (0.385)  | 0.62949     | 0.13 | 1 |             |             |
|          | psi(sl)     | -0.089 (0.302) | 0.76677     | 0.12 | 1 |             |             |
| Badger   | psi(el)     | -1.058 (0.512) | 0.0388 *    | 1.00 | 4 | 0.54 (0.14) | 0.18 (0.05) |
|          | psi(ve)     | 2.156 (1.508)  | 0.1528      | 1.00 | 4 |             |             |
|          | p(modRec)   | -3.261 (0.690) | 2.3e-06 *** | 1.00 | 4 |             |             |
|          | p(cab)      | 0.166 (0.264)  | 0.5303      | 1.00 | 4 |             |             |
|          | p(homo)     | -0.322 (0.232) | 0.1644      | 1.00 | 4 |             |             |
|          | psi(sl)     | -0.397 (0.552) | 0.4724      | 0.18 | 1 |             |             |
|          | psi(el2)    | 0.175 (0.519)  | 0.7359      | 0.15 | 1 |             |             |
|          | psi(homo)   | -0.132 (0.636) | 0.8353      | 0.14 | 1 |             |             |

|            |             |                 |            |      |   |             |             |
|------------|-------------|-----------------|------------|------|---|-------------|-------------|
| Brown hare | psi(homo)   | 2.173 (1.027)   | 0.0344 *   | 1.00 | 4 | 0.45 (0.12) | 0.21 (0.07) |
|            | p(modRec)   | -1.547 (2.364)  | 0.0155 *   | 1.00 | 4 |             |             |
|            | p(trtrail)  | -1.053 (2.371)  | 0.1002     | 1.00 | 4 |             |             |
|            | p(trtrailS) | -3.778 (13.005) | 0.9370     | 1.00 | 4 |             |             |
|            | p(cab)      | 1.473 (1.114)   | 0.1859     | 1.00 | 4 |             |             |
|            | p(homo)     | -0.587 (1.014)  | 0.8740     | 1.00 | 4 |             |             |
|            | psi(ve)     | -2.153 (2.712)  | 0.4275     | 0.22 | 1 |             |             |
|            | psi(sl)     | -0.883 (1.713)  | 0.8877     | 0.13 | 1 |             |             |
|            | psi(el)     | 0.447 (1.601)   | 0.9440     | 0.13 | 1 |             |             |
| Marten     | psi(homo)   | 0.501 (0.348)   | 0.15001    | 0.58 | 4 | 0.29 (0.10) | 0.25 (0.06) |
|            | p(cab)      | -0.773 (0.287)  | 0.00694 ** | 1.00 | 6 |             |             |
|            | p(homo)     | 0.545 (0.251)   | 0.03015 *  | 1.00 | 6 |             |             |
|            | psi(ve)     | 0.327 (0.327)   | 0.31721    | 0.28 | 2 |             |             |
|            | psi(el)     | -0.211 (0.386)  | 0.58568    | 0.10 | 1 |             |             |
|            | psi(sl)     | 0.171 (0.381)   | 0.65387    | 0.09 | 1 |             |             |

Mod=camera model; tr=trail type; cab=distance from settlements; homo=capture rate of humans; ve=capture rate of vehicles; el=elevation; el2=elevation squared; sl=slope

**Table A.3** Predicted  $\psi$  for each species at each camera trap station (58 sites).

| Site        | Predicted $\psi$ |          |          |         |        |            |        |         |
|-------------|------------------|----------|----------|---------|--------|------------|--------|---------|
|             | Brown bear       | Red deer | Roe deer | Chamois | Badger | Brown hare | Marten | Red fox |
| CT-TNT-1-01 | 0.54             | 0.77     | 0.86     | 0.29    | 0.78   | 0.48       | 0.28   | 0.77    |
| CT-TNT-1-02 | 0.54             | 0.79     | 0.89     | 0.25    | 0.73   | 0.86       | 0.33   | 0.91    |
| CT-TNT-1-03 | 0.53             | 0.75     | 0.90     | 0.43    | 0.40   | 0.24       | 0.24   | 0.45    |
| CT-TNT-1-04 | 0.51             | 0.75     | 0.91     | 0.64    | 0.12   | 0.86       | 0.32   | 0.71    |
| CT-TNT-1-05 | 0.51             | 0.73     | 0.83     | 0.67    | 0.24   | 0.23       | 0.24   | 0.36    |
| CT-TNT-1-06 | 0.55             | 0.77     | 0.90     | 0.24    | 0.77   | 0.24       | 0.25   | 0.62    |
| CT-TNT-1-07 | 0.51             | 0.71     | 0.82     | 0.51    | 0.93   | 0.81       | 0.35   | 0.86    |
| CT-TNT-1-08 | 0.50             | 0.73     | 0.81     | 0.73    | 0.19   | 0.23       | 0.24   | 0.33    |
| CT-TNT-1-09 | 0.49             | 0.75     | 0.74     | 0.69    | 0.24   | 1.00       | 0.47   | 0.99    |
| CT-TNT-1-10 | 0.53             | 0.75     | 0.89     | 0.46    | 0.41   | 0.36       | 0.26   | 0.53    |
| CT-TNT-1-11 | 0.51             | 0.74     | 0.87     | 0.54    | 0.62   | 0.89       | 0.35   | 0.86    |

|             |      |      |      |      |      |      |      |      |
|-------------|------|------|------|------|------|------|------|------|
| CT-TNT-1-12 | 0.51 | 0.73 | 0.76 | 0.57 | 0.72 | 0.31 | 0.27 | 0.58 |
| CT-TNT-1-13 | 0.50 | 0.74 | 0.74 | 0.72 | 0.24 | 0.76 | 0.31 | 0.73 |
| CT-TNT-1-14 | 0.53 | 0.76 | 0.87 | 0.39 | 0.58 | 0.24 | 0.25 | 0.54 |
| CT-TNT-1-15 | 0.51 | 0.59 | 0.87 | 0.63 | 0.99 | 0.38 | 0.33 | 0.53 |
| CT-TNT-1-16 | 0.49 | 0.58 | 0.88 | 0.68 | 1.00 | 0.99 | 0.51 | 0.96 |
| CT-TNT-1-17 | 0.52 | 0.75 | 0.75 | 0.50 | 0.61 | 0.28 | 0.26 | 0.60 |
| CT-TNT-1-18 | 0.52 | 0.74 | 0.82 | 0.57 | 0.39 | 0.24 | 0.25 | 0.45 |
| CT-TNT-1-19 | 0.49 | 0.69 | 0.75 | 0.74 | 0.75 | 0.68 | 0.32 | 0.69 |
| CT-TNT-1-20 | 0.51 | 0.75 | 0.90 | 0.64 | 0.14 | 0.85 | 0.31 | 0.72 |
| CT-TNT-1-21 | 0.52 | 0.74 | 0.82 | 0.59 | 0.37 | 0.26 | 0.25 | 0.46 |
| CT-TNT-1-22 | 0.55 | 0.77 | 0.88 | 0.25 | 0.83 | 0.24 | 0.25 | 0.65 |
| CT-TNT-1-23 | 0.49 | 0.71 | 0.48 | 0.77 | 0.36 | 0.24 | 0.26 | 0.46 |
| CT-TNT-1-24 | 0.54 | 0.77 | 0.90 | 0.28 | 0.70 | 0.41 | 0.27 | 0.69 |
| CT-TNT-1-25 | 0.51 | 0.75 | 0.90 | 0.57 | 0.26 | 0.93 | 0.35 | 0.86 |
| CT-TNT-1-26 | 0.52 | 0.74 | 0.82 | 0.58 | 0.39 | 0.23 | 0.25 | 0.45 |
| CT-TNT-1-27 | 0.53 | 0.75 | 0.86 | 0.39 | 0.73 | 0.38 | 0.27 | 0.66 |
| CT-TNT-1-28 | 0.54 | 0.76 | 0.78 | 0.33 | 0.84 | 0.23 | 0.26 | 0.66 |
| CT-TNT-1-29 | 0.51 | 0.74 | 0.91 | 0.62 | 0.19 | 0.65 | 0.28 | 0.55 |
| CT-TNT-1-30 | 0.53 | 0.75 | 0.74 | 0.43 | 0.77 | 0.27 | 0.26 | 0.65 |
| CT-TNT-2-01 | 0.51 | 0.74 | 0.87 | 0.58 | 0.48 | 0.96 | 0.38 | 0.91 |
| CT-TNT-2-02 | 0.51 | 0.74 | 0.83 | 0.68 | 0.22 | 0.52 | 0.28 | 0.56 |
| CT-TNT-2-03 | 0.52 | 0.73 | 0.83 | 0.50 | 0.71 | 0.27 | 0.26 | 0.54 |
| CT-TNT-2-04 | 0.52 | 0.77 | 0.90 | 0.43 | 0.39 | 0.80 | 0.31 | 0.81 |
| CT-TNT-2-05 | 0.48 | 0.68 | 0.86 | 0.60 | 0.97 | 1.00 | 0.64 | 1.00 |
| CT-TNT-2-06 | 0.53 | 0.76 | 0.83 | 0.42 | 0.62 | 0.27 | 0.26 | 0.59 |
| CT-TNT-2-07 | 0.49 | 0.72 | 0.71 | 0.82 | 0.14 | 0.42 | 0.27 | 0.42 |
| CT-TNT-2-08 | 0.53 | 0.76 | 0.88 | 0.42 | 0.51 | 0.29 | 0.25 | 0.55 |
| CT-TNT-2-10 | 0.52 | 0.74 | 0.85 | 0.57 | 0.33 | 0.26 | 0.25 | 0.45 |
| CT-TNT-2-11 | 0.55 | 0.78 | 0.92 | 0.22 | 0.73 | 0.23 | 0.25 | 0.59 |
| CT-TNT-2-12 | 0.51 | 0.74 | 0.84 | 0.65 | 0.25 | 0.24 | 0.25 | 0.37 |
| CT-TNT-2-13 | 0.53 | 0.76 | 0.82 | 0.37 | 0.76 | 0.51 | 0.29 | 0.77 |
| CT-TNT-2-14 | 0.51 | 0.75 | 0.89 | 0.62 | 0.18 | 0.54 | 0.27 | 0.52 |
| CT-TNT-2-15 | 0.51 | 0.74 | 0.84 | 0.63 | 0.28 | 0.25 | 0.25 | 0.40 |
| CT-TNT-2-16 | 0.53 | 0.75 | 0.86 | 0.44 | 0.58 | 0.27 | 0.25 | 0.54 |
| CT-TNT-2-17 | 0.50 | 0.72 | 0.72 | 0.78 | 0.20 | 0.31 | 0.26 | 0.40 |

|             |      |      |      |      |      |      |      |      |
|-------------|------|------|------|------|------|------|------|------|
| CT-TNT-2-18 | 0.53 | 0.75 | 0.89 | 0.46 | 0.40 | 0.27 | 0.25 | 0.48 |
| CT-TNT-2-19 | 0.51 | 0.75 | 0.76 | 0.51 | 0.68 | 0.90 | 0.35 | 0.91 |
| CT-TNT-2-20 | 0.55 | 0.77 | 0.85 | 0.25 | 0.85 | 0.23 | 0.25 | 0.66 |
| CT-TNT-2-21 | 0.55 | 0.78 | 0.91 | 0.19 | 0.84 | 0.39 | 0.27 | 0.75 |
| CT-TNT-2-23 | 0.53 | 0.76 | 0.87 | 0.41 | 0.58 | 0.28 | 0.26 | 0.56 |
| CT-TNT-2-24 | 0.51 | 0.50 | 0.82 | 0.49 | 1.00 | 0.27 | 0.38 | 0.65 |
| CT-TNT-2-25 | 0.52 | 0.74 | 0.87 | 0.63 | 0.22 | 0.26 | 0.25 | 0.37 |
| CT-TNT-2-26 | 0.53 | 0.75 | 0.79 | 0.42 | 0.78 | 0.33 | 0.27 | 0.66 |
| CT-TNT-2-27 | 0.52 | 0.75 | 0.78 | 0.50 | 0.57 | 0.24 | 0.25 | 0.54 |
| CT-TNT-2-28 | 0.51 | 0.74 | 0.80 | 0.61 | 0.36 | 0.28 | 0.25 | 0.48 |
| CT-TNT-2-29 | 0.54 | 0.76 | 0.83 | 0.31 | 0.85 | 0.42 | 0.28 | 0.76 |
| CT-TNT-2-30 | 0.54 | 0.76 | 0.80 | 0.33 | 0.82 | 0.25 | 0.26 | 0.66 |

---



## Appendix B. Spatial-temporal patterns of human avoidance by brown bears in a reintroduced population

**Supplementary material B.1** R and JAGS code for the single-species occupancy model fitted to the detection/non-detection data of the brown bear in the central Italian Alps.

```
##### model
modelFilename = "Bear.txt"
cat("
  model {

    # priors for psi
    alpha0<- log(mean.psi/(1-mean.psi))
    mean.psi ~ dunif(0,1)

    # year effects (corner constraint)
    year.eff.psi[1] <- 0
    for(t in 2:nyear){
      year.eff.psi[t] ~ dnorm(0,1/sqrt(2.25))
    }

    #year-specific intercepts
    Yeareff.psi.prob_y1 <- mean.psi
    Yeareff.psi.prob_y2 <- 1/(1+exp(-alpha0-year.eff.psi[2]))
    Yeareff.psi.prob_y3 <- 1/(1+exp(-alpha0-year.eff.psi[3]))
    Yeareff.psi.prob_y4 <- 1/(1+exp(-alpha0-year.eff.psi[4]))

    # priors for p
    beta0<- log(mean.p/(1-mean.p))
    mean.p ~ dunif(0,1)

    # year effects (corner constraint)
    year.eff.p[1] <- 0
    for(t in 2:nyear){
      year.eff.p[t] ~ dnorm(0,1/sqrt(2.25))   #year.eff.p[t]~dnorm(0,0.01)
    }

    Yeareff.p.prob_y1 <- mean.p
    Yeareff.p.prob_y2 <- 1/(1+exp(-beta0-year.eff.p[2]))
    Yeareff.p.prob_y3 <- 1/(1+exp(-beta0-year.eff.p[3]))
    Yeareff.p.prob_y4 <- 1/(1+exp(-beta0-year.eff.p[4]))

    alpha1 ~ dnorm(0,1/sqrt(2.25))

    beta1 ~ dnorm(0,1/sqrt(2.25))

    for(i in 1:nsite){
      for(t in 1:nyear){
```

```

all_std[i,t] ~ dnorm(0,1/sqrt(2.25))
}
}

## state process

for (i in 1:nsite){
for(t in 1:nyear){
Z[i,t] ~ dbern(psi[i,t])
logit(psi[i,t]) <- alpha0 + year.eff.psi[t] + alpha1 * all_std[i,t]

}
}

## observation process

for(i in 1:nsite){
for(t in 1:nyear){
y_bear[i,t] ~ dbin(p[i,t] * Z[i,t],K_tot[i,t])

logit(p[i,t]) <- beta0 + year.eff.p[t] + beta1 *Village[i]

}
}

## derived parameters

for(t in 1:nyear){
n_occ[t] <- sum(Z[,t])
psi_mean[t] <- mean(psi[,t])
p_mean[t] <- mean(p[,t])
}

}

## end model
", fill=TRUE, file=modelFilename)

# data for JAGS
bugs.data <- list(y_bear=y_bear,
                 nsite=dim(y_bear)[1], nyear=dim(y_bear)[2],
                 all_std=all_std, Village=Village, K_tot=K_tot)

## parameters to monitor

params <- c("psi_mean","p_mean","n_occ"," Yeareff.psi.prob_y1","
Yeareff.psi.prob_y2"," Yeareff.psi.prob_y3"," Yeareff.psi.prob_y4",
" Yeareff.p.prob_y1"," Yeareff.p.prob_y2"," Yeareff.p.prob_y3","
Yeareff.p.prob_y4","year.eff.psi","year.eff.p","alpha0","alpha1","beta0","beta
1")

## inits
zsti<-matrix(1,nrow=60,ncol=4)

jags.inits <- function(){ list(Z = zsti,
                              mean.psi=runif(1,0,1),
                              mean.p=runif(1,0,1),
                              alpha1 = runif(1, -3, 3),
                              beta1 = runif(1, -3, 3),
                              year.eff.psi = c(NA,runif(3, -3, 3))),

```

```

                                year.eff.p = c(NA,runif(3, -3, 3))
    })

# MCMC settings
n.adapt <- 1000
n.burnin <- 10000
n.iter <- 150000
n.thin <- 20
n.chains <- 3

start.time = Sys.time()

## adaptive phase to maximise MCMC efficiency

out_bear <- jags(data = bugs.data,
                inits=jags.inits,
                params,
                "Bear.txt",
                n.chains=n.chains,
                n.adapt=n.adapt,
                n.thin=n.thin,
                n.iter=n.iter,
                n.burnin=n.burnin)

end.time = Sys.time()

elapsed.time = round(difftime(end.time, start.time, units='mins'),2)
cat(paste(paste('Posterior computed in ', elapsed.time, sep=' '), 'minutes\n',
          sep=' '))

##### END

```

**Table B.2** Summary of posterior parameter estimates from the single-species occupancy model fitted to the detection/non-detection data of the brown bear in the central Italian Alps.  $\psi$ \_mean and  $p$ \_mean are the derived mean occupancy and detection probability for the brown bear in each year.  $N_{occ}$  is the estimated number of sites used by bears in each sampling season.  $\text{Yeareff.psi.prob}$  and  $\text{Yeareff.p.prob}$  are the fixed year effects (on the probability scale) on occupancy and detectability, respectively.  $\text{Year.eff.psi}$  and  $\text{year.eff.p}$  are the year-specific estimates for the fixed year-effect on occupancy and detectability, respectively (on the logit scale).  $\alpha_0$  and  $\beta_0$  are the intercept for occupancy and detectability, on the logit scale.  $\alpha_1$  is the effect of the number of human passages on occurrence probability.  $\beta_1$  is the effect of the distance from settlements on detection probability.

| Parameter    | Mean  | SD    | 2.5%  | 50%   | 97.5% |
|--------------|-------|-------|-------|-------|-------|
| psi_mean [1] | 0.352 | 0.103 | 0.181 | 0.342 | 0.580 |
| psi_mean [2] | 0.657 | 0.111 | 0.432 | 0.659 | 0.858 |
| psi_mean [3] | 0.590 | 0.130 | 0.344 | 0.589 | 0.840 |
| psi_mean [4] | 0.250 | 0.078 | 0.121 | 0.241 | 0.425 |
| p_mean [1]   | 0.106 | 0.032 | 0.053 | 0.103 | 0.176 |
| p_mean [2]   | 0.090 | 0.019 | 0.057 | 0.088 | 0.130 |
| p_mean [3]   | 0.078 | 0.021 | 0.044 | 0.076 | 0.124 |

|                     |        |       |        |        |        |
|---------------------|--------|-------|--------|--------|--------|
| p_mean [4]          | 0.185  | 0.042 | 0.111  | 0.182  | 0.275  |
| n_occ [1]           | 19.352 | 6.040 | 10.000 | 19.000 | 33.000 |
| n_occ [2]           | 40.406 | 6.169 | 28.000 | 41.000 | 52.000 |
| n_occ [3]           | 36.182 | 7.411 | 23.000 | 36.000 | 51.000 |
| n_occ [4]           | 14.668 | 3.668 | 10.000 | 14.000 | 24.000 |
| Yeareff.psi.prob_y1 | 0.321  | 0.106 | 0.152  | 0.308  | 0.565  |
| Yeareff.psi.prob_y2 | 0.660  | 0.129 | 0.405  | 0.661  | 0.896  |
| Yeareff.psi.prob_y3 | 0.583  | 0.148 | 0.310  | 0.577  | 0.874  |
| Yeareff.psi.prob_y4 | 0.218  | 0.077 | 0.098  | 0.207  | 0.393  |
| Yeareff.p.prob_y1   | 0.080  | 0.029 | 0.036  | 0.076  | 0.148  |
| Yeareff.p.prob_y2   | 0.066  | 0.017 | 0.038  | 0.064  | 0.104  |
| Yeareff.p.prob_y3   | 0.056  | 0.018 | 0.029  | 0.054  | 0.098  |
| Yeareff.p.prob_y4   | 0.154  | 0.045 | 0.080  | 0.150  | 0.254  |
| year.eff.psi[2]     | 1.521  | 0.722 | 0.152  | 1.502  | 2.987  |
| year.eff.psi[3]     | 1.171  | 0.746 | -0.213 | 1.139  | 2.723  |
| year.eff.psi[4]     | -0.545 | 0.614 | -1.784 | -0.532 | 0.642  |
| year.eff.p[2]       | -0.182 | 0.434 | -1.008 | -0.190 | 0.690  |
| year.eff.p[3]       | -0.363 | 0.461 | -1.263 | -0.367 | 0.538  |
| year.eff.p[4]       | 0.761  | 0.469 | -0.153 | 0.760  | 1.678  |
| $\alpha_0$          | -0.792 | 0.501 | -1.719 | -0.810 | 0.260  |
| $\alpha_1$          | -0.944 | 0.323 | -1.638 | -0.923 | -0.373 |
| $\beta_0$           | -2.504 | 0.397 | -3.300 | -2.496 | -1.754 |
| $\beta_1$           | 0.913  | 0.170 | 0.585  | 0.912  | 1.249  |

---

## Appendix C. When parks work: effect of anthropogenic disturbance on occupancy of tropical forest mammals

**Table C.1.** Species detected by camera traps during 2009-2016 in Mwanihana forest (Udzungwa Mountains National Park, Tanzania) with the number of independent detection events (i.e. separated by 1 day). In bold are the 8 species targeted by the analyses.

|    | <b>Species</b>                         | <b>2009</b> | <b>2010</b> | <b>2011</b> | <b>2012</b> | <b>2013</b> | <b>2014</b> | <b>2015</b> | <b>2016</b> |
|----|--|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| 1  | <i>Atilax paludinosus</i>              | 3           | 3           | 12          | 5           | 6           | 4           | 1           | 6           |
| 2  | <b><i>Bdeogale crassicauda</i></b>     | <b>126</b>  | <b>267</b>  | <b>259</b>  | <b>259</b>  | <b>336</b>  | <b>304</b>  | <b>289</b>  | <b>341</b>  |
| 3  | <b><i>Cephalophus harveyi</i></b>      | <b>281</b>  | <b>197</b>  | <b>228</b>  | <b>260</b>  | <b>290</b>  | <b>344</b>  | <b>293</b>  | <b>356</b>  |
| 4  | <b><i>Cephalophus spadix</i></b>       | <b>59</b>   | <b>51</b>   | <b>50</b>   | <b>29</b>   | <b>50</b>   | <b>51</b>   | <b>50</b>   | <b>72</b>   |
| 5  | <b><i>Cercocebus sanjei</i></b>        | <b>71</b>   | <b>95</b>   | <b>113</b>  | <b>142</b>  | <b>124</b>  | <b>142</b>  | <b>136</b>  | <b>130</b>  |
| 6  | <i>Cercopithecus mitis</i>             | 21          | 9           | 12          | 21          | 18          | 26          | 27          | 41          |
| 7  | <i>Civettictis civetta</i>             | 1           | 0           | 0           | 0           | 0           | 0           | 1           | 0           |
| 8  | <i>Colobus angolensis</i>              | 1           | 2           | 1           | 2           | 3           | 1           | 3           | 1           |
| 9  | <b><i>Cricetomys gambianus</i></b>     | <b>215</b>  | <b>293</b>  | <b>301</b>  | <b>267</b>  | <b>334</b>  | <b>405</b>  | <b>328</b>  | <b>333</b>  |
| 10 | <i>Crocota crocuta</i>                 | 0           | 3           | 2           | 0           | 0           | 0           | 0           | 0           |
| 11 | <i>Dendrohyrax validus</i>             | 23          | 39          | 34          | 48          | 51          | 31          | 48          | 55          |
| 12 | <b><i>Genetta servalina</i></b>        | <b>18</b>   | <b>60</b>   | <b>51</b>   | <b>57</b>   | <b>36</b>   | <b>64</b>   | <b>41</b>   | <b>52</b>   |
| 13 | <i>Hystrix africaeaustralis</i>        | 10          | 1           | 0           | 2           | 0           | 2           | 4           | 0           |
| 14 | <i>Leptailurus serval</i>              | 0           | 0           | 1           | 0           | 0           | 0           | 0           | 0           |
| 15 | <i>Loxodonta africana</i>              | 10          | 5           | 7           | 12          | 9           | 5           | 7           | 6           |
| 16 | <i>Mellivora capensis</i>              | 6           | 6           | 7           | 13          | 11          | 9           | 16          | 24          |
| 17 | <i>Mungos mungo</i>                    | 2           | 7           | 1           | 0           | 2           | 9           | 2           | 1           |
| 18 | <i>Nandinia binotata</i>               | 2           | 7           | 9           | 11          | 9           | 6           | 12          | 20          |
| 19 | <b><i>Nesotragus moschatus</i></b>     | <b>97</b>   | <b>113</b>  | <b>79</b>   | <b>77</b>   | <b>136</b>  | <b>155</b>  | <b>89</b>   | <b>123</b>  |
| 20 | <i>Orycteropus afer</i>                | 0           | 0           | 0           | 0           | 0           | 0           | 0           | 2           |
| 21 | <i>Panthera pardus</i>                 | 8           | 2           | 7           | 6           | 3           | 4           | 2           | 3           |
| 22 | <i>Papio cynocephalus</i>              | 3           | 0           | 2           | 0           | 1           | 3           | 1           | 3           |
| 23 | <i>Paraxerus vexillarius</i>           | 46          | 57          | 55          | 38          | 55          | 69          | 38          | 73          |
| 24 | <i>Petrodromus tetradactylus</i>       | 2           | 6           | 29          | 11          | 10          | 1           | 16          | 4           |
| 25 | <i>Potamochoerus larvatus</i>          | 18          | 23          | 16          | 21          | 24          | 42          | 23          | 30          |
| 26 | <i>Procolobus gordonorum</i>           | 5           | 2           | 8           | 2           | 3           | 2           | 10          | 10          |
| 27 | <i>Rhynchocyon cirnei</i>              | 4           | 3           | 8           | 0           | 1           | 6           | 5           | 4           |
| 28 | <b><i>Rhynchocyon udzungwensis</i></b> | <b>45</b>   | <b>74</b>   | <b>81</b>   | <b>57</b>   | <b>65</b>   | <b>50</b>   | <b>53</b>   | <b>46</b>   |

|    |                                |   |   |   |   |   |   |   |   |
|----|--------------------------------|---|---|---|---|---|---|---|---|
| 29 | <i>Syncerus caffer</i>         | 4 | 4 | 3 | 3 | 7 | 1 | 4 | 0 |
| 30 | <i>Thryonomys swinderianus</i> | 0 | 0 | 2 | 4 | 1 | 1 | 0 | 0 |
| 31 | <i>Tragelaphus scriptus</i>    | 0 | 4 | 2 | 7 | 2 | 3 | 7 | 7 |

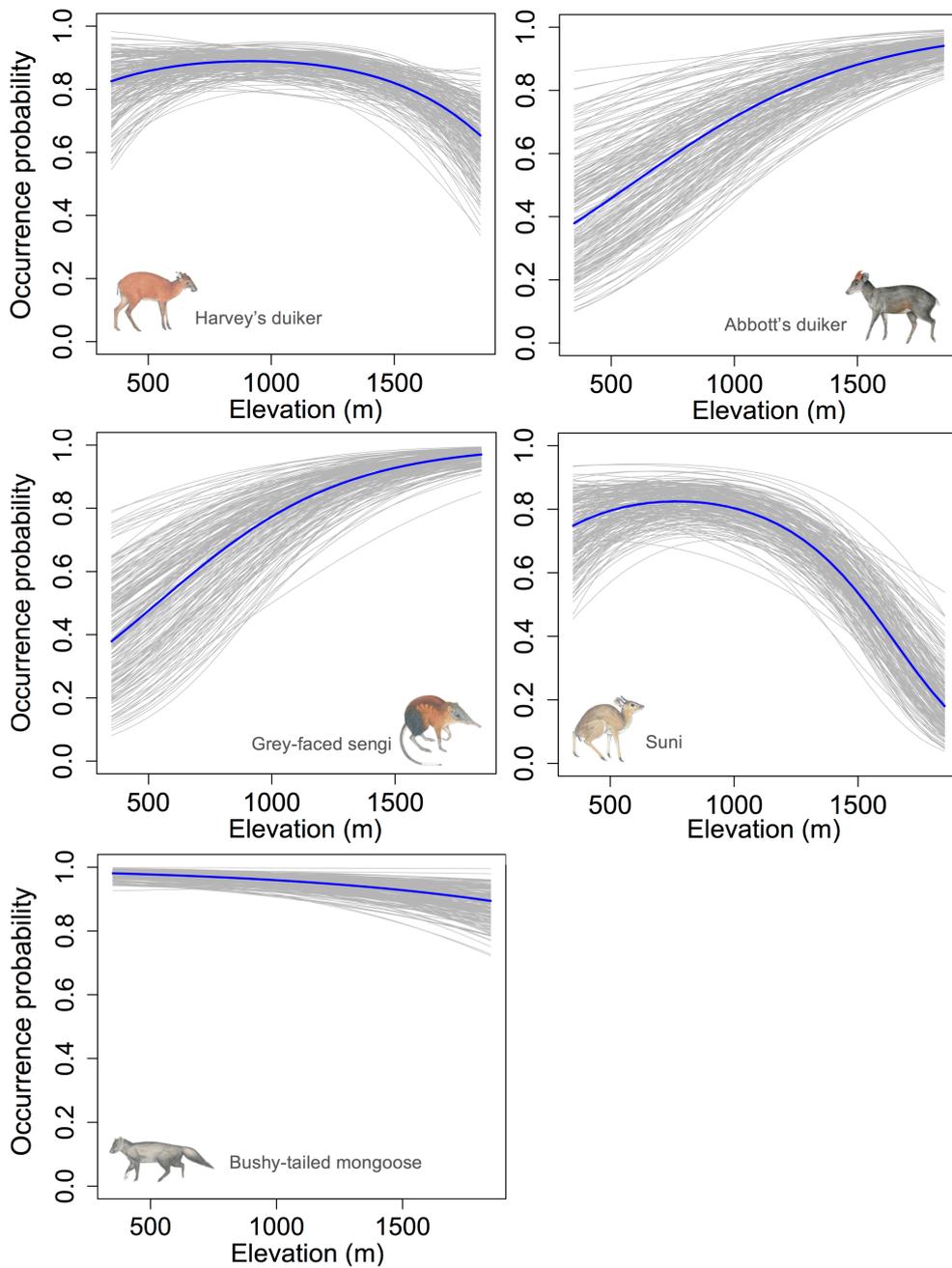
**Table C.2.** Posterior parameter estimates (mean  $\pm$  SD, and 95% Bayesian credible interval quantiles, BCI) for the  $\alpha$  and  $\beta$  coefficients (logit scale) from the single-species occupancy models of forest mammals in Mwanihana forest, Udzungwa Mountains of Tanzania. Asterisks indicates no overlap of the 95% BCIs with zero.

| Species                 | Parameter     | Mean ( $\pm$ SD)      | 95% BCI               |                 |
|-------------------------|---------------|-----------------------|-----------------------|-----------------|
| <b>Harvey's duiker</b>  | $\alpha_0$    | 0.896 ( $\pm$ 0.377)  | 0.184 – 1.658         |                 |
|                         | $\alpha_1$    | 1.090 ( $\pm$ 0.334)  | 0.429 – 1.730         |                 |
|                         | $\alpha_S$    | -0.485 ( $\pm$ 0.140) | -0.762 – -0.212       | *               |
|                         | $\alpha_E$    | -0.301 ( $\pm$ 0.139) | -0.581 – -0.037       | *               |
|                         | $\alpha_{E2}$ | -0.235 ( $\pm$ 0.130) | -0.485 – 0.027        |                 |
|                         | $\alpha_B$    | 0.246 ( $\pm$ 0.303)  | -0.358 – 0.828        |                 |
|                         | $\alpha_2$    | 2.067 ( $\pm$ 0.420)  | 1.297 – 2.941         |                 |
|                         | $\beta_0$     | -0.140 ( $\pm$ 0.041) | -0.221 – -0.061       |                 |
|                         | $\beta_B$     | 0.138 ( $\pm$ 0.041)  | 0.059 – 0.218         | *               |
| <b>Grey-faced sengi</b> | $\alpha_0$    | -2.385 ( $\pm$ 0.415) | -3.253 – -1.618       |                 |
|                         | $\alpha_1$    | 4.031 ( $\pm$ 0.461)  | 3.175 – 4.984         |                 |
|                         | $\alpha_E$    | 0.998 ( $\pm$ 0.213)  | 0.604 – 1.438         | *               |
|                         | $\alpha_{E2}$ | -0.184 ( $\pm$ 0.195) | -0.580 – 0.190        |                 |
|                         | $\alpha_B$    | -0.409 ( $\pm$ 0.427) | -1.261 – 0.418        |                 |
|                         | $\alpha_2$    | -0.982 ( $\pm$ 0.362) | -1.692 – -0.272       |                 |
|                         | $\beta_0$     | -0.686 ( $\pm$ 0.085) | -0.853 – -0.522       |                 |
|                         | $\beta_B$     | 0.276 ( $\pm$ 0.100)  | 0.082 – 0.470         | *               |
|                         | Suni          | $\alpha_0$            | -1.436 ( $\pm$ 0.323) | -2.093 – -0.828 |
| $\alpha_1$              |               | 2.591 ( $\pm$ 0.325)  | 1.982 – 3.251         |                 |
| $\alpha_S$              |               | 0.013 ( $\pm$ 0.122)  | -0.229 – 0.256        |                 |
| $\alpha_E$              |               | -0.766 ( $\pm$ 0.153) | -1.069 – -0.472       | *               |
| $\alpha_{E2}$           |               | -0.372 ( $\pm$ 0.142) | -0.656 – -0.100       | *               |
| $\alpha_B$              |               | 0.485 ( $\pm$ 0.303)  | -0.094 – 1.086        | (*)             |
| $\alpha_2$              |               | 0.148 ( $\pm$ 0.312)  | -0.462 – 0.763        |                 |
| $\beta_0$               |               | -0.486 ( $\pm$ 0.063) | -0.610 – -0.365       |                 |
| $\beta_B$               |               | -0.122 ( $\pm$ 0.066) | -0.251 – 0.004        |                 |
| <b>Sanje mangabey</b>   | $\alpha_0$    | 1.114 ( $\pm$ 0.378)  | 0.405 – 1.894         |                 |
|                         | $\alpha_1$    | 1.422 ( $\pm$ 0.421)  | 0.641 – 2.297         |                 |
|                         | $\alpha_S$    | 0.263 ( $\pm$ 0.144)  | -0.011 – 0.550        |                 |
|                         | $\alpha_E$    | 0.135 ( $\pm$ 0.130)  | -0.116 – 0.392        |                 |
|                         | $\alpha_{E2}$ | -0.535 ( $\pm$ 0.134) | -0.802 – -0.273       |                 |
|                         | $\alpha_B$    | -0.170 ( $\pm$ 0.361) | -0.919 – 0.508        |                 |
|                         | $\alpha_2$    | 0.705 ( $\pm$ 0.326)  | 0.084 – 1.362         |                 |
|                         | $\beta_0$     | -0.777 ( $\pm$ 0.051) | -0.878 – -0.678       |                 |

|                                  |               |                        |                 |   |
|----------------------------------|---------------|------------------------|-----------------|---|
|                                  | $\beta_B$     | -0.022 ( $\pm 0.051$ ) | -0.120 – 0.079  |   |
| <b>Giant pouched rat</b>         | $\alpha_0$    | 0.347 ( $\pm 0.288$ )  | -0.208 – 0.926  |   |
|                                  | $\alpha_1$    | 1.950 ( $\pm 0.266$ )  | 1.443 – 2.476   |   |
|                                  | $\alpha_S$    | 0.045 ( $\pm 0.117$ )  | -0.181 – 0.273  |   |
|                                  | $\alpha_E$    | 0.096 ( $\pm 0.125$ )  | -0.145 – 0.342  |   |
|                                  | $\alpha_{E2}$ | 0.126 ( $\pm 0.119$ )  | -0.104 – 0.362  |   |
|                                  | $\alpha_B$    | -0.892 ( $\pm 0.302$ ) | -1.504 – -0.318 | * |
|                                  | $\alpha_2$    | 0.008 ( $\pm 0.283$ )  | -0.548 – 0.563  |   |
|                                  | $\beta_0$     | 0.199 ( $\pm 0.043$ )  | 0.115 – 0.285   |   |
|                                  | $\beta_B$     | 0.172 ( $\pm 0.044$ )  | 0.086 – 0.259   | * |
| <b>Bushy-tailed<br/>mongoose</b> | $\alpha_0$    | 2.120 ( $\pm 0.545$ )  | 1.146 – 3.282   |   |
|                                  | $\alpha_1$    | 0.846 ( $\pm 0.454$ )  | -0.067 – 1.691  |   |
|                                  | $\alpha_S$    | 0.137 ( $\pm 0.155$ )  | -0.165 – 0.444  |   |
|                                  | $\alpha_E$    | -0.452 ( $\pm 0.163$ ) | -0.778 – -0.139 | * |
|                                  | $\alpha_{E2}$ | -0.131 ( $\pm 0.150$ ) | -0.418 – 0.173  |   |
|                                  | $\alpha_B$    | -0.721 ( $\pm 0.434$ ) | -1.635 – 0.069  |   |
|                                  | $\alpha_2$    | 1.209 ( $\pm 0.342$ )  | 0.560 – 1.907   |   |
|                                  | $\beta_0$     | -0.095 ( $\pm 0.040$ ) | -0.173 – -0.017 |   |
|                                  | $\beta_B$     | -0.215 ( $\pm 0.040$ ) | -0.291 – -0.135 | * |
| <b>Abbott's duiker</b>           | $\alpha_0$    | 0.405 ( $\pm 0.574$ )  | -0.603 – 1.676  |   |
|                                  | $\alpha_1$    | 0.856 ( $\pm 0.702$ )  | -0.522 – 2.275  |   |
|                                  | $\alpha_S$    | 0.032 ( $\pm 0.184$ )  | -0.329 – 0.395  |   |
|                                  | $\alpha_E$    | 0.819 ( $\pm 0.245$ )  | 0.400 – 1.357   | * |
|                                  | $\alpha_{E2}$ | -0.226 ( $\pm 0.171$ ) | -0.566 – 0.104  |   |
|                                  | $\alpha_B$    | -0.222 ( $\pm 0.416$ ) | -1.084 – 0.563  |   |
|                                  | $\alpha_2$    | 1.038 ( $\pm 0.615$ )  | 0.025 – 2.462   |   |
|                                  | $\beta_0$     | -1.728 ( $\pm 0.108$ ) | -1.940 – -1.522 |   |
|                                  | $\beta_B$     | 0.440 ( $\pm 0.101$ )  | 0.245 – 0.637   | * |
| <b>Lowe's genet</b>              | $\alpha_0$    | -0.249 ( $\pm 0.303$ ) | -0.835 – 0.363  |   |
|                                  | $\alpha_1$    | 1.339 ( $\pm 0.380$ )  | 0.635 – 2.119   |   |
|                                  | $\alpha_S$    | 0.144 ( $\pm 0.129$ )  | -0.106 – 0.404  |   |
|                                  | $\alpha_E$    | 0.003 ( $\pm 0.155$ )  | -0.314 – 0.298  |   |
|                                  | $\alpha_{E2}$ | 0.062 ( $\pm 0.126$ )  | -0.180 – 0.315  |   |
|                                  | $\alpha_B$    | -0.493 ( $\pm 0.304$ ) | -1.114 – 0.079  |   |
|                                  | $\alpha_2$    | -0.678 ( $\pm 0.366$ ) | -1.402 – 0.042  |   |
|                                  | $\beta_0$     | -1.493 ( $\pm 0.095$ ) | -1.680 – -1.312 |   |
|                                  | $\beta_B$     | 0.338 ( $\pm 0.111$ )  | 0.119 – 0.556   | * |

( $\alpha_0 + \alpha_1$ )= intercept of occupancy;  $\alpha_S$ =effect of the number of snares on occupancy;  $\alpha_E$ =effect of elevation on occupancy;  $\alpha_{E2}$ =effect of the square term of elevation on occupancy;  $\alpha_B$ =effect of the firewood collection ban on occupancy;  $\alpha_2$ = intercept for occupancy in the first year;  $\beta_0$ = intercept of detection probability;  $\beta_B$ = effect of the distance from park border on detection probability.

**Figure C.3.** Significant effects of elevation on occupancy for the species camera-trapped in Mwanihana forest, Tanzania. Drawings by J. Kingdon reproduced with permission.



**Supplementary material C.4.** R and JAGS code for the single-species occupancy model fitted to the detection/non-detection data of eight mammal species. As an example, we provide the script for the Harvey's duiker (below).

```
# load data
# y_harvey: 3D matrix with the detection history for the Harvey's duiker, for
each site i in sampling occasion j during year k
```

```

# snares_std: standardized number of snares collected in each site i (array)
during year k (year-site covariate)
# elev: standardized elevation (site covariate)
# elev2: standardized square term of elevation (site covariate)
# border: standardized distance from park border (site covariate)
# ban_35: binary covariate for the firewood collection activity status in each
year k (year covariate)

modelFilename = "Harvey.txt"
cat("
  model {

    ## specify priors
    # Intercept psi_y1
    alpha6 <- log(mean.psi_y1/(1-mean.psi_y1))
    mean.psi_y1 ~ dunif(0,1)

    # Intercept psi_yy
    alpha0 <- log(mean.psi_yy/(1-mean.psi_yy))
    mean.psi_yy ~ dunif(0,1)

    # Intercept p
    beta0 <- log(mean.p/(1-mean.p))
    mean.p ~ dunif(0,1)

    # occupancy
    alpha1 ~ dnorm(0,0.01)
    alpha2 ~ dnorm(0,0.01)
    alpha3 ~ dnorm(0,0.01)
    alpha4 ~ dnorm(0,0.01)
    alpha5 ~ dnorm(0,0.01)

    # detection
    beta1 ~ dnorm(0,0.01)

    ##ecological submodel
    for(i in 1:nsite){

      z[i,1] ~ dbern(psi[i,1])

      logit(psi[i,1]) <- alpha6 + alpha2 * snares_std[i,1] + alpha3 * elev[i] +
alpha4 * elev2[i]

      for(k in 2:nyear){
        z[i,k] ~ dbern(psi[i,k])
      }

      for(i in 1:nsite){
        for(k in 2:(nyear)){
          logit(psi[i,k]) <- alpha0 + alpha1 * z[i,k-1] + alpha2 *snares_std[i,k] +
alpha3 * elev[i] + alpha4 * elev2[i]
          + alpha5 * ban_35[k]
        }
      }

    # observational model
    for(i in 1:nsite){
      for(j in 1:nrep){
        for(k in 1:nyear){

```

```

muy[i,j,k] <- z[i,k]*p[i]

y[i,j,k] ~ dbern(muy[i,j,k])
} } }

for(i in 1:nsite){
logit(p[i]) <- beta0 + beta1 * border[i] }

## derived parameters
n.occ[1]<- sum(z[1:nsite,1])
p_mean<-mean(p[])

for(k in 2:nyear){
n.occ[k] <- sum(z[1:nsite,k])
}

for(k in 1:nyear){
psi_year[k]<-mean(psi[,k])
} }
## end model
", fill=TRUE, file=modelFilename)

# data for JAGS
bugs.data <- list(y=y, nsite=dim(y)[1], nrep=dim(y)[2], nyear=dim(y)[3],
elev=elev, elev2=elev2, border=border, snares_std=snares_std, ban_35=ban_35)

## parameters to monitor
params <-
c("psi_year","n.occ","p_mean","alpha0","alpha1","alpha2","alpha3","alpha4","alpha5",
"alpha6","beta0","beta1","mean.psi_y1","mean.psi_yy","mean.p")

## inits
zst <- apply(y_harvey, c(1, 3), sum, na.rm=T)
zsti<-ifelse(zst>0,1,0)

jags.inits <- function(){ list(z = zsti,
mean.psi_y1=runif(1,0,1),
mean.psi_yy=runif(1,0,1), mean.p=runif(1,0,1),
alpha1 = runif(1, -3, 3), alpha2 = runif(1, -3,
3), alpha3 = runif(1, -3, 3),
alpha4 = runif(1, -3, 3), alpha5 = runif(1, -3, 3), beta1 =
runif(1, -3, 3) )}

# MCMC settings
n.adapt <- 1000
n.burnin <- 5000
n.iter <- 100000
n.thin <- 20
n.chains <- 3
start.time = Sys.time()

## adaptive phase to maximise MCMC efficiency
out_harvey_final <- jags(data = bugs.data,
inits=jags.inits,
params,
"Harvey.txt",
n.chains=n.chains,
n.adapt=n.adapt,

```

```
        n.thin=n.thin,  
        n.iter=n.iter,  
        n.burnin=n.burnin)  
  
end.time = Sys.time()  
elapsed.time = round(difftime(end.time, start.time, units='mins'),2)  
cat(paste(paste('Posterior computed in ', elapsed.time, sep=' '), 'minutes\n',  
sep=' '))  
  
#### END
```



## Appendix D. Poor management in protected areas is associated with lowered tropical mammal diversity

**Supplementary material D.1.** R and JAGS code for the multi-region community model fitted to detection/non-detection data.

```
#load data
#M: total number of species in the augmented dataset
#yaug: 3D matrix with the total number of detections for the ith species, in
site j of region r during the entire sampling period
#nsite: number of sites sampled in each region r
#nspec: number of observed species in each region r
#guild: trophic guild for the ith species of region r (1= carnivore; 2=
herbivore; 3= insectivore; 4= omnivore)
#K_tot: total number of sampling occasions in site j of region r
#Elev: standardized elevation (site-region covariate)
#Elev2: standardized square term of elevation (site-region covariate)
#Bord: standardized distance from park/reserve border (site-region covariate)
#Model: binary covariate for the camera trap type used at each site j in
region r (site-region covariate)

# model
modelFilename = "multiregion.txt"
cat("
  model {
    ##Priors
for (r in 1:nreg) {
  omega[r] <- min(0.999,max(0.001,sum(lambda[r,])/M))  }

  for (r in 1:nreg){
# community mean occupancy
b[r] <- log(psi.mean[r]) - log(1 - psi.mean[r]) ## logit(psi.mean)
psi.mean[r] ~ dunif(0,1)
tau.psi[r] <- pow(sigma.psi[r],-2)
sigma.psi[r] ~ dunif(0,7)

# community mean detectability
a[r] <- log(p.mean[r]) - log(1 - p.mean[r])  ## logit(p.mean)
p.mean[r] ~ dunif(0,1)
tau.p[r] <- pow(sigma.p[r],-2)
sigma.p[r] ~ dunif(0,7) # dunif(0,10)
var.p[r] <- tau.p[r]/(1.-pow(rho[r],2))

# correlation coefficient
rho[r] ~ dunif(-1,1)
}
}
```

```

# prior for betal.psi (Elevation) on psi
for (i in 1:M){
  for (r in 1:nreg){
    betal.psi[i,r] ~ dnorm(mu.betal.psi[r],tau.betal.psi[r])
  }

  for (r in 1:nreg){
    mu.betal.psi[r] ~ dnorm(0,0.01)
    tau.betal.psi[r] <- pow(sigma.betal.psi[r],-2)
    sigma.betal.psi[r] ~ dunif(0,7) # dunif(0,10)
  }

  # prior for beta2.psi (Elevation2) on psi
for (i in 1:M){
  for (r in 1:nreg){
    beta2.psi[i,r] ~ dnorm(mu.beta2.psi[r],tau.beta2.psi[r])
  }

  for (r in 1:nreg){
    mu.beta2.psi[r] ~ dnorm(0,0.01)
    tau.beta2.psi[r] <- pow(sigma.beta2.psi[r],-2)
    sigma.beta2.psi[r] ~ dunif(0,7) # dunif(0,10)
  }

  # prior for betal.p (Border) on p
  for (i in 1:M){
    for (r in 1:nreg){
      betal.p[i,r] ~ dnorm(mu.betal.p[r],tau.betal.p[r])
    }

    for (r in 1:nreg){
      mu.betal.p[r] ~ dnorm(0,0.01)
      tau.betal.p[r] <- pow(sigma.betal.p[r],-2)
      sigma.betal.p[r] ~ dunif(0,7) # dunif(0,10)
    }

    ## prior for beta2.p constant
    beta2.p ~ dnorm(0,0.01)

    ## model for region- and guild-specific species richness
    for (r in 1:nreg){
      for (g in 1:nguild){
        log(lambda[r,g]) <- mu.lambda[r,g]
        pi[r,g] <- lambda[r,g]/sum(lambda[r,])
        mu.lambda[r,g] ~ dunif(-5,5)
      }

      ## Likelihood
      for (i in 1:M){
        for (r in 1:nreg) {

          # state process
          w[i,r] ~ dbern(omega[r])
          is.censored.alpha.psi[i,r] ~ dinterval(alpha.psi[i,r], lim[])
          is.censored.alpha.p[i,r] ~ dinterval(alpha.p[i,r], lim[])
          alpha.psi[i,r] ~ dnorm(b[r],tau.psi[r]) ## intercept for occupancy
          alpha.p[i,r] ~ dnorm(mu.p[i,r],var.p[r]) ## intercept for detectability
        }
      }
    }
  }
}

```

```

mu.p[i,r] <- a[r] + (rho[r]*sigma.p[r]/sigma.psi[r])*(alpha.psi[i,r] -
b[r])

## occupancy
for (j in 1:nsite[r]){
  logit(psi[i,j,r]) <- alpha.psi[i,r] + beta1.psi[i,r] * Elev[j,r] +
beta2.psi[i,r] * Elev2[j,r]
  Z[i,j,r] ~ dbern(psi[i,j,r] * w[i,r])

## observation process
logit(p[i,j,r]) <- alpha.p[i,r] + beta1.p[i,r] * Bord[j,r] + beta2.p *
Model[j,r]
Y[i,j,r] ~ dbin(p[i,j,r]*Z[i,j,r],K[j,r]) }

guild[i,r] ~ dcat(pi[r,1:nguild])
} }

## derived parameters
for (r in 1:nreg){
  N[r] <- sum(w[,r])
}
## mean occupancy and detection probability for each observed species

for(r in 1:nreg){
  for(i in 1:nspec[r]){
    logit(alpha.psi.species[i,r]) <- alpha.psi[i,r]
    logit(alpha.p.species[i,r]) <- alpha.p[i,r]
  } } }
## end model
", fill=TRUE, file=modelFilename)

# data for JAGS
nguild <- 4
nreg <- dim(yaug)[3]
w <- matrix(NA,M,nreg)
for (r in 1:nreg){
  w[,r] <- c(rep(1, nspec[r]),rep(NA,M-nspec[r]))
}

bugs.data <- list(M=M, nsite=nsite, nreg=nreg,K=K_tot,Y=yaug,
  is.censored.alpha.psi=matrix(1,nrow=M,ncol=nreg),
  is.censored.alpha.p=matrix(1,nrow=M,ncol=nreg),
  lim=c(-20,20), nguild=nguild, guild=guild,nspec=nspec,
Bord=Bord, Elev=Elev, Elev2=Elev2,
  Model=Model, w=w, Z=(yaug>0)*1)

## parameters to monitor
params <-
c("N","guild","w","psi.mean","sigma.psi","p.mean","sigma.p","rho","pi","lambda
","beta1.psi",
      "beta2.psi","mu.beta1.psi","sigma.beta1.psi",
"mu.beta2.psi","sigma.beta2.psi","beta1.p",
      "mu.beta1.p",
"sigma.beta1.p","beta2.p","alpha.psi.species","alpha.p.species")

## initial values
length(table(guild))
inits <- function(){
  list(rho=runif(nreg,0.5,0.8),

```

```

psi.mean=runif(nreg,0,1),
sigma.psi=runif(nreg,0,2),
p.mean=runif(nreg,0,1),
sigma.p=runif(nreg,0,2),
mu.beta1.psi=rnorm(nreg,-1,1),
sigma.beta1.psi=runif(nreg,0,2),
mu.beta2.psi=rnorm(nreg,-1,1),
sigma.beta2.psi=runif(nreg,0,2),
mu.beta1.p=rnorm(nreg,-1,1),
sigma.beta1.p=runif(nreg,0,2),
beta2.p=runif(1,-1,1),
mu.lambda=matrix(runif(nreg*nguild,1,3),nreg,nguild) )

# MCMC settings
n.adapt <- 1000
n.burnin <- 15000
n.iter <- 150000
n.thin <- 20
n.chains <- 3

start.time = Sys.time()

## adaptive phase to maximise MCMC efficiency
out_updated_5days <- jags(data = bugs.data,
  inits=inits,
  params,
  "multiregion.txt",
  n.chains=n.chains,
  n.adapt=n.adapt,
  n.thin=n.thin,
  n.iter=n.iter,
  n.burnin=n.burnin)

end.time = Sys.time()

elapsed.time = round(difftime(end.time, start.time, units='mins'),2)
cat(paste(paste('Posterior computed in ', elapsed.time, sep=' '), 'minutes\n',
  sep=' '))

#### End of script

```

**Table D.2.** Medium-to-large mammals detected by camera trapping in Mwanihana and/or Uzungwa Scarp, with body mass (kg), functional guild and naïve occupancy (n. of occupied sites divided by total n. of sites), by increasing body mass.

|           |                    |                                  | <b>Mass</b> | <b>Functional</b> | <b>Naïve</b>     |           |
|-----------|--------------------|----------------------------------|-------------|-------------------|------------------|-----------|
|           |                    |                                  | <b>(kg)</b> | <b>guild</b>      | <b>occupancy</b> |           |
| <b>##</b> | <b>Common name</b> | <b>Latin name</b>                |             |                   | <b>MW</b>        | <b>US</b> |
| 1         | Four-toed sengi    | <i>Petrodromus tetradactylus</i> | 0.1875      | Insectivore       | 0.05             | 0.00      |
| 2         | Checkered sengi    | <i>Rhynchocyon cirnei</i>        | 0.4900      | Insectivore       | 0.03             | 0.31      |

|    |                              |                                 |           |             |      |      |
|----|------------------------------|---------------------------------|-----------|-------------|------|------|
| 3  | Tanganyika mountain squirrel | <i>Paraxerus vexillarius</i>    | 0.6750    | Herbivore   | 0.25 | 0.26 |
| 4  | Grey-faced sengi             | <i>Rhynchocyon udzungwensis</i> | 0.7500    | Insectivore | 0.25 | 0.00 |
| 5  | Lowe's genet                 | <i>Genetta servalina lowei</i>  | 1.0550    | Carnivore   | 0.40 | 0.33 |
| 6  | Giant pouched rat            | <i>Cricetomys gambianus</i>     | 1.2850    | Omnivore    | 0.68 | 0.80 |
| 7  | Bushy-tailed mongoose        | <i>Bdeogale crassicauda</i>     | 1.5000    | Carnivore   | 0.83 | 0.41 |
| 8  | Banded mongoose              | <i>Mungos mungo</i>             | 1.9250    | Insectivore | 0.02 | 0.02 |
| 9  | African palm civet           | <i>Nandinia binotata</i>        | 2.0000    | Omnivore    | 0.15 | 0.11 |
| 10 | Tree hyrax                   | <i>Dendrohyrax validus</i>      | 2.4300    | Herbivore   | 0.33 | 0.07 |
| 11 | Marsh mongoose               | <i>Atilax paludinosus</i>       | 3.3000    | Carnivore   | 0.08 | 0.00 |
| 12 | Greater cane rat             | <i>Thrynomys swinderianus</i>   | 4.0600    | Herbivore   | 0.00 | 0.02 |
| 13 | Sykes' monkey                | <i>Cercopithecus mitis</i>      | 5.0000    | Herbivore   | 0.32 | 0.13 |
| 14 | Blue duiker                  | <i>Philatomba monticola</i>     | 6.2500    | Herbivore   | 0.00 | 0.22 |
| 15 | Suni                         | <i>Nesotragus moschatus</i>     | 6.4999    | Herbivore   | 0.47 | 0.39 |
| 16 | Sanje mangabey               | <i>Cercocebus sanjei</i>        | 8.0000    | Herbivore   | 0.72 | 0.31 |
| 17 | Honey badger                 | <i>Mellivora capensis</i>       | 9.0000    | Carnivore   | 0.27 | 0.04 |
| 18 | Black-and-white colobus      | <i>Colobus angolensis</i>       | 9.8500    | Herbivore   | 0.02 | 0.00 |
| 19 | Udzungwa red colobus         | <i>Procolobus gordonorum</i>    | 10.0000   | Herbivore   | 0.15 | 0.00 |
| 20 | Harvey's duiker              | <i>Cephalophus harveyi</i>      | 14.5001   | Herbivore   | 0.85 | 0.52 |
| 21 | Yellow baboon                | <i>Papio cynocephalus</i>       | 18.4000   | Omnivore    | 0.05 | 0.05 |
| 22 | Bushbuck                     | <i>Tragelaphus scriptus</i>     | 43.2504   | Herbivore   | 0.08 | 0.04 |
| 23 | Aardvark                     | <i>Orycteropus afer</i>         | 52.3504   | Insectivore | 0.02 | 0.00 |
| 24 | Leopard                      | <i>Panthera pardus</i>          | 54.9997   | Carnivore   | 0.05 | 0.00 |
| 25 | Abbott's duiker              | <i>Cephalophus spadix</i>       | 56.0003   | Herbivore   | 0.55 | 0.09 |
| 26 | Bush pig                     | <i>Potamochoerus larvatus</i>   | 97.5000   | Omnivore    | 0.27 | 0.13 |
| 27 | African elephant             | <i>Loxodonta africana</i>       | 3940.0343 | Herbivore   | 0.07 | 0.00 |

**Table D.3.** Summary of posterior parameter estimates from the multi-region community occupancy model fitted to the mammalian community data from two regions.  $N_r$  is the total species richness for each region  $r$  (with  $r = MW$  for Mwanihana or  $US$  for Uzungwa Scarp);  $\mu_{p,r}$  and  $\sigma_{p,r}$  are the region-specific mean and standard deviation for the species-specific intercepts of occurrence probability;  $\mu_{p,r}$  and  $\sigma_{p,r}$  are the

region-specific mean and standard deviation for the species-specific random intercepts of detection probability;  $\rho_r$  is the region-specific coefficient for the correlation between occupancy and detection probabilities;  $\pi_{r,g}$  is the proportion of species belonging to functional guild  $g$  (with  $g = \text{CARN}$  for carnivores,  $\text{HERB}$  for herbivores,  $\text{INS}$  for insectivores and  $\text{OMN}$  for omnivores) in each region;  $\lambda_{r,g}$  is the expected number of species in each functional guild and region. Mean ( $\mu_x$ ) and standard deviation ( $\sigma_x$ ) for each species- and region-specific random slopes ( $x=\{\alpha_1, \alpha_2, \beta_1\}$ ) are also reported, where  $\alpha_1$  is the coefficient for the effect of elevation on occurrence probability,  $\alpha_2$  is the coefficient for the effect of the square term of elevation on occurrence probability and  $\beta_1$  is the effect of the distance from forest border on detection probability.  $\beta_2$  is the coefficient for the effect of the type of camera trap used on detection probability. Mean of the random intercepts are given in probability scale, standard deviations and mean of the random slopes are in logit scale.

| <b>Parameter</b>   | <b>Mean</b> | <b>SD</b> | <b>2.5%</b> | <b>50%</b> | <b>97.5%</b> |
|--------------------|-------------|-----------|-------------|------------|--------------|
| $N_{MW}$           | 29.036      | 3.810     | 25.000      | 28.000     | 39.000       |
| $N_{US}$           | 21.789      | 3.092     | 19.000      | 21.000     | 30.000       |
| $\mu_{\psi,MW}$    | 0.138       | 0.066     | 0.032       | 0.131      | 0.285        |
| $\mu_{\psi,US}$    | 0.118       | 0.055     | 0.027       | 0.112      | 0.244        |
| $\sigma_{\psi,MW}$ | 2.303       | 0.510     | 1.530       | 2.230      | 3.505        |
| $\sigma_{\psi,US}$ | 1.939       | 0.537     | 1.178       | 1.843      | 3.216        |
| $\mu_{p,MW}$       | 0.242       | 0.039     | 0.163       | 0.243      | 0.315        |
| $\mu_{p,US}$       | 0.169       | 0.029     | 0.113       | 0.169      | 0.228        |
| $\sigma_{p,MW}$    | 0.816       | 0.174     | 0.542       | 0.794      | 1.219        |
| $\sigma_{p,US}$    | 0.612       | 0.172     | 0.362       | 0.585      | 1.024        |
| $Q_{MW}$           | 0.847       | 0.096     | 0.598       | 0.869      | 0.964        |
| $Q_{US}$           | 0.783       | 0.176     | 0.317       | 0.833      | 0.979        |
| $\pi_{MW,CARN}$    | 0.200       | 0.079     | 0.071       | 0.192      | 0.375        |
| $\pi_{US,CARN}$    | 0.158       | 0.082     | 0.036       | 0.146      | 0.348        |
| $\pi_{MW,HERB}$    | 0.439       | 0.098     | 0.255       | 0.438      | 0.632        |
| $\pi_{US,HERB}$    | 0.525       | 0.113     | 0.306       | 0.525      | 0.742        |
| $\pi_{MW,INS}$     | 0.200       | 0.079     | 0.072       | 0.192      | 0.378        |
| $\pi_{US,INS}$     | 0.105       | 0.069     | 0.014       | 0.091      | 0.275        |

|                        |        |       |        |        |        |
|------------------------|--------|-------|--------|--------|--------|
| $\pi_{MW,OMN}$         | 0.160  | 0.073 | 0.047  | 0.151  | 0.326  |
| $\pi_{US,OMN}$         | 0.211  | 0.092 | 0.064  | 0.200  | 0.417  |
| $\lambda_{MW,CARN}$    | 5.765  | 2.574 | 1.883  | 5.367  | 11.778 |
| $\lambda_{US,CARN}$    | 3.409  | 1.976 | 0.703  | 3.026  | 8.259  |
| $\lambda_{MW,HERB}$    | 12.647 | 3.840 | 6.329  | 12.251 | 21.336 |
| $\lambda_{US,HERB}$    | 11.330 | 3.693 | 5.369  | 10.886 | 19.802 |
| $\lambda_{MW,INS}$     | 5.765  | 2.569 | 1.891  | 5.358  | 11.854 |
| $\lambda_{US,INS}$     | 2.271  | 1.613 | 0.280  | 1.895  | 6.345  |
| $\lambda_{MW,OMN}$     | 4.616  | 2.332 | 1.269  | 4.212  | 10.236 |
| $\lambda_{US,OMN}$     | 4.554  | 2.291 | 1.264  | 4.189  | 10.046 |
| $\mu_{\alpha 1,MW}$    | 1.037  | 0.543 | -0.062 | 1.035  | 2.158  |
| $\mu_{\alpha 1,US}$    | -0.110 | 0.232 | -0.559 | -0.112 | 0.351  |
| $\sigma_{\alpha 1,MW}$ | 0.597  | 0.292 | 0.048  | 0.614  | 1.152  |
| $\sigma_{\alpha 1,US}$ | 0.881  | 0.218 | 0.535  | 0.854  | 1.388  |
| $\mu_{\alpha 2,MW}$    | -1.138 | 0.549 | -2.268 | -1.136 | -0.014 |
| $\mu_{\alpha 2,US}$    | 0.180  | 0.101 | -0.024 | 0.181  | 0.370  |
| $\sigma_{\alpha 2,MW}$ | 0.530  | 0.286 | 0.030  | 0.541  | 1.089  |
| $\sigma_{\alpha 2,US}$ | 0.105  | 0.089 | 0.002  | 0.084  | 0.327  |
| $\mu_{\beta 1,MW}$     | 0.067  | 0.055 | -0.048 | 0.069  | 0.169  |
| $\mu_{\beta 1,US}$     | 0.037  | 0.086 | -0.124 | 0.035  | 0.214  |
| $\sigma_{\beta 1,MW}$  | 0.090  | 0.066 | 0.003  | 0.079  | 0.246  |
| $\sigma_{\beta 1,US}$  | 0.146  | 0.108 | 0.007  | 0.127  | 0.399  |
| $\beta 2$              | 0.442  | 0.130 | 0.188  | 0.441  | 0.701  |

---



## Appendix E. Co-occurrence of snow leopard *Panthera uncia*, Siberian ibex *Capra sibirica* and livestock: potential relationships and effects

**Supplementary material E.1** Model formulation and parameter constraints applied to fit the two scenarios, and model fitting procedures

The latent binary variable  $z_j^i \sim \text{Bern}(\Psi_j^i)$ , with  $i = \{\text{LI,IB,SL}\}$  for livestock, ibex, and snow leopard, respectively, and probability of occurrence  $\Psi_j^i$ , indicates whether species  $i$  was present ( $z_j^i = 1$ ) or absent ( $z_j^i = 0$ ) from site  $j$  (with  $j = 1, \dots, J = 49$  camera trap stations). Livestock occurrence probability was modelled as a function of elevation ('elev'):

$$\text{logit}(\Psi_j^{\text{LI}}) = \beta_0^{\text{LI}} + \beta_{\text{elev}}^{\text{LI}} \text{elev}_j$$

where the average occurrence probability is  $\bar{\Psi}^{\text{LI}} = \text{expit}(\beta_0^{\text{LI}})$ , where expit is the inverse-logit function. Ibex occurrence was assumed to depend on the occurrence of livestock, with an additional effect of distance of site  $j$  to herders' houses and camps, as a proxy of anthropic disturbance ('dist'):

$$\text{logit}(\Psi_j^{\text{IB}}) = \beta_0^{\text{IB|LI}} z_j^{\text{LI}} + \beta_0^{\text{IB|\bar{LI}}} (1 - z_j^{\text{LI}}) + \beta_{\text{dist}}^{\text{IB}} \text{dist}_j$$

where  $\bar{\Psi}^{\text{IB|LI}} = \text{expit}(\beta_0^{\text{IB|LI}}) = \Pr(z_j^{\text{IB}} = 1 | z_j^{\text{LI}} = 1)$  is the conditional average probability of ibex occurrence given that livestock is present, and  $\bar{\Psi}^{\text{IB|\bar{LI}}} = \text{expit}(\beta_0^{\text{IB|\bar{LI}}}) = \Pr(z_j^{\text{IB}} = 1 | z_j^{\text{LI}} = 0)$  is the conditional average probability of ibex occurrence given that livestock is absent. The full linear predictor for snow leopard occurrence, i.e. the one that explicitly account for co-occurrence with both livestock and ibex, in addition to the effect of previous mentioned covariates, was as follows:

$$\begin{aligned} \text{logit}(\Psi_j^{\text{SL}}) = & \beta_0^{\text{SL|LI,IB}} z_j^{\text{LI}} z_j^{\text{IB}} + \beta_0^{\text{SL|\bar{LI},IB}} (1 - z_j^{\text{LI}}) z_j^{\text{IB}} + \\ & \beta_0^{\text{SL|LI,\bar{IB}}} z_j^{\text{LI}} (1 - z_j^{\text{IB}}) + \beta_0^{\text{SL|\bar{LI},\bar{IB}}} (1 - z_j^{\text{LI}}) (1 - z_j^{\text{IB}}) + \\ & \beta_{\text{elev}}^{\text{SL}} \text{elev}_j + \beta_{\text{dist}}^{\text{SL}} \text{dist}_j \end{aligned}$$

where  $\bar{\Psi}^{\text{SL|LI,IB}} = \text{expit}(\beta_0^{\text{SL|LI,IB}}) = \Pr(z_j^{\text{SL}} = 1 | z_j^{\text{LI}} = 1, z_j^{\text{IB}} = 1)$  is the conditional average probability of snow leopard occurrence given that livestock and ibex are present,  $\bar{\Psi}^{\text{SL|\bar{LI},IB}} = \text{expit}(\beta_0^{\text{SL|\bar{LI},IB}}) = \Pr(z_j^{\text{SL}} = 1 | z_j^{\text{LI}} = 0, z_j^{\text{IB}} = 1)$  is the conditional average probability of snow leopard occurrence given that livestock is absent and ibex is present,

$\bar{\psi}^{SL|LI,\bar{IB}} = \text{expit}(\beta_0^{SL|LI,\bar{IB}}) = \Pr(z_j^{SL} = 1 | z_j^{LI} = 1, z_j^{IB} = 0)$  is the conditional average probability of snow leopard occurrence given that livestock is present and ibex is absent, and  $\bar{\psi}^{SL|\bar{LI},\bar{IB}} = \text{expit}(\beta_0^{SL|\bar{LI},\bar{IB}}) = \Pr(z_j^{SL} = 1 | z_j^{LI} = 0, z_j^{IB} = 0)$  is the conditional average probability of snow leopard occurrence given that livestock and ibex are absent. The two scenarios were expressed by specifying the following constraints: (scenario 1) snow leopard occurrence depends on livestock occurrence only,  $\bar{\psi}^{SL|LI} = \bar{\psi}^{SL|LI,IB} = \bar{\psi}^{SL|LI,\bar{IB}}$  and  $\bar{\psi}^{SL|\bar{LI}} = \bar{\psi}^{SL|\bar{LI},IB} = \bar{\psi}^{SL|\bar{LI},\bar{IB}}$ ; (scenario 2) snow leopard occurrence depends on ibex occurrence only,  $\bar{\psi}^{SL|IB} = \bar{\psi}^{SL|LI,IB} = \bar{\psi}^{SL|\bar{LI},IB}$  and  $\bar{\psi}^{SL|\bar{IB}} = \bar{\psi}^{SL|LI,\bar{IB}} = \bar{\psi}^{SL|\bar{LI},\bar{IB}}$ .

In the encounter model, the observations were  $y_{jk}^i$ , for species  $i$ , site  $j$  and sampling occasion (day)  $k$ , with  $k = 1, \dots, K$  and  $K$  ranging from 25 to 68 days (median 46) between sites, where  $y_{jk}^i = 1$  if species  $i$  was detected at site  $j$  in sampling occasion  $k$ , and  $y_{jk}^i = 0$  if the species was not encountered. The site totals  $y_j^i = \sum_{k=1}^{K_j} y_{jk}^i$  were modeled as  $y_j^i \sim \text{Bin}(K_j, p_j^i)$ , where encounter probability  $p_j^i$  was modeled differently for each species. Livestock encounter probability was assumed to be constant and independent of occurrence of other species,  $\text{logit}(p_j^{LI}) = \alpha_0^{LI}$ , with average encounter probability  $\bar{p}^{LI} = \text{expit}(\alpha_0^{LI})$ . Ibex encounter probability was tested for an effect of distance to herders' houses and camps ('dist'):

$$\text{logit}(p_j^{IB}) = \alpha_0^{IB|LI} z_j^{LI} + \alpha_0^{IB|\bar{LI}} (1 - z_j^{LI}) + \alpha_{\text{dist}}^{IB} \text{dist}_j$$

where  $\bar{p}^{IB|LI} = \text{expit}(\alpha_0^{IB|LI}) = \Pr(y_j^{IB} = 1 | z_j^{LI} = 1)$  is the conditional probability that ibex is encountered given that livestock is present, and  $\bar{p}^{IB|\bar{LI}} = \text{expit}(\alpha_0^{IB|\bar{LI}}) = \Pr(y_j^{IB} = 1 | z_j^{LI} = 0)$  is the conditional probability that ibex is encountered given that livestock is absent. In our case, due to data paucity, we fixed average ibex encounter probability independent of livestock presence, i.e.  $\bar{p}^{IB} = \bar{p}^{IB|LI} = \bar{p}^{IB|\bar{LI}}$ . The full linear predictor for snow leopard encounter probability was as follows:

$$\begin{aligned} \text{logit}(p_j^{SL}) = & \alpha_0^{SL|LI,IB} z_j^{LI} z_j^{IB} + \alpha_0^{SL|\bar{LI},IB} (1 - z_j^{LI}) z_j^{IB} + \\ & \alpha_0^{SL|LI,\bar{IB}} z_j^{LI} (1 - z_j^{IB}) + \alpha_0^{SL|\bar{LI},\bar{IB}} (1 - z_j^{LI}) (1 - z_j^{IB}) + \alpha_{\text{dist}}^{SL} \text{dist}_j \end{aligned}$$

where average encounter probability was differently constrained under the two scenarios: (scenario 1) snow leopard encounter probability depended on whether livestock was present,  $\bar{p}^{SL|LI} = \bar{p}^{SL|LI,IB} = \bar{p}^{SL|LI,\bar{IB}}$  and  $\bar{p}^{SL|\bar{LI}} = \bar{p}^{SL|\bar{LI},IB} = \bar{p}^{SL|\bar{LI},\bar{IB}}$ ; (scenario 2) snow leopard encounter probability was independent of whether livestock and ibex were present, i.e.  $\bar{p}^{SL} = \bar{p}^{SL|LI,IB} = \bar{p}^{SL|\bar{LI},IB} = \bar{p}^{SL|LI,\bar{IB}} = \bar{p}^{SL|\bar{LI},\bar{IB}}$ . Note that snow leopard encounter probability was a function of distance to herders' houses and camps.

Models were fitted using the Markov chain Monte Carlo (MCMC) framework. We used Normal (0,100) prior distributions for  $\beta_{\text{elev}}^i$ ,  $\beta_{\text{dist}}^i$ , and  $\alpha_{\text{dist}}^i$  parameters and Uniform(0,1) prior distributions for all parameters. Summaries of the posterior distribution generated from a three Markov chains initialized with random starting values, run for 15,000 iterations after a 2,000

burn-in, and without thinning. The  $\hat{R}$  diagnostics (Brooks 1998) used to assess convergence was  $<1.006$  for all parameters.

#### Reference

Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7, 434–455.

#### Supplementary material E.2. R and JAGS model code to fit the co-occurrence occupancy models for the two scenarios.

```
#####
### Co-occurrence model for scenario 1
#####
# Legend:
#DOM = livestock
#UNG = ibex
#LEO = snow leopard

# BUGS model
modelFileName = 'model_LEO_covs.txt'
cat("
model {
### PRIORS FOR OCCUPANCY PARAMETERS
# Livestock
mean.psi.DOM ~ dunif(0,1)
mu.psi.DOM <- log(mean.psi.DOM) - log(1-mean.psi.DOM)

# Ibex
psi.UNG_withDOM ~ dunif(0,1)
psi.UNG_withoutDOM ~ dunif(0,1)
mu.psi.UNG_withDOM <- log(psi.UNG_withDOM) - log(1-psi.UNG_withDOM)
mu.psi.UNG_withoutDOM <- log(psi.UNG_withoutDOM) - log(1-psi.UNG_withoutDOM)

# Snow leopard
psi.LEO_withDOM_withUNG <- equal.psi.LEO_withDOM
psi.LEO_withoutDOM_withUNG <- equal.psi.LEO_withoutDOM
psi.LEO_withDOM_withoutUNG <- equal.psi.LEO_withDOM
psi.LEO_withoutDOM_withoutUNG <- equal.psi.LEO_withoutDOM
equal.psi.LEO_withDOM ~ dunif(0,1)
equal.psi.LEO_withoutDOM ~ dunif(0,1)

mu.psi.LEO_withDOM_withUNG <- log(psi.LEO_withDOM_withUNG) - log(1-
psi.LEO_withDOM_withUNG)
mu.psi.LEO_withoutDOM_withUNG <- log(psi.LEO_withoutDOM_withUNG) - log(1-
psi.LEO_withoutDOM_withUNG)
mu.psi.LEO_withDOM_withoutUNG <- log(psi.LEO_withDOM_withoutUNG) - log(1-
psi.LEO_withDOM_withoutUNG)
mu.psi.LEO_withoutDOM_withoutUNG <- log(psi.LEO_withoutDOM_withoutUNG) - log(1-
psi.LEO_withoutDOM_withoutUNG)

### PRIORS FOR DETECTION PARAMETERS
# Livestock
mean.p.DOM ~ dunif(0,1)
mu.p.DOM <- log(mean.p.DOM) - log(1-mean.p.DOM)

# Ibex
mean.p.UNG_withDOM <- equal.p.UNG
mean.p.UNG_withoutDOM <- equal.p.UNG
equal.p.UNG ~ dunif(0,1)

mu.p.UNG_withDOM <- log(mean.p.UNG_withDOM) - log(1-mean.p.UNG_withDOM)
mu.p.UNG_withoutDOM <- log(mean.p.UNG_withoutDOM) - log(1-mean.p.UNG_withoutDOM)

# Snow leopard
mean.p.LEO_withDOM_withUNG <- equal.p.LEO_withDOM
mean.p.LEO_withoutDOM_withUNG <- equal.p.LEO_withoutDOM
```

```

mean.p.LEO_withDOM_withoutUNG <- equal.p.LEO_withDOM
mean.p.LEO_withoutDOM_withoutUNG <- equal.p.LEO_withoutDOM
equal.p.LEO_withDOM ~ dunif(0,1)
equal.p.LEO_withoutDOM ~ dunif(0,1)

mu.p.LEO_withDOM_withUNG <- log(mean.p.LEO_withDOM_withUNG) - log(1-
mean.p.LEO_withDOM_withUNG)
mu.p.LEO_withoutDOM_withUNG <- log(mean.p.LEO_withoutDOM_withUNG) - log(1-
mean.p.LEO_withoutDOM_withUNG)
mu.p.LEO_withDOM_withoutUNG <- log(mean.p.LEO_withDOM_withoutUNG) - log(1-
mean.p.LEO_withDOM_withoutUNG)
mu.p.LEO_withoutDOM_withoutUNG <- log(mean.p.LEO_withoutDOM_withoutUNG) - log(1-
mean.p.LEO_withoutDOM_withoutUNG)

### PRIORS FOR SLOPES
# occurrence
beta.psi.DOM.elev ~ dnorm(0,0.01)
beta.psi.DOM.dist ~ dnorm(0,0.01)
beta.psi.UNG.dist ~ dnorm(0,0.01)
beta.psi.LEO.elev ~ dnorm(0,0.01)
beta.psi.LEO.dist ~ dnorm(0,0.01)
# detectability
beta.p.UNG.dist ~ dnorm(0,0.01)
beta.p.LEO.dist ~ dnorm(0,0.01)

# MODEL OF OCCURRENCES
for (i in 1:nsites) {
  # Livestock
  psi.DOM.def[i] <- ifelse(DOM.limits[i]==1,psi.DOM[i],0)
  z.DOM[i] ~ dbern(psi.DOM.def[i])
  logit(psi.DOM[i]) <- mu.psi.DOM + beta.psi.DOM.elev * elev[i] + beta.psi.DOM.dist *
dist[i]
  # Ibex
  z.UNG[i] ~ dbern(psi.UNG.def[i])
  logit(psi.UNG.def[i]) <- z.DOM[i] * mu.psi.UNG_withDOM + (1-z.DOM[i]) *
mu.psi.UNG_withoutDOM +
      beta.psi.UNG.dist * dist[i]
  # Snow leopard
  z.LEO[i] ~ dbern(psi.LEO.def[i])
  logit(psi.LEO.def[i]) <- z.DOM[i] * z.UNG[i] * mu.psi.LEO_withDOM_withUNG +
(1-z.DOM[i]) * z.UNG[i] * mu.psi.LEO_withoutDOM_withUNG +
z.DOM[i] * (1-z.UNG[i]) * mu.psi.LEO_withDOM_withoutUNG +
(1-z.DOM[i]) * (1-z.UNG[i]) *
mu.psi.LEO_withoutDOM_withoutUNG +
      beta.psi.LEO.elev * elev[i] + beta.psi.LEO.dist * dist[i]
}

# MODEL OF DETECTIONS
for (i in 1:nsites) {
  # Livestock
  y_DOM[i] ~ dbinom(p.DOM.def[i],K[i])
  p.DOM.def[i] <- z.DOM[i] * p.DOM[i]
  logit(p.DOM[i]) <- mu.p.DOM
  # Ibex
  y_UNG[i] ~ dbinom(p.UNG.def[i],K[i])
  p.UNG.def[i] <- z.UNG[i] * p.UNG[i]
  logit(p.UNG[i]) <- mu.p.UNG_withDOM * z.DOM[i] + mu.p.UNG_withoutDOM * (1-
z.DOM[i]) +
      beta.p.UNG.dist * dist[i]
  # Snow leopard
  y_LEO[i] ~ dbinom(p.LEO.def[i],K[i])
  p.LEO.def[i] <- z.LEO[i] * p.LEO[i]
  logit(p.LEO[i]) <- mu.p.LEO_withDOM_withUNG * z.DOM[i] * z.UNG[i] +
mu.p.LEO_withoutDOM_withUNG * (1-z.DOM[i]) * z.UNG[i] +
mu.p.LEO_withDOM_withoutUNG * z.DOM[i] * (1-z.UNG[i]) +
mu.p.LEO_withoutDOM_withoutUNG * (1-z.DOM[i]) * (1-z.UNG[i]) +
      beta.p.LEO.dist * dist[i]
}
} ", fill=TRUE, file=modelFileName)

# data
bugs.data <-
list(nsites=nsites,y_DOM=y_DOM,y_UNG=y_UNG,y_LEO=y_LEO,K=K,DOM.limits=DOM.limits,
      elev=covs_st$El,dist=covs_st$Dis
)

# data structure

```

```

#str(bugs.data)
#List of 8
# $ nsites      : int 49
# $ y_DOM       : num [1:49] 13 11 1 31 1 15 6 1 14 0 ...
# $ y_UNG       : num [1:49] 0 0 0 0 0 0 0 0 0 0 ...
# $ y_LEO       : num [1:49] 0 3 0 25 0 5 0 0 5 0 ...
# $ K           : int [1:49] 44 43 43 44 44 44 43 43 42 47 ...
# $ DOM.limits : num [1:49] 1 1 1 1 1 1 1 1 1 0 ...
# $ elev        : num [1:49] -1.3941 -0.7505 0.0895 -1.07 -0.5587 ...
# $ dist        : num [1:49] -1.0264 -0.6178 -0.1643 -0.3798 0.0871 ...

# Legend:
#nsites = number of sites
#y_DOM, y_UNG, y_LEO = species-specific detection frequencies
#K = site-specific number of sampling occasions (days)
#DOM.limits = site accessibility for livestock (0=not accessible, 1=accessible)
#elev = standardized site elevation
#dist = standardized distance to herder's houses and camps

# initial values
inits <- function() {list(mean.psi.DOM=runif(1,0.5,1),

psi.UNG_withDOM=runif(1,0.5,1),psi.UNG_withoutDOM=runif(1,0.5,1),

psi.LEO_withDOM_withUNG=runif(1,0.5,1),psi.LEO_withoutDOM_withUNG=runif(1,0.5,1),

psi.LEO_withDOM_withoutUNG=runif(1,0.5,1),psi.LEO_withoutDOM_withoutUNG=runif(1,0.5,1),
      mean.p.DOM=runif(1,0.5,1),equal.p.UNG=runif(1,0.5,1),

equal.p.LEO_withDOM=runif(1,0.5,1),equal.p.LEO_withoutDOM=runif(1,0.5,1),
      beta.psi.DOM.elev=runif(1,-1,1),beta.psi.DOM.dist=runif(1,-
1,1),
      beta.psi.UNG.dist=runif(1,-1,1),
      beta.psi.LEO.elev=runif(1,-1,1),beta.psi.LEO.dist=runif(1,-
1,1),
      beta.p.UNG.dist=runif(1,-1,1),beta.p.LEO.dist=runif(1,-1,1),

z.DOM=DOM.limits,z.UNG=rep(1,length(y_DOM)),z.LEO=rep(1,length(y_DOM))
      )
      }

# parameters to monitor
parameters<-c("mean.psi.DOM","psi.UNG_withDOM","psi.UNG_withoutDOM",
"equal.psi.LEO_withDOM","equal.psi.LEO_withoutDOM",
"mean.p.DOM","equal.p.UNG",
"equal.p.LEO_withDOM","equal.p.LEO_withoutDOM",
"beta.psi.DOM.elev","beta.psi.DOM.dist","beta.psi.UNG.dist","beta.psi.LEO.elev","beta.ps
i.LEO.dist",
"beta.p.UNG.dist","beta.p.LEO.dist"
)

# MCMC settings
n.adapt <- 1000
n.burnin <- 2000
n.iter <- 15000
thin <- 1
chains <- 3

# run the model for scenario 1
out <- jags(data = bugs.data,
      inits = inits,
      parameters.to.save = parameters,
      model.file = "model_LEO_covs.txt",
      n.chains = chains,
      n.adapt = n.adapt,
      n.iter = n.iter,
      n.burnin = n.burnin,
      n.thin = thin,seed=2446,
      parallel=T)

###~#####
### Co-occurrence model for scenario 2
###~#####
# Legend:
#DOM = livestock
#UNG = ibex
#LEO = snow leopard

```

```

# BUGS model
modelFileName = 'model_LEO_covs_sc3a.txt'
cat("
model {
### PRIORS FOR OCCUPANCY PARAMETERS
# Livestock
mean.psi.DOM ~ dunif(0,1)
mu.psi.DOM <- log(mean.psi.DOM) - log(1-mean.psi.DOM)

# Ibex
psi.UNG_withDOM ~ dunif(0,1)
psi.UNG_withoutDOM ~ dunif(0,1)
mu.psi.UNG_withDOM <- log(psi.UNG_withDOM) - log(1-psi.UNG_withDOM)
mu.psi.UNG_withoutDOM <- log(psi.UNG_withoutDOM) - log(1-psi.UNG_withoutDOM)

# Snow leopard
psi.LEO_withDOM_withUNG <- equal.psi.LEO_withUNG
psi.LEO_withoutDOM_withUNG <- equal.psi.LEO_withUNG
psi.LEO_withDOM_withoutUNG <- equal.psi.LEO_withoutUNG
psi.LEO_withoutDOM_withoutUNG <- equal.psi.LEO_withoutUNG
equal.psi.LEO_withUNG ~ dunif(0,1)
equal.psi.LEO_withoutUNG ~ dunif(0,1)
mu.psi.LEO_withDOM_withUNG <- log(psi.LEO_withDOM_withUNG) - log(1-
psi.LEO_withDOM_withUNG)
mu.psi.LEO_withoutDOM_withUNG <- log(psi.LEO_withoutDOM_withUNG) - log(1-
psi.LEO_withoutDOM_withUNG)
mu.psi.LEO_withDOM_withoutUNG <- log(psi.LEO_withDOM_withoutUNG) - log(1-
psi.LEO_withDOM_withoutUNG)
mu.psi.LEO_withoutDOM_withoutUNG <- log(psi.LEO_withoutDOM_withoutUNG) - log(1-
psi.LEO_withoutDOM_withoutUNG)

### PRIORS FOR DETECTION PARAMETERS
# Livestock
mean.p.DOM ~ dunif(0,1)
mu.p.DOM <- log(mean.p.DOM) - log(1-mean.p.DOM)

# Ibex
mean.p.UNG_withDOM <- equal.p.UNG
mean.p.UNG_withoutDOM <- equal.p.UNG
equal.p.UNG ~ dunif(0,1)
mu.p.UNG_withDOM <- log(mean.p.UNG_withDOM) - log(1-mean.p.UNG_withDOM)
mu.p.UNG_withoutDOM <- log(mean.p.UNG_withoutDOM) - log(1-mean.p.UNG_withoutDOM)

# Snow leopard
mean.p.LEO_withDOM_withUNG <- equal.p.LEO
mean.p.LEO_withoutDOM_withUNG <- equal.p.LEO
mean.p.LEO_withDOM_withoutUNG <- equal.p.LEO
mean.p.LEO_withoutDOM_withoutUNG <- equal.p.LEO
equal.p.LEO ~ dunif(0,1)
mu.p.LEO_withDOM_withUNG <- log(mean.p.LEO_withDOM_withUNG) - log(1-
mean.p.LEO_withDOM_withUNG)
mu.p.LEO_withoutDOM_withUNG <- log(mean.p.LEO_withoutDOM_withUNG) - log(1-
mean.p.LEO_withoutDOM_withUNG)
mu.p.LEO_withDOM_withoutUNG <- log(mean.p.LEO_withDOM_withoutUNG) - log(1-
mean.p.LEO_withDOM_withoutUNG)
mu.p.LEO_withoutDOM_withoutUNG <- log(mean.p.LEO_withoutDOM_withoutUNG) - log(1-
mean.p.LEO_withoutDOM_withoutUNG)

### PRIORS FOR SLOPES
beta.psi.DOM.elev ~ dnorm(0,0.01)
beta.psi.DOM.dist ~ dnorm(0,0.01)
beta.psi.UNG.dist ~ dnorm(0,0.01)
beta.psi.LEO.elev ~ dnorm(0,0.01)
beta.psi.LEO.dist ~ dnorm(0,0.01)
beta.p.UNG.dist ~ dnorm(0,0.01)
beta.p.LEO.dist ~ dnorm(0,0.01)

# MODEL OF OCCURRENCES
for (i in 1:nsites) {
# Livestock
psi.DOM.def[i] <- ifelse(DOM.limits[i]==1,psi.DOM[i],0)
z.DOM[i] ~ dbern(psi.DOM.def[i])
logit(psi.DOM[i]) <- mu.psi.DOM + beta.psi.DOM.elev * elev[i] + beta.psi.DOM.dist *
dist[i]
# Ibex
z.UNG[i] ~ dbern(psi.UNG.def[i])

```

```

logit(psi.UNG.def[i]) <- z.DOM[i] * mu.psi.UNG_withDOM + (1-z.DOM[i]) *
mu.psi.UNG_withoutDOM +
      beta.psi.UNG.dist * dist[i]
# Snow leopard
z.LEO[i] ~ dbern(psi.LEO.def[i])
logit(psi.LEO.def[i]) <- z.DOM[i] * z.UNG[i] * mu.psi.LEO_withDOM_withUNG +
      (1-z.DOM[i]) * z.UNG[i] * mu.psi.LEO_withoutDOM_withUNG +
      z.DOM[i] * (1-z.UNG[i]) * mu.psi.LEO_withDOM_withoutUNG +
      (1-z.DOM[i]) * (1-z.UNG[i]) *
mu.psi.LEO_withoutDOM_withoutUNG +
      beta.psi.LEO.elev * elev[i] + beta.psi.LEO.dist * dist[i]
}
# MODEL OF DETECTIONS
for (i in 1:nsites) {
  # Livestock
  y_DOM[i] ~ dbinom(p.DOM.def[i],K[i])
  p.DOM.def[i] <- z.DOM[i] * p.DOM[i]
  logit(p.DOM[i]) <- mu.p.DOM
  # Ibex
  y_UNG[i] ~ dbinom(p.UNG.def[i],K[i])
  p.UNG.def[i] <- z.UNG[i] * p.UNG[i]
  logit(p.UNG[i]) <- mu.p.UNG_withDOM * z.DOM[i] + mu.p.UNG_withoutDOM * (1-
z.DOM[i]) +
      beta.p.UNG.dist * dist[i]
  # Snow leopard
  y_LEO[i] ~ dbinom(p.LEO.def[i],K[i])
  p.LEO.def[i] <- z.LEO[i] * p.LEO[i]
  logit(p.LEO[i]) <- mu.p.LEO_withDOM_withUNG * z.DOM[i] * z.UNG[i] +
      mu.p.LEO_withoutDOM_withUNG * (1-z.DOM[i]) * z.UNG[i] +
      mu.p.LEO_withDOM_withoutUNG * z.DOM[i] * (1-z.UNG[i]) +
      mu.p.LEO_withoutDOM_withoutUNG * (1-z.DOM[i]) * (1-z.UNG[i]) +
      beta.p.LEO.dist * dist[i]
}
}"; fill=TRUE, file=modelFileName)
# data
bugs.data <-
list(nsites=nsites,y_DOM=y_DOM,y_UNG=y_UNG,y_LEO=y_LEO,K=K,DOM.limits=DOM.limits,
      elev=covs_st$El,dist=covs_st$Dis
)
# data structure
#str(bugs.data)
#List of 8
# $ nsites      : int 49
# $ y_DOM       : num [1:49] 13 11 1 31 1 15 6 1 14 0 ...
# $ y_UNG       : num [1:49] 0 0 0 0 0 0 0 0 0 0 ...
# $ y_LEO       : num [1:49] 0 3 0 25 0 5 0 0 5 0 ...
# $ K           : int [1:49] 44 43 43 44 44 44 43 43 42 47 ...
# $ DOM.limits: num [1:49] 1 1 1 1 1 1 1 1 1 0 ...
# $ elev        : num [1:49] -1.3941 -0.7505 0.0895 -1.07 -0.5587 ...
# $ dist        : num [1:49] -1.0264 -0.6178 -0.1643 -0.3798 0.0871 ...

# Legend:
#nsites = number of sites
#y_DOM, y_UNG, y_LEO = species-specific detection frequencies
#K = site-specific number of sampling occasions (days)
#DOM.limits = site accessibility for livestock (0=not accessible, 1=accessible)
#elev = standardized site elevation
#dist = standardized distance to herder's houses and camps
# initial values
inits <- function() {list(mean.psi.DOM=runif(1,0.5,1),
psi.UNG_withDOM=runif(1,0.5,1),psi.UNG_withoutDOM=runif(1,0.5,1),
equal.psi.LEO_withUNG=runif(1,0.1,0.2),equal.psi.LEO_withoutUNG=runif(1,0.3,0.5),
      mean.p.DOM=runif(1,0.5,1),equal.p.UNG=runif(1,0.5,1),
      equal.p.LEO=runif(1,0.08,0.1),
      beta.psi.DOM.elev=runif(1,-1,1),beta.psi.DOM.dist=runif(1,-
1,1),
      beta.psi.UNG.dist=runif(1,-1,1),
      beta.psi.LEO.elev=runif(1,-1,1),beta.psi.LEO.dist=runif(1,-
1,1),
      beta.p.UNG.dist=runif(1,-1,1),beta.p.LEO.dist=runif(1,-1,1),
z.DOM=DOM.limits,z.UNG=rep(1,length(y_DOM)),z.LEO=rep(1,length(y_DOM))
)
}
# parameters to monitor

```

```

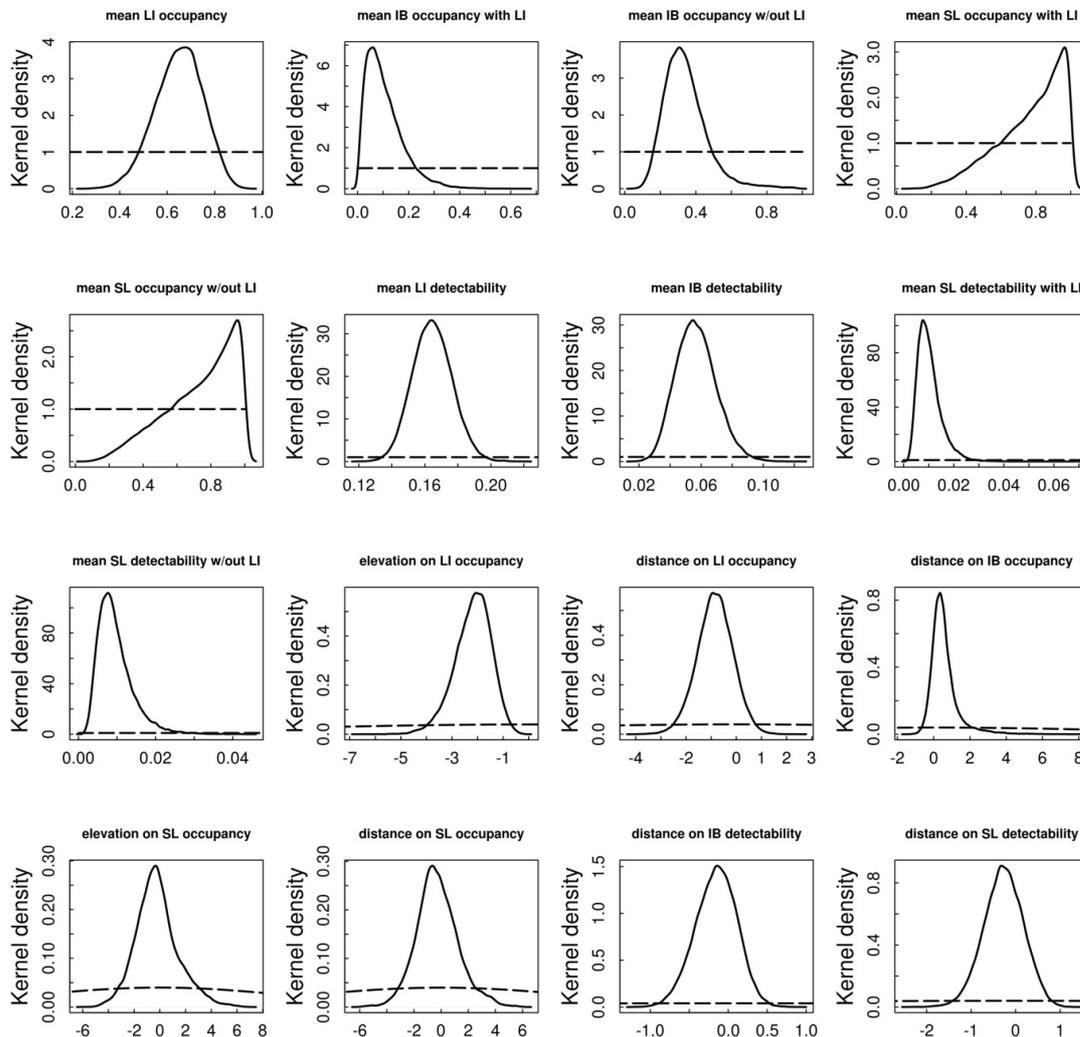
parameters<-c("mean.psi.DOM","psi.UNG_withDOM","psi.UNG_withoutDOM",
"equal.psi.LEO_withUNG","equal.psi.LEO_withoutUNG",
"mean.p.DOM","equal.p.UNG",
"equal.p.LEO",
"beta.psi.DOM.elev","beta.psi.DOM.dist","beta.psi.UNG.dist","beta.psi.LEO.elev","beta.ps
i.LEO.dist",
"beta.p.UNG.dist","beta.p.LEO.dist"
)
# MCMC settings
n.adapt <- 1000
n.burnin <- 2000
n.iter <- 15000
thin <- 1
chains <- 3

# run the model for scenario 1
out <- jags(data = bugs.data,
inits = inits,
parameters.to.save = parameters,
model.file = "model_LEO_covs_sc3a.txt",
n.chains = chains,
n.adapt = n.adapt,
n.iter = n.iter,
n.burnin = n.burnin,
n.thin = thin,
parallel=T)

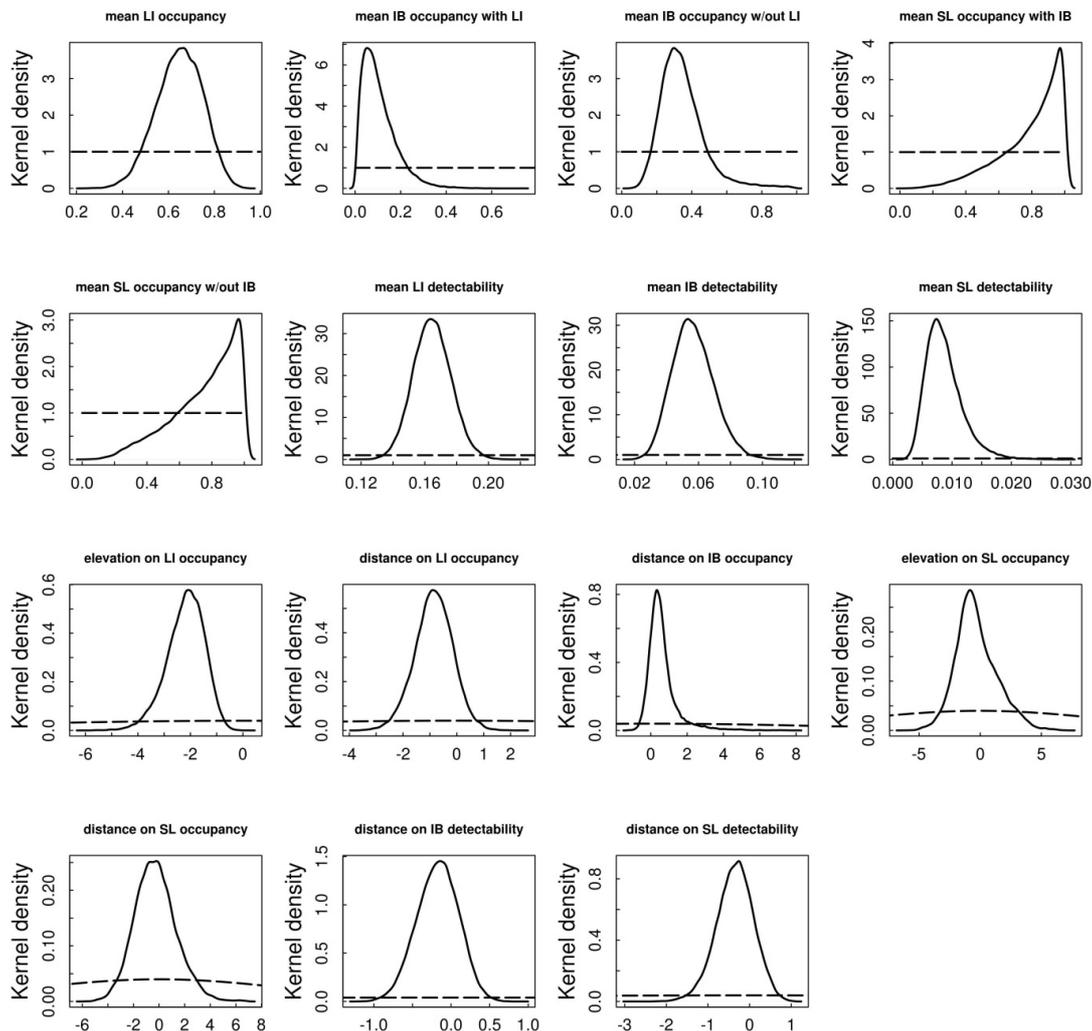
## End of code

```

**Figure E.3** Posterior (solid line) and prior (dashed line) parameter distribution for each parameter estimated under the first scenario.



**Figure E.4** Posterior (solid line) and prior (dashed line) parameter distribution for each parameter estimated under the second scenario.



**Table E.5** Wild mammals and other species detected by camera trapping, with raw indices of capture, ordered by decreasing naïve occupancy

| Species                                 | No. of photographs | No. of events | Relative abundance index | Naïve occupancy |
|---|--------------------|---------------|--------------------------|-----------------|
| <b>Wild mammals</b>                     |                    |               |                          |                 |
| Red fox <i>Vulpes vulpes</i>            | 85                 | 81            | 3.64                     | 0.69            |
| Siberian marmot <i>Marmota sibirica</i> | 354                | 276           | 12.40                    | 0.49            |
| Snow leopard <i>Panthera uncia</i>      | 17                 | 14            | 0.63                     | 0.27            |
| Siberian ibex <i>Capra sibirica</i>     | 88                 | 33            | 1.48                     | 0.18            |
| Pallas' cat <i>Otocolobus manul</i>     | 11                 | 11            | 0.49                     | 0.18            |
| Wolf <i>Canis lupus</i>                 | 28                 | 10            | 0.45                     | 0.16            |

|  |    |    |      |      |
|--|----|----|------|------|
| Beech marten <i>Martes foina</i>         | 10 | 10 | 0.45 | 0.16 |
| Steppe polecat <i>Mustela eversmanii</i> | 27 | 25 | 1.12 | 0.16 |
| Arctic hare <i>Lepus timidus</i>         | 19 | 18 | 0.81 | 0.12 |
| Wolverine <i>Gulo gulo</i>               | 6  | 6  | 0.27 | 0.12 |
| Pika <i>Pika</i> spp.                    | 14 | 9  | 0.40 | 0.02 |
| Red squirrel <i>Sciurus vulgaris</i>     | 1  | 1  | 0.04 | 0.02 |

**Domestic mammals & people**

|                      |      |     |       |      |
|----------------------|------|-----|-------|------|
| Goats                | 940  | 138 | 6.20  | 0.29 |
| Cattle and yaks      | 397  | 163 | 7.33  | 0.27 |
| Sheep                | 226  | 50  | 2.25  | 0.24 |
| Horses               | 83   | 50  | 2.25  | 0.22 |
| Dogs                 | 28   | 28  | 1.26  | 0.20 |
| Camels               | 11   | 11  | 0.49  | 0.04 |
| All domestic animals | 1685 | 367 | 16.49 | 0.43 |
| People               | 195  | 105 | 4.72  | 0.35 |

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Original investigation

# The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping



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## ABSTRACT

As human activities increase in natural areas, so do threats to wildlife, potentially leading to immediate and long-term impacts on species distribution, activity, reproduction and survival. This is particularly relevant for large-bodied vertebrates that are especially sensitive to human presence and human-driven habitat changes. Assessing the impact of anthropogenic disturbance requires data on distribution and activity patterns of target species in relation to human presence and infrastructures. Here, we used camera trap data to study the influence of anthropogenic disturbance on the community of medium-to-large mammals in a mountainous area in the eastern Italian Alps, with emphasis on the local population of brown bear (*Ursus arctos*). In 2015, we sampled a study area of 220 km<sup>2</sup> with 60 camera trap locations adopting a systematic grid. Such design was inspired by the terrestrial vertebrate monitoring protocol developed by the TEAM Network, a pan-tropical biodiversity programme. Camera traps run for 30 days in each site and cumulated 1978 camera trapping days, yielding 1514 detection events of 12 species of mammals. For the 8 most recorded species, we used detection/non-detection data to model estimated occupancy and detection probability in relation to a suite of environmental and disturbance covariates. Our analysis revealed that human disturbance plays a significant role in influencing species-specific detection probability, while we found little evidence of significant relationship between occupancy and anthropogenic disturbance. For example, we found that brown bear's detectability was negatively correlated with capture rate of humans at sampling sites, and positively correlated with distance from settlements. We also assessed species-specific daily activity patterns and found that, for all species, the overlap with human diel pattern decreased significantly at sites with higher human presence. We also discuss the potential of our approach for cost-efficient and long-term monitoring of mammals.

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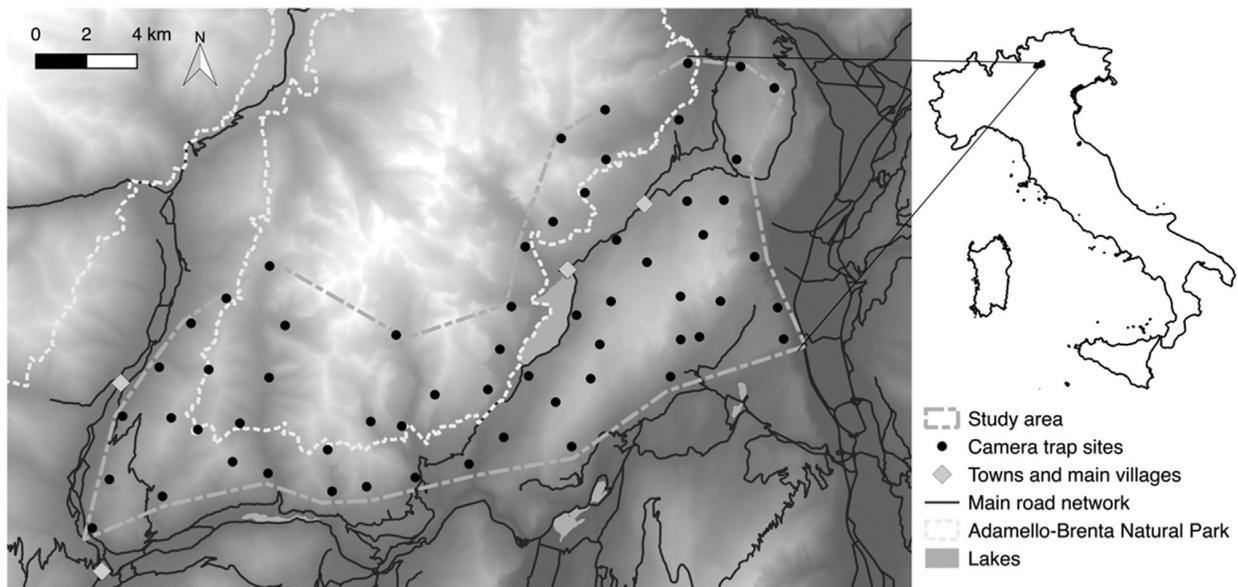
## Introduction

In human-dominated landscapes, increased habitat fragmentation and accessibility to natural areas are bringing humans in closer contact with wild populations (Preisler et al., 2006). Outdoor recreation is typically assumed to be compatible with biodiversity conservation and permitted in most protected areas worldwide, but its effect is still a relatively unknown topic in the conservation science literature (Taylor and Knight, 2003; Blumstein et al., 2005; Sutherland, 2007). Human recreation and diversification of outdoor

activities have become of major conservation concern as tourism expands into natural parks (Margules and Pressey, 2000). Recreation is important for maintaining public support for protected areas and connecting people with nature (Kays et al., 2016), but at the same time it could also be a major disturbance to wildlife (Baker, 1992; Hobbs and Huenneke, 1992; Larson et al., 2016). In addition to habitat degradation resulting from the development of recreational facilities and infrastructure, which can cause an array of impacts on the distribution, reproduction and survival of wildlife (George and Crooks, 2006; Reed and Merenlender, 2008), human disturbance can elicit costly behavioral responses such as flight (Arlettaz et al., 2007; Thiel et al., 2007), feeding disruption (Fernandez-Juricic and Tellería, 2000) or changes in spatial/temporal habitat use (Rogala et al., 2011). Species with large spatial requirements

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**Fig. 1.** Map of the study area (left) in western Trentino province, Northern Italy. The 60 camera trap locations are shown as black dots and the border of the Adamello-Brenta Natural Park is also shown. The background is a Digital Terrain Model, with brighter tones corresponding to higher elevation. The geographic location of the study area in Italy is shown in the map on the right.

and low population densities, typically the large carnivores, are especially sensitive to human infrastructure and activities (Crooks, 2002). Stankowich (2008) indicates that experience with humans and their recreational activities also has a significant impact on ungulate behaviour. For these reasons, larger mammals are considered a proxy of ecosystem health and habitat connectivity (Crooks et al., 2011; e.g. Peters et al., 2015); hence, understanding how their spatio-temporal patterns of habitat use are locally affected by human disturbance becomes an increasingly important research question (Larson et al., 2016).

Here, we examined habitat preferences and the influence of human disturbance on spatial and temporal patterns of medium-to-large terrestrial mammals in a human-disturbed mountainous area in the eastern Italian Alps. The Alps represent a priority area for conservation globally (Olson and Dinerstein, 2002), being one of the richest biodiversity hot spots of Europe and at the same time one of the most intensively exploited mountain ecosystems in the world (Lassen and Savoia, 2005). This mountain range, despite the natural fragility of its ecosystems, is the first destination for outdoor winter sports in the world, which is emblematic of the anthropogenic pressure (Elsasser and Messerli, 2001). The study area is partially inside a protected mountain area (Adamello Brenta Natural Park, PNAB) of particular faunal importance for the historical presence of the last alpine population of brown bear (*Ursus arctos*) that was recently reintroduced (Preatoni et al., 2005), as well as for the current recolonization of the wolf (*Canis lupus*; Ražen et al., 2015).

The on-going expansion of tourism and recreation into wildlife habitats calls for measures to mitigate the negative effects of anthropogenic disturbance (Sutherland, 2007). Mitigating such disturbance requires knowledge on how humans impact wildlife occurrence and activity patterns. We aimed to study the potential influence of human disturbance on spatial (i.e. occupancy and detectability) and temporal (daily activity) patterns of wildlife in the study area, especially in relation to the high presence of tourism in the summer. Our specific objectives were: (1) to assess species' probability of occurrence by estimating occupancy and detection probability, (*sensu* MacKenzie et al. (2002)), (2) to determine anthropogenic and habitat drivers of variations in these metrics, and (3) to assess daily activity patterns of the species in the study

area and investigate the relationship between these and human presence.

## Material and methods

### Study area

We conducted the camera trap survey between June and August 2015 in an area of about 220 km<sup>2</sup> within Trento Province, NE Italy (centred on 46°06'45"N and 10°55'50"E; Fig. 1). This mountainous area encompasses the southern part of Brenta, the westernmost Dolomite group, and its adjacent valleys, which are partially included within the PNAB. While this is formally a protected area, not being a National Park its regulations allow for activities such as hunting, logging and road building, and therefore we assumed that human disturbance does not differ inside and outside the protected area. Therefore, the most relevant feature for our study aims was that some of the sampling sites within the PNAB were more distant from settlements and trafficked roads, and at relatively higher elevation. The sampling area holds part of the core area of the brown bear population (Groff et al., 2015) and represents a large variation in both habitat type and altitudinal range (300–2800 m a.s.l.), with a dominant mountainous terrain. The vegetation composition 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*). Above the treeline (at about 1800 m) vegetation is dominated by mountain pine (*Pinus mugo*) and open habitats comprised of alpine herbaceous species. The climate of the study area varies from continental to alpine, in relation to altitude. The average resident population density is of 32.2/km<sup>2</sup> (<http://www.urbistat.it/AdminStat/it/>) and occurs along the main valleys to the west, south and east of the core study area, with intense tourism presence in the summer. Tourists contribute largely to human activity in summer across the study area.

### Data collection: camera trapping

We designed our sampling protocol by adapting the one developed by the Tropical Ecology Assessment and Monitoring (TEAM)

**Table 1**

List of environmental and disturbance covariates on detection probability ( $p$ ) and occupancy ( $\psi$ ) respectively, as used in occupancy analysis, and the assumed relationship with  $p$  and  $\psi$ .

| Covariates                         | Hypothesized relationship  |
|------------------------------------|--|
| Covariates on detection ( $p$ )    |  |
| Camera model                       | IR+ cameras have larger detection zone hence greater detectability especially for smaller species.   |
| Trail type                         | Trails are less disturbed by the passage of vehicles, but some are intensively frequented by tourists during the summer season.  |
| Distance from settlements          | Noisy and disturbing human activities and presence may affect the behaviour of the species.  |
| Capture rate of humans             | The passage of people can decrease animal detection.   |
| Capture rate of vehicles           | The passage of noisy vehicles can decrease animal detection.   |
| Covariates on occupancy ( $\psi$ ) |  |
| Elevation                          | Elevation reflects habitat and forest variation, and is also correlated with distance from settlements (increase in elevation corresponds to decrease in permanent human disturbance). |
| Elevation squared                  | Quadratic term was used to test whether the relationship with elevation was linear or not.   |
| Slope                              | Species may avoid or prefer steep sites.   |
| Capture rate of humans             | Noising and disturbing human activities may affect animal behaviour and can cause avoidance and fleeing responses.   |
| Capture rate of vehicles           | The noisy passage of vehicles can cause avoidance of roads and surrounding areas.  |

Network (TEAM Network, 2011; Jansen et al., 2014), a pan-tropical biodiversity monitoring programme (Rovero and Ahumada, 2017). We used QGIS version 2.8.2 (QGIS Development Team, 2013) to design a regular grid of 60 camera trap stations evenly spaced and initially positioned at random across the study area to cover an altitudinal gradient from 500 to 1900 m a.s.l., i.e. with no sampling sites above the tree line. Relative to TEAM's, our protocol differed because we set one camera trap site every 4 km<sup>2</sup> instead of 2 km<sup>2</sup>. This compromised between maximizing the overall area monitored, especially given the large home range of brown bears (Preatoni et al., 2005; Groff et al., 2015), and avoiding too large gaps between camera trap sites (Fig. 1). In addition, being the area diffusely covered by forestry roads and trails, which we considered suitable sites for detecting passing wildlife, sampling sites were chosen to fall equally on these categories. Hence, 30 sites were located on forestry roads and 30 on trails (of which 10 were hiking trails and 20 other types of trails, mostly used by hunters). Field sampling was done through two sequential arrays of 30 camera traps each, for easier implementation and due to limited equipment available. Each camera trap sampled for a minimum of 30 consecutive days.

We used two digital camera trap models that mount an infrared flash array, distributed randomly and in equal number across sites: (1) Reconyx HC 500 (Reconyx Inc., Holmen, WI, USA) with a 0.20 s trigger delay, and (2) UOVision UV572 IR+ (UOVision Technology, Shenzhen, China) with 1 s trigger delay. We set camera traps on suitably located trees, i.e. at a distance of 5–6 m from the target trail for the IR+ and 3–4 m for the Reconyx, based on flash intensity and trigger speed of these models, and at an average height of 50 cm, depending on terrain morphology. Cameras were fastened with locks. We cleaned the ground in front of the camera traps of debris and vegetation that could cover the animals or reflect light. We used rechargeable high-performance NiMH batteries. Date and time were stamped in each image and camera traps saved on SD memory cards (Verbatim Premium SDHC cards, 4/8 GB). Cameras were set to take photos with no delay between consecutive triggers. We checked cameras approx. 15 days after the placement, to avoid prolonged malfunctioning. We recorded the location of the camera trap sites by using handheld GPS units (Garmin GPSMap 64 s). We did not use any bait for attracting animals.

#### Data collection: covariates

We downloaded road network and settlement digital maps and Digital Elevation Model (DEM) raster at 10 m spatial resolution from the PAT Geoportal (<http://www.territorio.provincia.tn.it>), and used them in software GRASS 7.0 (GRASS Development Team, 2015) and QGIS 2.8.2 (QGIS Development Team, 2013). We derived elevation and slope of the sites from the DEM, and measured distance from

settlements and from the main road network as potential proxies of disturbance. Thus, the covariates at the camera trap sites were: (1) elevation (in m a.s.l.); (2) slope expressed in radians; (3) distance (m) from main (paved) road network; (4) distance (m) from settlements; (6) trail type in 3 categories: hiking trails, other types of trails, mostly used by hunters, and forestry, unpaved roads; (7) capture rate of humans as computed from sampling data; (8) capture rate of vehicles as computed from sampling data; (9) camera model as resulted from the placement across sites. Elevation and slope were taken as representative of the trap sites, being the DEM accuracy diffused by the 10 m spatial resolution. For variable (7), we checked if capture rate of humans was different inside and outside the park border, and found no significant difference (Welch Two Sample  $t$ -test,  $N_1 = 18$ ,  $N_2 = 40$ ,  $P$ -value = 0.24).

#### Photo processing

At sampling completion, we recovered camera traps and extracted images from the memory cards for identification using dedicated open-access software, Wild.ID (Fegraus and MacCarthy, 2016). After we annotated all of the images, we exported the entire data set to a comma-separated values (.csv) file used for further analyses. Species identification of clear images was straightforward with the exception of distinguishing with a sufficient degree of certainty between beech marten (*Martes foina*) and pine marten (*Martes martes*), because: (1) the only evident (i.e. potentially observable in the collected images) difference between the two species in dimensions and coat lies in the colour of the chest stain, but most of the images were recorded by night and so monochrome (due to the cameras' features) and (2) the two species are sympatric on a large part of the Italian Alps (Boitani et al., 2003). Therefore, we classified all these images as *Martes spp.*

#### Data analysis

We analysed data using a hierarchical modelling approach that allows to explicitly consider imperfect detection (MacKenzie, 2006). Thus, occupancy ( $\psi$ ) is defined as the proportion of area, patches or sites occupied by a species (MacKenzie et al., 2002) and is considered a surrogate of abundance (MacKenzie and Nichols, 2004). We extracted matrices for analysis by processing the raw data in the software R (R Development Core Team, 2015), using scripts prepared by the TEAM Network and available through Rovero and Spitale (2016). We first derived standard descriptors of species and community by filtering the image records for each species to get the number of independent events. We defined the minimum time between two independent events as 15 min, hence mostly avoiding that images of the same individual pausing in front of the camera trap were scored as multiple events. This interval is

**Table 2**

Checklist of mammals detected by camera trapping in the eastern Alps, ordered by decreasing number of events. Naïve occupancy ( $\psi$ ) is computed as the number of sites the species was trapped divided by all sites sampled ( $n = 58$ ). The capture rate (or RAI, relative abundance index) was computed as the number of events divided by sampling effort and multiplied by 100 (i.e. events per 100 days of camera trapping).

| Latin name                 | Common name   | Taxonomic order | Functional guild | Events | Capture rate | Naïve $\psi$ |
|----------------------------|---------------|-----------------|------------------|--------|--------------|--------------|
| <i>Vulpes vulpes</i>       | Red fox       | Carnivora       | Omnivore         | 562    | 28.41        | 0.621        |
| <i>Capreolus capreolus</i> | Roe deer      | Ungulates       | Herbivore        | 302    | 15.27        | 0.793        |
| <i>Cervus elaphus</i>      | Red deer      | Ungulates       | Herbivore        | 208    | 10.52        | 0.638        |
| <i>Rupicapra rupicapra</i> | Chamois       | Ungulates       | Herbivore        | 166    | 8.39         | 0.448        |
| <i>Lepus europaeus</i>     | Brown hare    | Lagomorpha      | Herbivore        | 114    | 5.76         | 0.293        |
| <i>Meles meles</i>         | Badger        | Carnivora       | Omnivore         | 64     | 3.24         | 0.328        |
| <i>Martes sp.</i>          | Marten        | Carnivora       | Carnivore        | 49     | 2.48         | 0.241        |
| <i>Ursus arctos</i>        | Brown bear    | Carnivora       | Omnivore         | 38     | 1.92         | 0.328        |
| <i>Sciurus vulgaris</i>    | Red squirrel  | Rodentia        | Rodent           | 8      | 0.40         | 0.086        |
| <i>Canis lupus</i>         | Wolf          | Carnivora       | Carnivore        | 1      | 0.05         | 0.017        |
| <i>Marmota marmota</i>     | Alpine marmot | Rodentia        | Rodent           | 1      | 0.05         | 0.017        |
| <i>Mustela nivalis</i>     | Least weasel  | Carnivora       | Carnivore        | 1      | 0.05         | 0.017        |

smaller than usually found in the literature (1 h the most common; e.g. Tobler et al., 2009), but Kays and Parsons (2014) and F. Rovero (unpublished data) found that a few minutes generally suffice. We then computed a capture rate, or relative abundance index (RAI), as the number of events divided by sampling effort (camera days) and multiplied by 100 (i.e. events per 100 days of camera trapping; e.g. Rovero et al., 2014). Camera days were computed as the number of 24-h periods from camera deployment until retrieval, or until the last image was taken in cases when the memory card filled up before camera retrieval. We also computed the naïve occupancy as the number of camera trap sites occupied on sites sampled.

We built a species accumulation curve with cumulative camera trap days to assess if survey effort was sufficient for the curve to level off, i.e. to capture the majority of species present in the community. The order in which samples (they consisted of number of events per 15 min) were included in the curve was randomized 1000 times and results were used to derive 95% confidence intervals around the mean, using the package ‘vegan’ in R (Gotelli and Colwell, 2001). Even though this approach ignores imperfect detection of individual species, it is useful for comparison with other studies.

For species detected with >20 events, we performed occupancy analysis using the package ‘unmarked’ in R (Fiske and Chandler, 2011, 2015). For each species, we built detection/non-detection matrices of sites by surveys using a sampling occasion of 5 days. Such occasion length compromised between losing information to estimate detectability – and hence precision in the estimates – when increasing, and incurring in convergence problems when decreasing (Rovero and Spitale, 2016). We used these matrices as the input for the single-season occupancy model (MacKenzie, 2006). We used a common set of models for all the species of interest. In addition to the null model, that assumes constant  $\psi$  and  $p$  (i.e.  $\psi(\cdot), p(\cdot)$ ), for other models  $p$  and  $\psi$  were allowed to vary by subsets of covariates, as reported in Table 1. Our hypothesis was that probability of detection would have been influenced by sources of anthropic disturbance, and we also wanted to test possible differences in performance among camera models. Prior to the analysis, we standardized covariates to have a mean of zero and unit SD, and we tested them for collinearity, which resulted in dropping ‘distance from paved roads’ as it was significantly correlated with ‘distance from settlements’ ( $r = 0.7$ ). We used the Akaike Information Criterion (AIC; Burnham and Anderson, 2002; Zuur et al., 2009) to rank candidate models. In the case of top-ranked models with similar AIC (with  $\Delta AIC < 2$ ), we applied a model-averaging technique to estimate occupancy from these multiple models with the function available in the R package ‘MuMIn’ (Bartoń, 2015). The relative importance of the model parameters was calculated with the R package ‘AICmodavg’ (Mazerolle, 2012). We first determined the

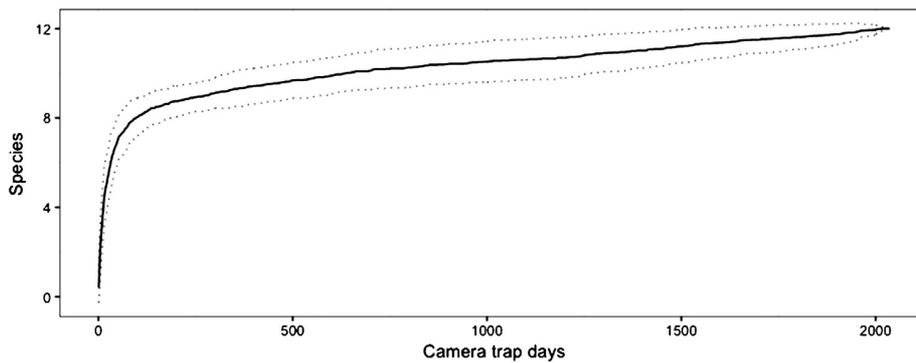
best species-specific models for detectability among the 31 models obtained by combination of 5 covariates of interest. A set of best models for each species was selected and from the model average the most significant variables were retained based on relative variable importance criterion ( $>0.20$ ). Once we fixed the model part for detection, we fitted the one for occupancy.

For the same pool of species analysed in occupancy framework, we also investigated diel activity pattern and its relationship with human activity. By following the procedures described by Ridout and Linkie (2009), we subsampled the raw data for consecutive detections of a given species at each site recorded within 30 min (Zimmermann et al., 2016). We considered each camera site as either having high or low human disturbance based on capture rate of humans, using the mean value as threshold, and this resulted in 41 low and 17 high disturbance camera trap sites. For each of the two disturbance levels, we then performed pairwise comparisons of activity patterns between wild mammals and humans by estimating the coefficient of overlapping  $\Delta$  (ranging from 0, no overlap, to 1, complete overlap) using the package ‘overlap’ (Meredith and Ridout, 2016) in R. We hypothesized overlap to be smaller where human disturbance was greater. To assess the significance of this difference, we generated distributions of overlap values by randomly resampling 1000 times the data set of detections for each species and calculating each time  $\Delta$ . Then, for each species, we used the Welch Two-Sample  $t$ -test to assess if the two generated distributions of  $\Delta$  values were significantly different.

## Results

Of the 60 camera traps set two malfunctioned and did not yield enough data for analysis. The remaining 58 accumulated 1,978 camera days (mean per site 34.1). Sampling yielded 4,462 independent events overall, of which 1,514 were of wild mammals. Blank images were 16,074 (87% taken by IR+ cameras), while 1,499 had an unidentifiable subject, i.e. images where the subject appeared blurry, overexposed or outside the flash range. These were taken for 92% by the IR+ cameras. Twelve species of wild mammals were recorded (range 1–8, mean 3.8). The list of detected mammals and standard descriptors are reported in Table 2. The checklist matched the expectations based on knowledge of the local fauna, with no species representing new records in the area (see Discussion). We also recorded 6 bird species (11 events) and 5 domestic species (60 events), predominantly dogs. Humans were recorded both as pedestrians/bikers (1,952 events) and vehicles (925 events). The randomized species accumulation curve with sampling effort is shown in Fig. 2.

We could fit occupancy models for the eight most recorded species. Estimated  $\psi$  ranged from 0.29 to 0.83 and  $p$  ranged from



**Fig. 2.** Randomized species accumulation curve (solid line), with sampling effort for the community of medium-to-large mammals detected by camera trapping in the eastern Alps. Dotted lines indicate 95% confidence intervals.

0.13 to 0.54 (Table 3). The ‘null’ model (i.e. without covariates) was among the best supported for only one species, the brown bear, while at least one of the covariates affected significantly or marginally significantly  $\psi$  or  $p$  of all the others. Model selection indicated that no single model was demonstrably better (i.e. with  $\Delta$ AIC being 2 points greater than the following in rank) for any of the species. We therefore used model averaging. For the brown bear, significant correlations were only found for its detection probability (Table 3; Fig. 3). The average model included distance from settlements (positive relationship), and capture rate of humans (negative relationship). Among ungulates, predicted  $\psi$  for the chamois (*Rupicapra rupicapra*) at the camera trap stations was highly variable (range 0.19–0.82; Fig. 3), and both slope and elevation positively affected  $\psi$ . Capture rate of humans negatively affected red deer’s (*Cervus elaphus*) detectability; trail type significantly affected roe deer’s (*Capreolus capreolus*) detectability, with a positive influence of trails in relation to forestry roads. The three species of mesocarnivores had similar patterns, with a positive correlation between disturbance covariates and  $\psi$ , i.e. capture rate of humans with red fox (*Vulpes vulpes*) and marten’s (*Martes* sp.) occupancy, capture rate of vehicles with badger’s (*Meles meles*). For all the eight analysed species, camera model significantly affected species’ detectability, which was positively correlated with the IR+ model. For marten and red fox the differences in detection due to camera models were too high to be properly accounted for by the analysis; hence, for these two species we excluded camera model as a covariate in model selection. Results of model selection and of model averaging for each species are reported in Appendix A and Appendix B.

The results of the analysis of activity patterns are summarised in Fig. 4. For the majority of the target species, the analysis of the relationship between overlap and disturbance revealed significantly smaller overlap with greater disturbance. The red fox was the only species for which the coefficient of overlap slightly increased with greater disturbance. All  $t$ -tests for differences in activity overlap between low and high disturbance had a significant outcome ( $P < 0.001$ ).

## Discussion

Our study revealed that human disturbance plays a significant role in influencing the detection probability of target species, indicating that in this coupled human–natural system patterns of habitat association of larger mammals are inherently dependent on human-generated disturbance, and translating into processes of avoidance or, for certain species, tolerance. This also applies to the activity pattern, as for all species it resulted significantly influenced by human activity, supporting our hypothesis that the coefficient

of overlap in diel activity between human and wildlife is smaller where disturbance is greater.

For the brown bear population, that is of remarkable conservation attention (Peters et al., 2015), our results provide novel information on habitat associations as well as patterns in the responses of bears to disturbance. That no covariate of occupancy was retained in more than one model among the best ones suggests the lack of a marked preference for any particular habitat as well as tolerance to human presence. However, the capture rate of humans was negatively correlated with bears’ detectability, indicating that the presence of people, which is intense in the summer, may induce a behavioural response of increased shyness of bears at these sites. This is concordant with the comparable pattern of increased detectability with increasing distance from settlements, which may reflect bears’ elusiveness in proximity of a direct and permanent source of disturbance. Both results matched an earlier study in the same areas on detections of bears at rub trees (Tattoni et al., 2015) and other studies in Europe, where bears are known to avoid people (Swenson, 1999; Zedrosser et al., 2001). Interestingly, the brown bear had the lowest average detection probability, and this in turn resulted into a proportionally higher estimated occupancy relative to the naïve occupancy (i.e. from 0.33 to 0.52). The analysis of activity pattern of bears and people revealed clear temporal segregation overall; in addition, analysis of overlap in activity as computed for different disturbance levels showed a significant temporal shift in bear activity at the sites with greater human passage, indicating that bears adjust their movement patterns in time as well as in space to decrease chances of encountering humans. This matches findings of an earlier study (Tattoni et al., 2015) as well as studies from both North America and Europe reporting that in areas with low intensity of human utilization bears are largely diurnal, whereas in areas with high intensity of human utilization or during periods of frequent human access bears shift to nocturnal behaviour (Gibeau et al., 2002; Kaczensky et al., 2006; Moe et al., 2007). Our results support the assumption that the nocturnal activity pattern observed in European brown bears is more likely an effect of individual learning than a genetically fixed trait (Kaczensky et al., 2006). These findings suggest both spatial and temporal displacement in response to human presence, an important prerequisite for the coexistence of brown bears and people in the study area and the Alps in general. This is especially relevant in the current context of increasing human–bear conflicts.

Occupancy analysis revealed co-occurrence of the three ungulates across the study area. Although the red deer is known as superior competitor to smaller ungulates with similar diets (e.g. roe deer and alpine chamois) and this competition can be high during summer (Lovari et al., 2014), habitat heterogeneity can promote coexistence between herbivores (Anderwald et al., 2016). The most

**Table 3**  
Summary of species-specific occupancy ( $\psi$ ) and detection probability ( $p$ ) estimates for the eight most detected species by camera trapping in the eastern Alps, ordered by decreasing estimated occupancy. Parameters are average values of predicted  $\psi$  and  $p$  from the final models at the 58 camera trap stations. Significant outcomes of the relationships between  $\psi$  or  $p$  and covariates are also indicated with their directionality (positive/negative relationship), shown in parenthesis when the significance is marginal ( $0.05 < p < 0.1$ ). Only the variables with at least one significant outcome are shown. Naïve occupancy values are also shown.

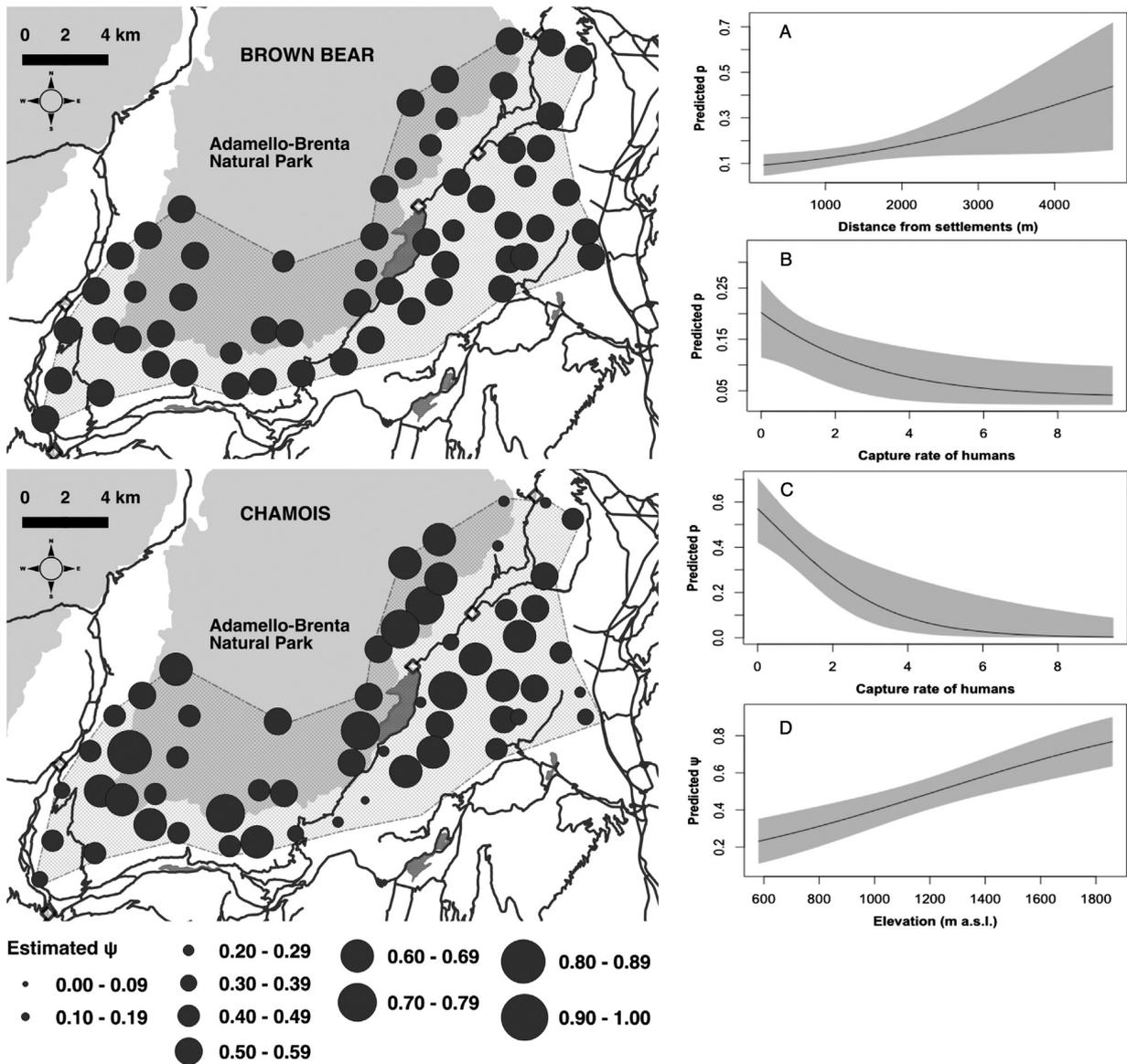
| Species            | Naïve $\psi$ | $\psi$ | SE ( $\psi$ ) | $p$  | SE ( $p$ ) | $\psi$ (elevation) | $\psi$ (capture rate of humans) | $p$ (camera model)[model] | $p$ (trail type)[type] | $p$ (distance from settlements) | $p$ (capture rate of humans) | $p$ (capture rate of vehicles) |
|--------------------|--------------|--------|---------------|------|------------|--------------------|---------------------------------|---------------------------|------------------------|---------------------------------|------------------------------|--------------------------------|
| Roe deer           | 0.79         | 0.83   | 0.09          | 0.42 | 0.06       |                    |                                 | - [Recomyx]               | + [trail/trails]       |                                 |                              |                                |
| Red deer           | 0.64         | 0.74   | 0.11          | 0.34 | 0.05       |                    |                                 | - [Recomyx]               |                        | (+)                             | -                            | +                              |
| Red fox            | 0.62         | 0.62   | 0.11          | 0.54 | 0.04       | (-)                | +                               | Not used                  |                        | (-)                             |                              | +                              |
| Badger             | 0.33         | 0.54   | 0.14          | 0.18 | 0.05       | -                  |                                 | - [Recomyx]               |                        |                                 |                              |                                |
| Brown bear         | 0.33         | 0.52   | 0.15          | 0.13 | 0.06       |                    |                                 | (-)[Recomyx]              |                        | (+)                             |                              |                                |
| Chamois            | 0.45         | 0.51   | 0.13          | 0.36 | 0.07       | (+)                |                                 | (-)[Recomyx]              |                        |                                 | (-)                          |                                |
| Brown hare         | 0.29         | 0.45   | 0.12          | 0.21 | 0.07       |                    | +                               | - [Recomyx]               |                        |                                 |                              |                                |
| <i>Martes</i> spp. | 0.24         | 0.29   | 0.10          | 0.25 | 0.06       |                    |                                 | Not used                  |                        | -                               | +                            |                                |

distinct patterns among the ungulates are related to the chamois, as indeed for this species the estimated occupancy varied markedly among the 58 sites (Appendix C). Results of increasing occupancy with increasing elevation and slope are of straightforward interpretation, reflecting how well adapted is this species to rugged and rocky terrain (Corlatti et al., 2011). At the same time, the negative influence of elevation and slope on both deer's occupancy may be evidence of spatial, i.e. altitudinal, segregation with the chamois, whose results included the same spatial drivers, but with converse relationships, as already documented in the Alps (Anderwald et al., 2016). That capture rate of humans was included in model average as negatively affecting roe deer's probability of occurrence is consistent with the fact that this species proved to be rather active during the day as well as people, even if with crepuscular peaks of activity, with a pattern that seemed to be relatively unaffected by different levels of human passage. The roe deer was the only species for which the trail type was retained as significantly affecting detectability, showing that the passage of vehicles decreases detections. A negative relationship of capture rate of humans with red deer's detection probability and a positive relationship with distance from settlements suggest a certain level of shyness of this species towards human activities and avoidance of permanent sources of human disturbance. For this species, daily activity pattern showed a low coefficient of overlap with humans, with little difference between levels of disturbance. For the chamois, the activity pattern analysis in the sites with low disturbance revealed a typical diurnal behaviour, and the coefficient of overlap with human activity was the highest among all species. In contrast, the daily pattern in the sites with higher disturbance was predominantly crepuscular, suggesting a clear shift in diel activity related to human disturbance.

Results for the red fox and marten are similar in suggesting a high level of tolerance to human presence, which could depend on the availability of human-driven food resources and shelters, and a high heterogeneity of potential ecological niches (Červinka et al., 2014). Their occupancy was positively correlated to the capture rate of both humans and vehicles. Such apparent spatial association with proxies of human disturbance is, however, counterbalanced by an evident temporal segregation between mesocarnivores and people. Indeed, they all showed a typical nocturnal behaviour. Results for the badger suggest secretive habits and higher shyness of this species in response to human disturbance as compared to red fox and marten.

Overall, the checklist of 12 species matched the expectations based on previous accounts (Boitani et al., 2003), indicating that sampling effort was sufficient to detect the great majority of the mammal community, including species that are known to be very rare or localised. Indeed, the record of a wolf as species of conservation concern is of interest and confirms the current, natural recolonization of this species in the eastern Alps (Groff et al., 2015). No lynx (*Lynx lynx*) has been recorded, according to the fact that today the only animal known to be present in Trento province is a male that originally dispersed from Switzerland and has recently moved its home range to the SW part of the province (Groff et al., 2015). On the contrary, we did not record the mouflon (*Ovis musimon*), though it is known to be present over some of the focal part of the study area (data from Servizio Foreste e Fauna of Trento Province). Lastly, that we did not record the alpine ibex (*Capra ibex*) is not surprising as this species occurs only in the western part of the PNAB (data from Servizio Foreste e Fauna of Trento Province); furthermore, it is not a forest-dweller and in the summer season it occupies areas at higher altitudes than the area sampled in our study (Aublet et al., 2009).

As general considerations, an important aspect related to the main goal of assessing human disturbance is that the area we sampled is a complex matrix of intermingled disturbance sources

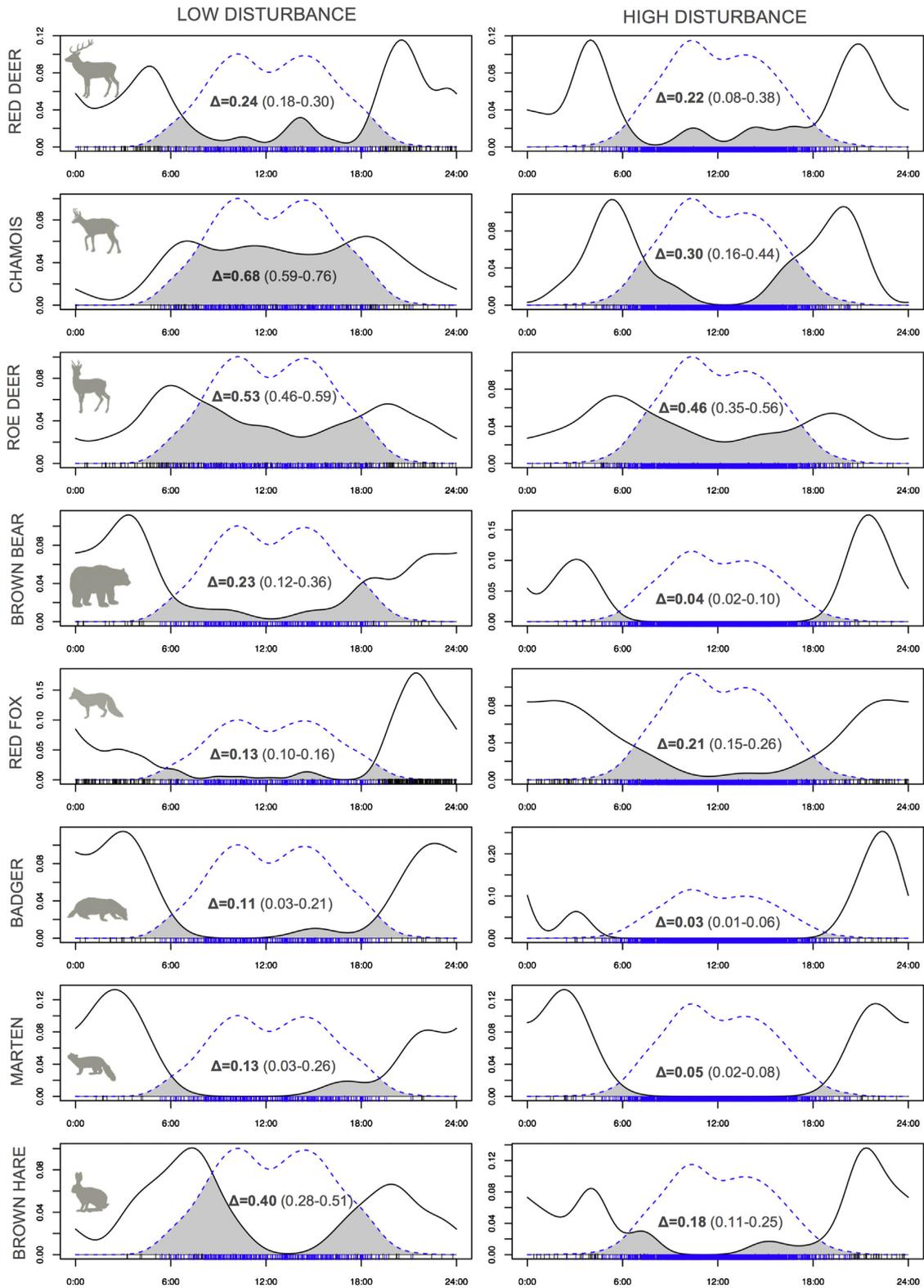


**Fig. 3.** Map of the distribution of the brown bear and chamois in the study area, eastern Alps, with locations of camera traps shown as dots of size proportional to their estimated occupancy. Charts show the influence of significant covariates on occupancy ( $\psi$ ) or detectability ( $p$ ).

in space and time (settlements, infrastructures, road networks, touristic facilities, hikers, etc.). The lack of a clear and unidirectional disturbance gradient, from outside the protected area to its interior, complicates the analysis and interpretation of results. A similar assessment in a national park with stricter regulations and a stronger gradient of disturbance may therefore reveal clearer patterns of human-wildlife interactions. However, we believe that the context we studied may be more representative of the general environmental settings in the Alps. From a methodological perspective, we inspired our design to a systematic protocol developed by the TEAM Network to monitor medium-to-large mammal communities in the tropics. We introduced differences that should be considered for multi-year monitoring, the most limiting being the use of different camera trap models. Indeed the performances of the two models caused clear differences in estimated detection probability. Seemingly, Reconyx cameras had lower sensitivity than the IR+, with increasing significance for the smaller-sized species. The difference was likely due to the much wider detection angle of

the IR+ model ( $100^\circ$ , as compared to  $33^\circ$  of the Reconyx), resulting in higher detectability of target species. However, the IR+ yielded a much higher rate of blank/unidentifiable images and two camera malfunctioned, hence overall performing less well. The two models were set on a nearly equal number of trails and roads, suggesting that the difference in detection efficiency are indeed to be attributed to differences in camera performance and not to differences in species' occurrence between trails and forestry roads.

In conclusion, while we found little evidence for a direct impact of human presence on mammals' occurrence in the study area, we found an effect on their detectability, and, interestingly, on their activity pattern. Our results are relevant for protected area managers to assess the degree at which biodiversity conservation is compatible with infrastructural development, and overall human presence in the Alps. Key recommendations for replicating the study towards setting-up a long-term monitoring include consistency in camera model, camera sites and field routines over the years. These in turn require a solid and collaborative institutional



**Fig. 4.** Diel activity patterns (kernel density curves) for the eight most detected species in the study area, eastern Italian Alps. The overlap with human activity is shown for low and high disturbance levels. The activity pattern of people is shown as dotted lines. The coefficients of overlap ( $\Delta$ ) are also reported, along with their confidence intervals. The wild species names are reported on the left of the respective charts.

set-up. Sampling is cost-efficient as it requires relatively modest field work (human effort deployed amounts to approximately 60 man/days per year). Data from multiple years can eventually be used to derive globally-set indicators for assessing biodiversity change, such as the Wildlife Picture Index (O'Brien et al., 2010).

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### Appendix A. Top-ranked models for each species in the study area, the eastern Alps (the null model ( $\psi(\cdot) p(\cdot)$ ) is also shown). Change in Akaike information criterion ( $\Delta AIC$ ) is the difference in AIC values between each model with the lowest AIC model, $nPars$ is the number of parameters in the model and $w_i$ is the AIC model weight

| Species    | Models                                       | AIC    | $\Delta AIC$ | nPars | $w_i$ |
|------------|--|--------|--------------|-------|-------|
| Red deer   | $\psi(\sim ve) p(\sim mod+cab+homo+ve)$      | 459.51 | 0.00         | 7     | 0.13  |
|            | $\psi(\cdot) p(\sim mod+cab+homo+ve)$        | 459.60 | 0.09         | 6     | 0.12  |
|            | $\psi(\sim el) p(\sim mod+cab+homo+ve)$      | 460.50 | 0.99         | 7     | 0.08  |
|            | $\psi(\sim homo+ve) p(\sim mod+cab+homo+ve)$ | 460.58 | 1.07         | 8     | 0.07  |
|            | $\psi(\sim el+ve) p(\sim mod+cab+homo+ve)$   | 460.93 | 1.42         | 8     | 0.06  |
|            | $\psi(\sim sl+ve) p(\sim mod+cab+homo+ve)$   | 460.94 | 1.43         | 8     | 0.06  |
|            | $\psi(\sim sl) p(\sim mod+cab+homo+ve)$      | 461.03 | 1.52         | 7     | 0.05  |
|            | $\psi(\cdot) p(\cdot)$                       | 475.33 | 15.82        |       |       |
| Roe deer   | $\psi(\sim sl) p(\sim mod+tr+cab)$           | 557.37 | 0.00         | 7     | 0.16  |
|            | $\psi(\cdot) p(\sim mod+tr+cab)$             | 558.24 | 0.87         | 6     | 0.09  |
|            | $\psi(\sim sl+homo) p(\sim mod+tr+cab)$      | 559.08 | 1.71         | 8     | 0.07  |
|            | $\psi(\sim sl+el) p(\sim mod+tr+cab)$        | 559.10 | 1.73         | 8     | 0.07  |
|            | $\psi(\sim sl+ve) p(\sim mod+tr+cab)$        | 559.24 | 1.87         | 8     | 0.06  |
|            | $\psi(\cdot) p(\cdot)$                       | 564.85 | 7.48         |       |       |
|            |  |        |              |       |       |
| Chamois    | $\psi(\sim sl+el) p(\sim mod+homo)$          | 339.91 | 0.00         | 6     | 0.16  |
|            | $\psi(\sim el) p(\sim mod+homo)$             | 340.59 | 0.69         | 5     | 0.12  |
|            | $\psi(\sim sl+el+homo) p(\sim mod+homo)$     | 341.56 | 1.65         | 7     | 0.07  |
|            | $\psi(\sim sl+el+el2) p(\sim mod+homo)$      | 341.66 | 1.75         | 7     | 0.07  |
|            | $\psi(\sim sl+el+ve) p(\sim mod+homo)$       | 341.89 | 1.98         | 7     | 0.06  |
|            | $\psi(\cdot) p(\cdot)$                       | 348.99 | 9.08         |       |       |
|            |  |        |              |       |       |
| Brown bear | $\psi(\cdot) p(\sim mod+cab+homo)$           | 221.15 | 0.00         | 5     | 0.16  |
|            | $\psi(\cdot) p(\cdot)$                       | 221.27 | 0.12         | 2     | 0.14  |
|            | $\psi(\sim el) p(\sim mod+cab+homo)$         | 222.21 | 1.06         | 6     | 0.10  |
|            | $\psi(\sim sl) p(\sim mod+cab+homo)$         | 222.43 | 1.28         | 6     | 0.08  |
|            | $\psi(\sim homo) p(\sim mod+cab+homo)$       | 223.04 | 1.89         | 6     | 0.06  |
|            | $\psi(\sim ve) p(\sim mod+cab+homo)$         | 223.07 | 1.92         | 6     | 0.06  |
|            |  |        |              |       |       |
| Marten     | $\psi(\sim homo) p(\sim cab+homo)$           | 198.47 | 0.00         | 5     | 0.17  |
|            | $\psi(\cdot) p(\sim cab+homo)$               | 199.14 | 0.67         | 4     | 0.11  |
|            | $\psi(\sim ve) p(\sim cab+homo)$             | 199.48 | 1.02         | 5     | 0.10  |
|            | $\psi(\sim homo+ve) p(\sim cab+homo)$        | 199.90 | 1.43         | 6     | 0.08  |
|            | $\psi(\sim el+homo) p(\sim cab+homo)$        | 200.17 | 1.71         | 6     | 0.07  |
|            | $\psi(\sim sl+homo) p(\sim cab+homo)$        | 200.26 | 1.80         | 6     | 0.07  |
|            | $\psi(\cdot) p(\cdot)$                       | 204.08 | 5.61         |       |       |
|            |  |        |              |       |       |
| Red fox    | $\psi(\sim el+homo) p(\sim cab+ve)$          | 454.24 | 0.00         | 6     | 0.26  |
|            | $\psi(\sim el+el2+homo) p(\sim cab+ve)$      | 455.94 | 1.70         | 7     | 0.11  |
|            | $\psi(\sim el+homo+ve) p(\sim cab+ve)$       | 455.97 | 1.74         | 7     | 0.10  |
|            | $\psi(\sim homo) p(\sim cab+ve)$             | 455.98 | 1.74         | 5     | 0.10  |
|            | $\psi(\sim sl+el+homo) p(\sim cab+ve)$       | 456.15 | 1.91         | 7     | 0.10  |
|            | $\psi(\cdot) p(\cdot)$                       | 467.70 | 13.46        |       |       |
|            |  |        |              |       |       |
| Badger     | $\psi(\sim el+ve) p(\sim mod+cab+homo)$      | 232.11 | 0.00         | 7     | 0.27  |
|            | $\psi(\sim sl+el+ve) p(\sim mod+cab+homo)$   | 233.56 | 1.45         | 8     | 0.13  |
|            | $\psi(\sim el+el2+ve) p(\sim mod+cab+homo)$  | 234.00 | 1.89         | 8     | 0.11  |
|            | $\psi(\sim el+homo+ve) p(\sim mod+cab+homo)$ | 234.07 | 1.96         | 8     | 0.10  |
|            | $\psi(\cdot) p(\cdot)$                       | 259.11 | 27.00        |       |       |
|            |  |        |              |       |       |
| Brown hare | $\psi(\sim homo) p(\sim mod+tr+cab+homo)$    | 224.48 | 0.00         | 8     | 0.27  |
|            | $\psi(\sim homo+ve) p(\sim mod+tr+cab+homo)$ | 225.37 | 0.89         | 9     | 0.17  |
|            | $\psi(\sim sl+homo) p(\sim mod+tr+cab+homo)$ | 226.46 | 1.98         | 9     | 0.10  |
|            | $\psi(\sim el+homo) p(\sim mod+tr+cab+homo)$ | 226.47 | 1.99         | 9     | 0.10  |
|            | $\psi(\cdot) p(\cdot)$                       | 248.43 | 23.95        |       |       |
|            |  |        |              |       |       |

Mod=camera model; tr=trail type; cab=distance from settlements; homo=capture rate of humans; ve=capture rate of vehicles; el=elevation; el2=elevation squared; sl=slope.

**Appendix B. Summaries of model average for each species. NMod is the number of models that include each covariate;  $\psi$  and  $p$  are the mean occupancy and detectability, respectively, predicted by the average model at the camera trap sites**

| Species              | Covariates          | Estimate (SE)       | P value        | Rel. Imp. | N Mod | $\psi$ (SE) | $p$ (SE)    |             |             |             |
|----------------------|---------------------|---------------------|----------------|-----------|-------|-------------|-------------|-------------|-------------|-------------|
| Brown bear           | $p(\text{modRec})$  | -0.858 (0.510)      | 0.0924         | 0.62      | 5     | 0.52 (0.15) | 0.13 (0.06) |             |             |             |
|                      | $p(\text{cab})$     | 0.544 (0.290)       | 0.0613         | 0.62      | 5     |             |             |             |             |             |
|                      | $p(\text{homo})$    | -0.673 (0.390)      | 0.0845         | 0.62      | 5     |             |             |             |             |             |
|                      | $\psi(\text{el})$   | -0.464 (0.497)      | 0.3511         | 0.12      | 1     |             |             |             |             |             |
|                      | $\psi(\text{sl})$   | -0.365 (0.465)      | 0.4320         | 0.10      | 1     |             |             |             |             |             |
|                      | $\psi(\text{homo})$ | -0.272 (0.704)      | 0.6988         | 0.08      | 1     |             |             |             |             |             |
|                      | $\psi(\text{ve})$   | -0.115 (0.394)      | 0.7694         | 0.08      | 1     |             |             |             |             |             |
| Red deer             | $p(\text{modRec})$  | -0.589 (0.274)      | 0.03146        | 1.00      | 7     | 0.74 (0.11) | 0.34 (0.05) |             |             |             |
|                      | $p(\text{cab})$     | 0.254 (0.143)       | 0.07573        | 1.00      | 7     |             |             |             |             |             |
|                      | $p(\text{homo})$    | -1.509 (0.381)      | 7.42e-05       | 1.00      | 7     |             |             |             |             |             |
|                      | $p(\text{ve})$      | 0.721 (0.309)       | 0.01946        | 1.00      | 7     |             |             |             |             |             |
|                      | $\psi(\text{ve})$   | -0.482 (0.412)      | 0.24146        | 0.47      | 4     |             |             |             |             |             |
|                      | $\psi(\text{el})$   | -0.346 (0.371)      | 0.35156        | 0.21      | 2     |             |             |             |             |             |
|                      | $\psi(\text{sl})$   | -0.263 (0.349)      | 0.45076        | 0.18      | 2     |             |             |             |             |             |
|                      | $\psi(\text{homo})$ | 1.068 (1.260)       | 0.39643        | 0.09      | 1     |             |             |             |             |             |
|                      | Roe deer            | $\psi(\text{sl})$   | -0.755 (0.523) | 0.149372  | 0.68  |             |             | 4           | 0.83 (0.09) | 0.42 (0.06) |
| $p(\text{modRec})$   |                     | -0.699 (0.234)      | 0.002764       | 1.00      | 5     |             |             |             |             |             |
| $p(\text{trtrail})$  |                     | 0.549 (0.254)       | 0.031109       | 1.00      | 5     |             |             |             |             |             |
| $p(\text{trtrailS})$ |                     | 0.849 (0.344)       | 0.013579       | 1.00      | 5     |             |             |             |             |             |
| $p(\text{cab})$      |                     | -0.129 (0.114)      | 0.257554       | 1.00      | 5     |             |             |             |             |             |
| $\psi(\text{homo})$  |                     | -0.196 (0.340)      | 0.565100       | 0.11      | 1     |             |             |             |             |             |
| $\psi(\text{el})$    |                     | -0.230 (0.448)      | 0.608631       | 0.11      | 1     |             |             |             |             |             |
| $\psi(\text{ve})$    |                     | 0.160 (0.477)       | 0.736725       | 0.10      | 1     |             |             |             |             |             |
| Chamois              |                     | $\psi(\text{sl})$   | 0.568 (0.396)  | 0.15110   | 0.68  | 4           | 0.51 (0.13) | 0.36 (0.06) |             |             |
|                      | $\psi(\text{el})$   | 0.661 (0.349)       | 0.05838        | 1.00      | 5     |             |             |             |             |             |
|                      | $p(\text{modRec})$  | -0.632 (0.361)      | 0.07998        | 1.00      | 5     |             |             |             |             |             |
|                      | $p(\text{homo})$    | -1.074 (0.344)      | 0.00181        | 1.00      | 5     |             |             |             |             |             |
|                      | $\psi(\text{homo})$ | -0.359 (0.582)      | 0.53699        | 0.12      | 1     |             |             |             |             |             |
|                      | $\psi(\text{el2})$  | 0.162 (0.330)       | 0.62338        | 0.11      | 1     |             |             |             |             |             |
|                      | $\psi(\text{ve})$   | 0.037 (0.294)       | 0.90009        | 0.10      | 1     |             |             |             |             |             |
|                      | Red fox             | $\psi(\text{el})$   | -0.630 (0.336) | 0.06114   | 0.78  | 4           |             |             | 0.62 (0.11) | 0.54 (0.04) |
|                      |                     | $\psi(\text{homo})$ | 1.420 (0.698)  | 0.04177   | 1.00  | 5           |             |             |             |             |
| $p(\text{cab})$      |                     | -0.201 (0.121)      | 0.08269        | 1.00      | 5     |             |             |             |             |             |
| $p(\text{ve})$       |                     | 0.389 (0.146)       | 0.00768        | 1.00      | 5     |             |             |             |             |             |
| $\psi(\text{el2})$   |                     | -0.176 (0.322)      | 0.58378        | 0.13      | 1     |             |             |             |             |             |
| $\psi(\text{ve})$    |                     | 0.186 (0.385)       | 0.62949        | 0.13      | 1     |             |             |             |             |             |
| $\psi(\text{sl})$    |                     | -0.089 (0.302)      | 0.76677        | 0.12      | 1     |             |             |             |             |             |
| Badger               |                     | $\psi(\text{el})$   | -1.058 (0.512) | 0.0388    | 1.00  | 4           | 0.54 (0.14) | 0.18 (0.05) |             |             |
|                      |                     | $\psi(\text{ve})$   | 2.156 (1.508)  | 0.1528    | 1.00  | 4           |             |             |             |             |
|                      | $p(\text{modRec})$  | -3.261 (0.690)      | 2.3e-06        | 1.00      | 4     |             |             |             |             |             |
|                      | $p(\text{cab})$     | 0.166 (0.264)       | 0.5303         | 1.00      | 4     |             |             |             |             |             |
|                      | $p(\text{homo})$    | -0.322 (0.232)      | 0.1644         | 1.00      | 4     |             |             |             |             |             |
|                      | $\psi(\text{sl})$   | -0.397 (0.552)      | 0.4724         | 0.18      | 1     |             |             |             |             |             |
|                      | $\psi(\text{el2})$  | 0.175 (0.519)       | 0.7359         | 0.15      | 1     |             |             |             |             |             |
|                      | $\psi(\text{homo})$ | -0.132 (0.636)      | 0.8353         | 0.14      | 1     |             |             |             |             |             |
|                      | Brown hare          | $\psi(\text{homo})$ | 2.173 (1.027)  | 0.0344    | 1.00  | 4           |             |             | 0.45 (0.12) | 0.21 (0.07) |
| $p(\text{modRec})$   |                     | -1.547 (2.364)      | 0.0155         | 1.00      | 4     |             |             |             |             |             |
| $p(\text{trtrail})$  |                     | -1.053 (2.371)      | 0.1002         | 1.00      | 4     |             |             |             |             |             |
| $p(\text{trtrailS})$ |                     | -3.778 (13.005)     | 0.9370         | 1.00      | 4     |             |             |             |             |             |
| $p(\text{cab})$      |                     | 1.473 (1.114)       | 0.1859         | 1.00      | 4     |             |             |             |             |             |
| $p(\text{homo})$     |                     | -0.587 (1.014)      | 0.8740         | 1.00      | 4     |             |             |             |             |             |
| $\psi(\text{ve})$    |                     | -2.153 (2.712)      | 0.4275         | 0.22      | 1     |             |             |             |             |             |
| $\psi(\text{sl})$    |                     | -0.883 (1.713)      | 0.8877         | 0.13      | 1     |             |             |             |             |             |
| $\psi(\text{el})$    |                     | 0.447 (1.601)       | 0.9440         | 0.13      | 1     |             |             |             |             |             |
| Marten               |                     | $\psi(\text{homo})$ | 0.501 (0.348)  | 0.15001   | 0.58  | 4           | 0.29 (0.10) | 0.25 (0.06) |             |             |
|                      | $p(\text{cab})$     | -0.773 (0.287)      | 0.00694        | 1.00      | 6     |             |             |             |             |             |
|                      | $p(\text{homo})$    | 0.545 (0.251)       | 0.03015        | 1.00      | 6     |             |             |             |             |             |
|                      | $\psi(\text{ve})$   | 0.327 (0.327)       | 0.31721        | 0.28      | 2     |             |             |             |             |             |
|                      | $\psi(\text{el})$   | -0.211 (0.386)      | 0.58568        | 0.10      | 1     |             |             |             |             |             |
|                      | $\psi(\text{sl})$   | 0.171 (0.381)       | 0.65387        | 0.09      | 1     |             |             |             |             |             |

Mod=camera model; tr=trail type; cab=distance from settlements; homo=capture rate of humans; ve=capture rate of vehicles; el=elevation; el2=elevation squared; sl=slope.

### Appendix C. Predicted occupancy ( $\psi$ ) for each species at each camera trap station (58 sites)

| Site        | Predicted $\psi$ |          |          |         |        |            |        |         |
|-------------|------------------|----------|----------|---------|--------|------------|--------|---------|
|             | Brown bear       | Red deer | Roe deer | Chamois | Badger | Brown hare | Marten | Red fox |
| CT-TNT-1-01 | 0.54             | 0.77     | 0.86     | 0.29    | 0.78   | 0.48       | 0.28   | 0.77    |
| CT-TNT-1-02 | 0.54             | 0.79     | 0.89     | 0.25    | 0.73   | 0.86       | 0.33   | 0.91    |
| CT-TNT-1-03 | 0.53             | 0.75     | 0.90     | 0.43    | 0.40   | 0.24       | 0.24   | 0.45    |
| CT-TNT-1-04 | 0.51             | 0.75     | 0.91     | 0.64    | 0.12   | 0.86       | 0.32   | 0.71    |
| CT-TNT-1-05 | 0.51             | 0.73     | 0.83     | 0.67    | 0.24   | 0.23       | 0.24   | 0.36    |
| CT-TNT-1-06 | 0.55             | 0.77     | 0.90     | 0.24    | 0.77   | 0.24       | 0.25   | 0.62    |
| CT-TNT-1-07 | 0.51             | 0.71     | 0.82     | 0.51    | 0.93   | 0.81       | 0.35   | 0.86    |
| CT-TNT-1-08 | 0.50             | 0.73     | 0.81     | 0.73    | 0.19   | 0.23       | 0.24   | 0.33    |
| CT-TNT-1-09 | 0.49             | 0.75     | 0.74     | 0.69    | 0.24   | 1.00       | 0.47   | 0.99    |
| CT-TNT-1-10 | 0.53             | 0.75     | 0.89     | 0.46    | 0.41   | 0.36       | 0.26   | 0.53    |
| CT-TNT-1-11 | 0.51             | 0.74     | 0.87     | 0.54    | 0.62   | 0.89       | 0.35   | 0.86    |
| CT-TNT-1-12 | 0.51             | 0.73     | 0.76     | 0.57    | 0.72   | 0.31       | 0.27   | 0.58    |
| CT-TNT-1-13 | 0.50             | 0.74     | 0.74     | 0.72    | 0.24   | 0.76       | 0.31   | 0.73    |
| CT-TNT-1-14 | 0.53             | 0.76     | 0.87     | 0.39    | 0.58   | 0.24       | 0.25   | 0.54    |
| CT-TNT-1-15 | 0.51             | 0.59     | 0.87     | 0.63    | 0.99   | 0.38       | 0.33   | 0.53    |
| CT-TNT-1-16 | 0.49             | 0.58     | 0.88     | 0.68    | 1.00   | 0.99       | 0.51   | 0.96    |
| CT-TNT-1-17 | 0.52             | 0.75     | 0.75     | 0.50    | 0.61   | 0.28       | 0.26   | 0.60    |
| CT-TNT-1-18 | 0.52             | 0.74     | 0.82     | 0.57    | 0.39   | 0.24       | 0.25   | 0.45    |
| CT-TNT-1-19 | 0.49             | 0.69     | 0.75     | 0.74    | 0.75   | 0.68       | 0.32   | 0.69    |
| CT-TNT-1-20 | 0.51             | 0.75     | 0.90     | 0.64    | 0.14   | 0.85       | 0.31   | 0.72    |
| CT-TNT-1-21 | 0.52             | 0.74     | 0.82     | 0.59    | 0.37   | 0.26       | 0.25   | 0.46    |
| CT-TNT-1-22 | 0.55             | 0.77     | 0.88     | 0.25    | 0.83   | 0.24       | 0.25   | 0.65    |
| CT-TNT-1-23 | 0.49             | 0.71     | 0.48     | 0.77    | 0.36   | 0.24       | 0.26   | 0.46    |
| CT-TNT-1-24 | 0.54             | 0.77     | 0.90     | 0.28    | 0.70   | 0.41       | 0.27   | 0.69    |
| CT-TNT-1-25 | 0.51             | 0.75     | 0.90     | 0.57    | 0.26   | 0.93       | 0.35   | 0.86    |
| CT-TNT-1-26 | 0.52             | 0.74     | 0.82     | 0.58    | 0.39   | 0.23       | 0.25   | 0.45    |
| CT-TNT-1-27 | 0.53             | 0.75     | 0.86     | 0.39    | 0.73   | 0.38       | 0.27   | 0.66    |
| CT-TNT-1-28 | 0.54             | 0.76     | 0.78     | 0.33    | 0.84   | 0.23       | 0.26   | 0.66    |
| CT-TNT-1-29 | 0.51             | 0.74     | 0.91     | 0.62    | 0.19   | 0.65       | 0.28   | 0.55    |
| CT-TNT-1-30 | 0.53             | 0.75     | 0.74     | 0.43    | 0.77   | 0.27       | 0.26   | 0.65    |
| CT-TNT-2-01 | 0.51             | 0.74     | 0.87     | 0.58    | 0.48   | 0.96       | 0.38   | 0.91    |
| CT-TNT-2-02 | 0.51             | 0.74     | 0.83     | 0.68    | 0.22   | 0.52       | 0.28   | 0.56    |
| CT-TNT-2-03 | 0.52             | 0.73     | 0.83     | 0.50    | 0.71   | 0.27       | 0.26   | 0.54    |
| CT-TNT-2-04 | 0.52             | 0.77     | 0.90     | 0.43    | 0.39   | 0.80       | 0.31   | 0.81    |
| CT-TNT-2-05 | 0.48             | 0.68     | 0.86     | 0.60    | 0.97   | 1.00       | 0.64   | 1.00    |
| CT-TNT-2-06 | 0.53             | 0.76     | 0.83     | 0.42    | 0.62   | 0.27       | 0.26   | 0.59    |
| CT-TNT-2-07 | 0.49             | 0.72     | 0.71     | 0.82    | 0.14   | 0.42       | 0.27   | 0.42    |
| CT-TNT-2-08 | 0.53             | 0.76     | 0.88     | 0.42    | 0.51   | 0.29       | 0.25   | 0.55    |
| CT-TNT-2-10 | 0.52             | 0.74     | 0.85     | 0.57    | 0.33   | 0.26       | 0.25   | 0.45    |
| CT-TNT-2-11 | 0.55             | 0.78     | 0.92     | 0.22    | 0.73   | 0.23       | 0.25   | 0.59    |
| CT-TNT-2-12 | 0.51             | 0.74     | 0.84     | 0.65    | 0.25   | 0.24       | 0.25   | 0.37    |
| CT-TNT-2-13 | 0.53             | 0.76     | 0.82     | 0.37    | 0.76   | 0.51       | 0.29   | 0.77    |
| CT-TNT-2-14 | 0.51             | 0.75     | 0.89     | 0.62    | 0.18   | 0.54       | 0.27   | 0.52    |
| CT-TNT-2-15 | 0.51             | 0.74     | 0.84     | 0.63    | 0.28   | 0.25       | 0.25   | 0.40    |
| CT-TNT-2-16 | 0.53             | 0.75     | 0.86     | 0.44    | 0.58   | 0.27       | 0.25   | 0.54    |
| CT-TNT-2-17 | 0.50             | 0.72     | 0.72     | 0.78    | 0.20   | 0.31       | 0.26   | 0.40    |
| CT-TNT-2-18 | 0.53             | 0.75     | 0.89     | 0.46    | 0.40   | 0.27       | 0.25   | 0.48    |
| CT-TNT-2-19 | 0.51             | 0.75     | 0.76     | 0.51    | 0.68   | 0.90       | 0.35   | 0.91    |
| CT-TNT-2-20 | 0.55             | 0.77     | 0.85     | 0.25    | 0.85   | 0.23       | 0.25   | 0.66    |
| CT-TNT-2-21 | 0.55             | 0.78     | 0.91     | 0.19    | 0.84   | 0.39       | 0.27   | 0.75    |
| CT-TNT-2-23 | 0.53             | 0.76     | 0.87     | 0.41    | 0.58   | 0.28       | 0.26   | 0.56    |
| CT-TNT-2-24 | 0.51             | 0.50     | 0.82     | 0.49    | 1.00   | 0.27       | 0.38   | 0.65    |
| CT-TNT-2-25 | 0.52             | 0.74     | 0.87     | 0.63    | 0.22   | 0.26       | 0.25   | 0.37    |
| CT-TNT-2-26 | 0.53             | 0.75     | 0.79     | 0.42    | 0.78   | 0.33       | 0.27   | 0.66    |
| CT-TNT-2-27 | 0.52             | 0.75     | 0.78     | 0.50    | 0.57   | 0.24       | 0.25   | 0.54    |
| CT-TNT-2-28 | 0.51             | 0.74     | 0.80     | 0.61    | 0.36   | 0.28       | 0.25   | 0.48    |
| CT-TNT-2-29 | 0.54             | 0.76     | 0.83     | 0.31    | 0.85   | 0.42       | 0.28   | 0.76    |
| CT-TNT-2-30 | 0.54             | 0.76     | 0.80     | 0.33    | 0.82   | 0.25       | 0.26   | 0.66    |

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# Poor management in protected areas is associated with lowered tropical mammal diversity

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## Keywords

camera trapping; bushmeat hunting; species richness; hierarchical modeling; community occupancy; Tanzania.

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## Abstract

Numerous protected areas (PAs) have been created worldwide to safeguard wildlife and other natural resources from anthropogenic threats such as habitat destruction and bushmeat hunting. However, conservation efforts in many tropical PAs are still inadequate, revealing deficiencies in management effectiveness. It is therefore important to quantify how different protection regimes impact wildlife within PAs. We investigated the differences between forest mammal communities in two ecologically comparable PAs in the Udzungwa Mountains (Tanzania) with contrasting management regimes. One is a well-protected national park with efficient law enforcement; the other has suffered decades of inadequate protection, mainly resulting in high levels of illegal hunting. Using camera-trapping data, we assessed the target communities in terms of species richness, functional composition (i.e. proportions of trophic guilds) and species-specific occurrences, all while accounting for imperfect detection. We found striking differences between the two mammal communities: lower species richness, alteration in the trophic structure and reduced occurrence probabilities for most species in the forest with high disturbance. The difference in occurrence probability between the two PAs tended to be highest for larger-bodied species. Our results show that strictly enforced legal protection is required to maintain diverse mammal communities in tropical forests under ever-increasing anthropogenic threats. While PAs are the cornerstone of efforts to conserve tropical biodiversity, the future of biodiversity within them is closely tied to the effectiveness of enforcement.

## Introduction

Tropical rainforests are the richest terrestrial ecosystems on the planet (Myers *et al.*, 2000), harboring unparalleled diversity that provides important ecosystem services at local, regional and global levels (Kremen *et al.*, 2000). Mammals are key components within tropical ecosystems, playing integral roles as consumers, dispersers of seeds and spores, predators and prey (Ahumada *et al.*, 2011). Changes in the richness and structure of mammalian communities are therefore likely to have consequences for ecosystem stability (Derhé *et al.*, 2018). Mammals also tend to be charismatic species and are thus important flagships for conservation efforts (Rondinini, Rodrigues & Boitani, 2011). Bushmeat hunting is the most widespread form of resource extraction in tropical forests (Fa, Peres & Meeuwig, 2002; Ripple

*et al.*, 2016), and represents one of the main anthropogenic threats to wild mammals (Laurance *et al.*, 2012; Tilman *et al.*, 2017). The global bushmeat hunting crisis is difficult to address because it is intimately tied to human development challenges such as food insecurity, emergent disease risks and land-use change (Ripple *et al.*, 2016). To face this threat, numerous protected areas (PAs) have been created worldwide to safeguard wildlife and other natural resources. However, conservation efforts in most tropical PAs are still inadequate, as management is not always effective (Laurance *et al.*, 2012; Tranquilli *et al.*, 2014). With wildlife populations declining outside PAs, poaching pressure is also increasing in many parks and reserves (Ripple *et al.*, 2016), hence the notion of 'paper parks', that is PAs that only exist on paper, where ground conservation is minimal or non-existent (Bruner *et al.*, 2001; Joppa, Loarie & Pimm, 2008). It is

therefore critical to document and quantify how different protection regimes of PAs impact wildlife communities to develop effective conservation strategies.

Here, we investigate the differences between forest mammal communities in two ecologically comparable PAs with contrasting management regimes in the Udzungwa Mountains of Tanzania: Mwanihana and Uzungwa Scarp forests. The Udzungwa Mountains are of outstanding value for biological endemism and biodiversity conservation (Rovero *et al.*, 2014a). The main difference between the two PAs is the degree to which management and protective measures are enforced. The first one, Mwanihana, is a well-protected national park where active law enforcement is ensured and disturbance is virtually absent (DeFries *et al.*, 2010). In contrast, the other one, Uzungwa Scarp, has suffered decades of inadequate protection, mainly resulting in much higher levels of illegal hunting (Rovero *et al.*, 2012). For example, Rovero *et al.* (2010) showed an increase in disturbance in this reserve of 19% in just 10 years (1998–2008), including numerous snares for poaching, forest fires, gunshots, and tree harvesting. Notably, snare density in Uzungwa Scarp was among the highest in African tropical forests (Topp-Jørgensen *et al.*, 2009). Although logging and firewood collection may also partially affect mammal abundance (Rovero *et al.*, 2012), evidence suggests that the level of poaching is the main difference between these PAs and the main threat to wildlife (Topp-Jørgensen *et al.*, 2009; Rovero *et al.*, 2010, 2012; Hegerl *et al.*, 2015). The two target PAs share several ecological and climatic characteristics, making them an excellent model system to address our study objectives. They have similar extent and altitudinal range of forest cover, and remarkably comparable mean annual rainfall and temperature range (Hegerl *et al.*, 2015). This results in a high degree of overlap in tree species composition (Lovett & Wasser, 2008) and, until the last century, comparable mammal richness and diversity, with the exception of a few species with very limited range that do not occur in both PAs (Dinesen *et al.*, 2001).

We compared mammal communities using the same sampling design over the two study areas. We evaluated the target communities in terms of species richness, functional composition (i.e. richness and proportions of trophic guilds) and species-specific occurrence probabilities, which together provide critical information for conservation. While species richness represents the canonical, most direct and mainly used measurement of biodiversity (Gotelli & Colwell, 2001), functional composition (Petchey & Gaston, 2002), which links diversity to ecological processes, has been shown to be a good descriptor of ecosystem function, with growing applications in ecology and conservation science (Mouillot *et al.*, 2013; Derhé *et al.*, 2016). In addition, as many threatened mammal species remain poorly studied (Ripple *et al.*, 2016), species-specific metrics of occurrence are greatly valuable, particularly if communities hold rare and endemic species. We focused on terrestrial (i.e. predominantly ground-dwelling), medium- to large-bodied mammals that are relatively easily detected by camera traps. We modeled the data using a multi-species hierarchical occupancy approach (Dorazio

*et al.*, 2006), which allowed us to investigate the two communities while accounting for multiple sources of uncertainty including imperfect detection (Zipkin *et al.*, 2010; Rich *et al.*, 2016). Our analysis uses a recently proposed multi-region model that incorporates all species observed during sampling, regardless of sample sizes, and allows for hypothesis testing on guild- and community-specific species richness as well as estimation of species-specific occurrence probabilities (Tenan *et al.*, 2017). Our objective was to compare the target mammal communities in view of the different hunting and protection levels. Furthermore, given that vulnerability to disturbance may disproportionately impact larger-bodied species (Cardillo *et al.*, 2005; Ripple *et al.*, 2016), we also tested the correlation between average species-specific body mass and differences in estimated average occurrence probability in the two PAs. We hypothesized that (1) species richness and species-specific occurrence probabilities are inversely related to human disturbance, with large-bodied species showing the strongest correlation; and (2) the functional composition of the mammal community is modified in the disturbed forest in relation to the well-protected one as a result of changes in richness of the trophic guilds most sensitive to disturbance.

## Materials and methods

### Study area

The highland forests of Tanzania are among the most important areas in the world for biodiversity conservation due to the exceptional density of threatened and endemic species (Rovero *et al.*, 2014a). In particular, the Udzungwa Mountains are a stronghold for many rare species, including mammals (Rovero & De Luca, 2007), such as the recently discovered endemic gray-faced sengi *Rhynchocyon udzungwensis*, the IUCN-endangered Abbott's duiker *Cephalophus spadix*, a large-bodied forest antelope which is endemic of Tanzania and threatened by hunting and habitat loss (Bowkett *et al.*, 2014), and the ground-dwelling, IUCN-endangered (and Udzungwa's iconic monkey) Sanje mangabey *Cercocebus sanjei* (Rovero *et al.*, 2014a; IUCN 2016). Mwanihana (177 km<sup>2</sup>) is a forest within the Udzungwa Mountains National Park, while Uzungwa Scarp (200 km<sup>2</sup>) is a nature reserve (Fig. 1). Both forests are east-facing escarpment slopes, characterized by a unique continuous vegetation cover from lowland (300–800 m), sub-montane deciduous forest (800–1400 m) to evergreen moist montane forest (>1400 m; Lovett & Wasser, 2008). In both areas, the forest at lower elevation zones was historically degraded and hence has large portions of secondary, regenerating vegetation. The interior forest is comparatively undisturbed with large chunks of pristine, closed-canopy moist forest, although in Uzungwa Scarp these zones are generally more degraded than Mwanihana (Rovero *et al.*, 2014b). Shared ecological and climatic characteristics are reported in Fig. 1. Active law enforcement has taken place in Mwanihana since establishment of the area as a national park in 1992 (Rovero *et al.*, 2012). On the contrary, Uzungwa Scarp has not received

adequate protection over the same time period (Rovero *et al.*, 2010, 2012). Thus, anthropogenic disturbance in Uzungwa Scarp is much higher, primarily from illegal hunting through snares, but also because of habitat destruction and logging (Nielsen, 2006; Hegerl *et al.*, 2015). In addition, the anthropogenic pressure in Mwanihana comes from villages located only along the eastern side of the forest, with the other sides bordering drier but protected habitats within the national park. On the contrary, Uzungwa Scarp is an isolated forest completely surrounded by villages and hence with no protected natural habitat buffering the reserve. As an indication of poaching incidence, during the setting of camera traps in Uzungwa Scarp we found nearly 300 snares, while only 50 were found in Mwanihana. Additionally, Hegerl *et al.* (2015) reported a marked difference between Mwanihana and Uzungwa Scarp both in the annual budget allocated for forest management, (USD *c.* 400 000 vs. 1000 respectively), and in the number of permanent staff units (78 vs. 1 respectively).

## Data collection

We sampled both forests simultaneously during the dry season 2016 (July–November) according to a standardized protocol for monitoring terrestrial vertebrates (TEAM Network, 2011). We employed three arrays of 20 cameras in both forests for a total of 60 sampling locations in each PA (Fig. 1). Cameras were placed at a density of one camera per 2 km<sup>2</sup>. Locations were selected to be representative of the habitat and elevation gradient of each forest. Each camera was placed on a tree to record a trail segment approximately 2–3 m away and was deployed for 30–35 days. The area within the sensor field of the camera was cleared of ground vegetation for better visibility. In Mwanihana, data were collected through the Tropical Ecology Assessment and Monitoring (TEAM) Network project (Rovero & Ahumada, 2017) by deploying Reconyx HC500 camera traps (Reconyx Inc., Holmen, WI, USA). In Uzungwa Scarp, two different camera trap types were used according to availability and randomly placed across the sites: (1) Reconyx HC500 and (2) Cuddeback Ambush IR flash camera traps (Ambush IR, Cuddeback, De Pere, Wisconsin, USA). The realized sampling effort was 1922 (mean per camera 32.03) camera days in Mwanihana and 1816 (33.63) in Uzungwa Scarp respectively.

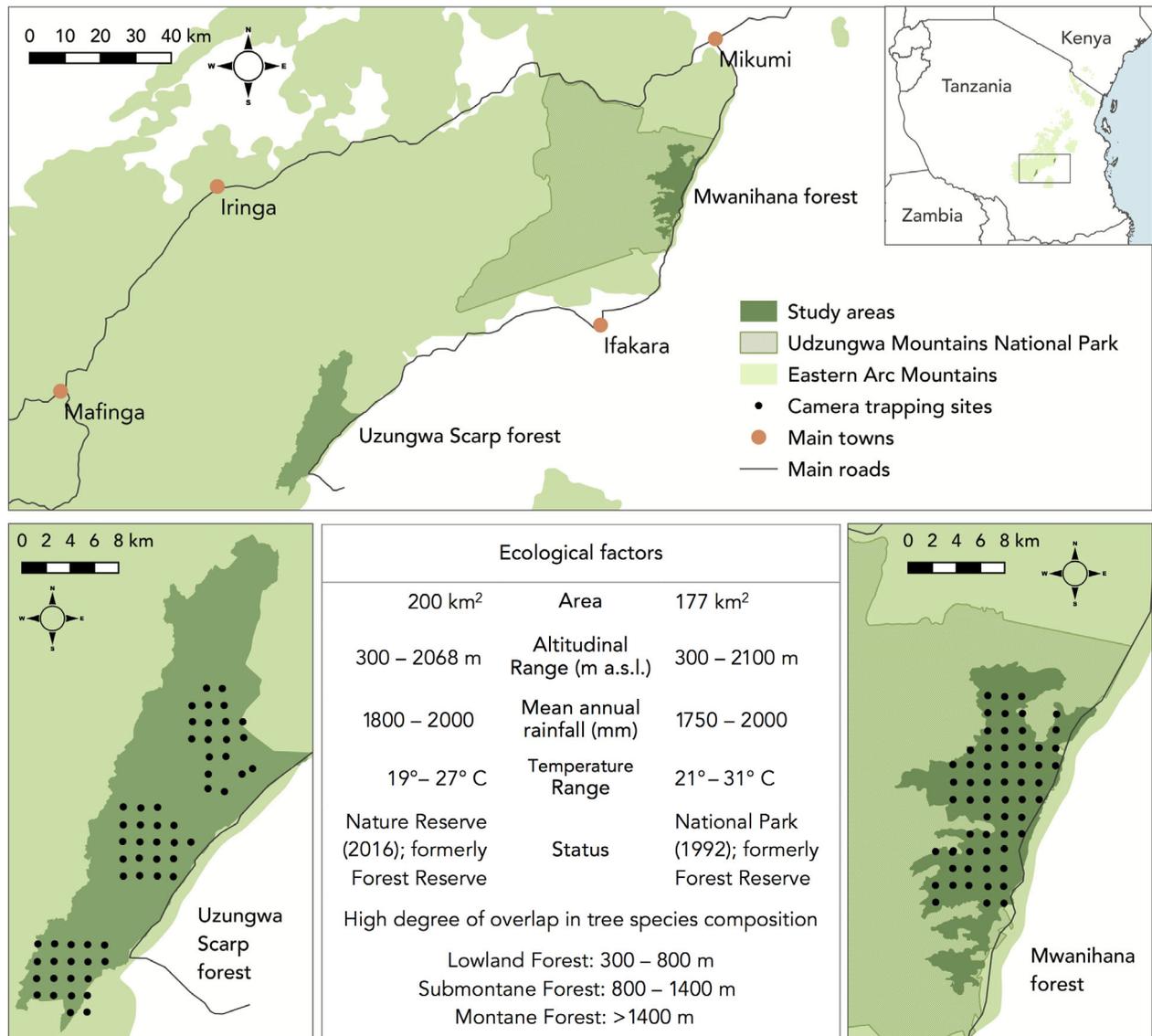
## Statistical analysis

Total number of detections of each species during the entire sampling period were summarized in an array,  $Y$ , with elements  $y_{i,j,r}$  for the  $i$ th species, in site  $j$  of region  $r$ . We used a sampling occasion of 5 days, which led to a median of 7 total sampling occasions  $K_{j,r}$  among different sites and regions. Sampling at each point  $j$  with  $K > 1$  sampling occasions over a short period (such that the community remained closed for the duration of the survey) allowed us to formally distinguish between species absence and non-detection.

We analyzed the data using a multi-region community occupancy model (Tenan *et al.*, 2017). We structured our model to compare species richness and community composition of the sampled mammal communities between the two regions (Mwanihana and Uzungwa Scarp,  $r = 2$ ) based on four trophic guilds ( $g = 4$ ), with the underlying model assumption that each species  $i = 1, 2, \dots, n_r$  (where  $n_r$  is the number of observed species in each region) can be assigned to only one guild. Each detected species was assigned to one of the following guilds (diet data sourced from Wilman *et al.*, 2014): (1) carnivore (>50% of diet based on vertebrates), (2) herbivore (include grazers, browsers, granivores and frugivores, with >50% plant material), (3) insectivore (>50% invertebrates), (4) omnivore (generally both plant and animal material; Robinson & Redford, 1986). Guild was thus known for all observed species but not for unobserved ones. We augmented the detection and guild data for both regions such that the total number of possible species in the community was  $M = 100$ , that is by  $M - n_r$  number of ‘all-zero’ encounter histories for each region, a proportion  $\Omega_r$  of which are the estimated unobserved species that exist in the community but that were never detected (Dorazio *et al.*, 2006). We chose  $M$  so that it was much larger than the total number of species in either communities and equal across regions (Sutherland *et al.*, 2016). The latent binary variable  $\omega_{i,r} \sim \text{Bern}(\Omega_r)$  denotes whether species  $i$  truly exists in community  $r$  ( $\omega_{i,r} = 1$ ) or not ( $\omega_{i,r} = 0$ ). For species that were observed in a region,  $\omega_{i,r} = 1$ . Variation across regions in guild-specific richness is assumed to be a Poisson process where  $N_{g,r} \sim \text{Poiss}(\lambda_{g,r})$  and  $\lambda_{g,r}$  is the expected guild- and region-specific richness. Following the model formulation of Tenan *et al.* (2017), we marginalized over a binomial prior distribution (assuming  $M$  trials each having probability  $\Omega_r$  of occurring) to estimate the total number of species in each community,  $N_r$ . We specified  $\Omega_r = (\sum_g \lambda_{g,r})/M$  and assumed a guild indicator variable  $g_{i,r} \sim \text{Cat}(\pi_r)$  that allowed the model to estimate guild membership for the augmented species, with  $\pi_r = (\pi_{1,r}, \dots, \pi_{G,r})$  and  $\pi_{g,r} = \lambda_{g,r} / \sum_g \lambda_{g,r}$ . Thus,  $\pi_{g,r}$  represented the derived probability that species  $i$ , in region  $r$ , belongs to guild  $g$ .

We define species-, site- and region-specific occurrence,  $z_{i,j,r}$ , as a binary variable in which  $z_{i,j,r} = 1$  if species  $i$  is present at camera trap site  $j$  in region  $r$ . The occurrence state is defined as the outcome of a Bernoulli process in which  $z_{i,j,r} \sim \text{Bern}(\psi_{i,j,r} * \omega_{i,r})$ , where  $\psi_{i,j,r}$  is the probability that species  $i$  occurred at site  $j$  in region  $r$ . We model occurrence as a function of elevation (ELEV), which in turn is a proxy for habitat type because elevation is the strongest driver of variation in forest composition over the study regions (Lovett & Wasser, 2008). We also included a square term on the effects of elevation (ELEV<sup>2</sup>) to account for potential mid-altitude peaks in species-specific distributions. We assume that the logit transformation of the occurrence probability (Kéry & Royle, 2008) is a linear combination of a species- and region-specific effect (intercept), and species-specific quadratic effects of elevation as follows:

$$\text{logit}(\psi_{i,j,r}) = \alpha 0_{i,r} + \alpha 1_{i,r} * \text{ELEV}_{j,r} + \alpha 2_{i,r} * \text{ELEV}_{j,r}^2$$



**Figure 1** Map of the study area, Udzungwa Mountains of Tanzania. Camera traps locations in the two forests (Mwanihana and Uzungwa Scarp) are shown as black dots. The geographic location of the study area in Tanzania is shown in the map on the upper right, and a summary of the main ecological factors of the two forests is also reported. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Thus, the inverse-logit of  $\alpha_{0,i,r}$  is the occurrence probability for species  $i$  in region  $r$  in sites with average elevation. Occurrence is imperfectly observed, which confounds the estimation of  $\psi_{i,j,r}$ . We therefore specify the detection model for the observational data,  $y_{i,j,r}$  for species  $i$  at site  $j$  in region  $r$  as  $y_{i,j,r} \sim \text{Bin}(p_{i,j,r} * z_{i,j,r} * K_{j,r})$ , where  $p$  is the detection probability of species  $i$  at site  $j$  in region  $r$ , conditional on species presence ( $z = 1$ ), and  $K_{j,r}$  is the number of sampling occasions at site  $j$  in region  $r$ . We expected detection probability  $p_{i,j,r}$  to vary based on distance from  $j$  to the park/reserve border ( $m$ , denoted BORDER). Our hypothesis was that animals would be more elusive near the border because of greater disturbance and, possibly, denser forest floor vegetation, both limiting detection by camera traps (Rovero *et al.*,

2014b). In addition, we also incorporated a binary covariate (0–1) corresponding to the camera type used at each  $j$  site in region  $r$  (CAM\_TYPE) to account for potential differences in performance:

$$\text{logit}(p_{i,j,r}) = \beta_{0,i,r} + \beta_{1,i,r} * \text{BORDER}_{j,r} + \beta_2 * \text{CAM\_TYPE}_{j,r}$$

We assume that the species-level parameters  $\alpha_0$ ,  $\alpha_1$ ,  $\alpha_2$ ,  $\beta_0$  and  $\beta_1$  are random effects, each governed by community-level hyper-parameters. For example, we assume that  $\alpha_{1,i,r} \sim N(\mu_{\alpha 1,r}, \sigma_{\alpha 1,r})$ , where  $\mu_{\alpha 1,r}$  is the mean community intercept (across species) and  $\sigma_{\alpha 1,r}$  is the standard deviation

(among species). To account for the fact that rare species may be more difficult to detect, we included a correlation structure between occupancy and detection probability with region-specific correlation parameters  $\rho_r$  (Dorazio & Royle, 2005; see Appendix S1 in Tenan *et al.*, 2017).

We fit the model with a Bayesian formulation and Markov chain Monte Carlo using JAGS (Plummer, 2003), called from R (R Development Core Team 2016) through the package 'jagsUI' (Kellner, 2016). We ran three chains of length 150 000, discarded the first 15 000 iterations as burn-in, and thinned the remaining chains by taking each 20th value. Continuous covariates were derived using geo-processing tools available in QGIS 2.18.0 (QGIS Development Team 2017), and standardized to have mean zero and unit variance. Elevation and distance from border were collinear, but this did not affect the analysis since their effect was tested on different parameters. We used uninformative priors (see Appendix S1) and verified convergence through visual inspection of the chains and with the Gelman-Rubin diagnostic (Brooks & Gelman, 1998). We considered an effect significant if the 95% Bayesian credible interval (BCI) for the related posterior distribution did not encompass zero. Finally, to test the relationship between species-specific body mass and related occurrence probability ( $\psi$ ), we calculated the Pearson's coefficient ( $r$ ) in a post-hoc correlation analysis, using the posterior distributions of the species-specific differences in estimated  $\psi$  between the two areas as a function of species-specific body mass (average values taken from Smith *et al.*, 2003). We then derived the 95% BCI for the correlation coefficient and the probability of a positive correlation, that is  $\Pr(r > 0)$ .

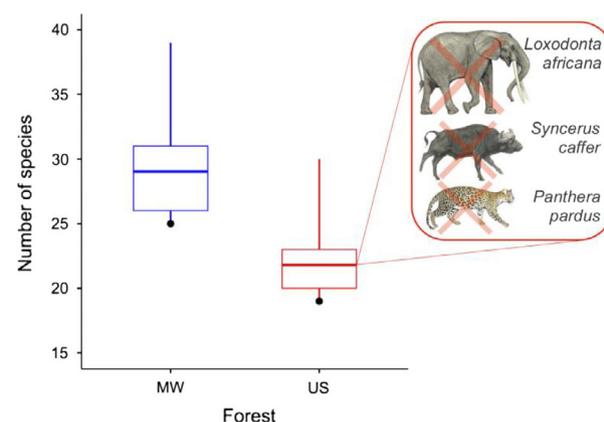
## Results

The number of detected species was 25 in Mwanihana and 19 in Uzungwa Scarp (see Appendix S2). Species detected in Uzungwa Scarp were a subset of the species detected in Mwanihana, except for two, the greater cane rat *Thryonomys swinderianus* and the blue duiker *Philantomba monticola*. Thus, 17 species were shared by the two PAs. Estimated species richness differed substantially between the two forests, with a median of 28 (mean 29.0, 95% BCI 25–39) in Mwanihana and 21 (mean 21.8, 95% BCI 19–30) in Uzungwa Scarp (Fig. 2). Insectivore richness was significantly lower in Uzungwa Scarp compared to Mwanihana (median 2 [95% BCI 2–4] as compared to 5 [95% BCI 5–9] in Mwanihana), and also comprised a lower proportion of the community (10%, vs. 20% in Mwanihana). Carnivores showed a similar gap, with a median of 5 species (95% BCI 5–6, proportion of the community 20%) in Mwanihana and only 3 (95% BCI 3–6, 16%) in Uzungwa Scarp. The estimated number of herbivore and omnivore species was similar between forests (herbivores: median 12 [95% BCI 11–18] in Mwanihana and 11 [95% BCI 10–16] in Uzungwa Scarp; omnivores: 4 [95% BCI 4–7] in Mwanihana and 4 [95% BCI 4–7] in Uzungwa Scarp), while the proportions in the community increased in Uzungwa Scarp, since the total number of species decreased (Fig. 3). For species detected in

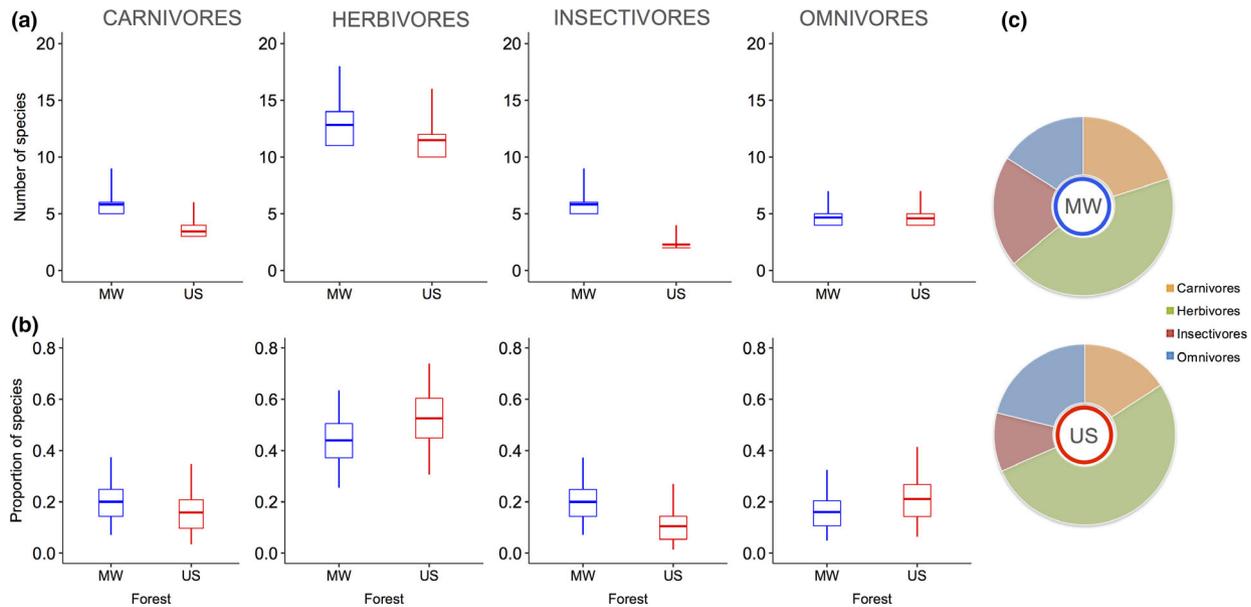
both forests, estimated occurrence probabilities were generally significantly lower in Uzungwa Scarp relative to Mwanihana (Fig. 4). For example, estimated median occupancy for the Uzungwa-endemic and flagship Sanje mangabey was 0.71 (95% BCI 0.58–0.81) in Mwanihana and 0.27 (95% BCI 0.16–0.40) in Uzungwa Scarp, and for the Tanzania-endemic and rare Abbott's duiker was 0.52 (95% BCI 0.37–0.66) in Mwanihana and only 0.08 (95% BCI 0.03–0.17) in Uzungwa Scarp. The opposite pattern, among species native to both regions, was found for only two species, the giant pouched rat *Cricetomys gambianus* and the checkered sengi *Rhynchocyon cirnei*. We also found a positive association between body mass and species-specific differences in average occurrence probabilities (Pearson's coefficient of  $r = 0.22$  [95% BCI 0.11–0.33], with  $\Pr(r > 0) = 0.999$ ; Fig. 5). At the species-specific level, the effects of elevation (both linear and squared term) on  $\psi$  were variable. We found no significant effect of distance to PA border on detection probability for any of the species, in either forest. The use of different camera types had a significant effect on species detectability, with greater detection using the Ambush IR camera, which was used at some sites in Uzungwa Scarp (see Appendix S3).

## Discussion

Our analyses revealed clear differences between target mammal communities under contrasting protection regimes. In line with our hypotheses, we found lower species richness and reduced occurrence probabilities for most mammal species in the forest with high disturbance (Uzungwa Scarp), with a tendency of greater decrease in occurrence probability by the larger-bodied species. We also found that the composition of trophic guilds varied between the two PAs. The significant loss of species in Uzungwa Scarp, as compared to Mwanihana, is alarming given the outstanding biological value of the area (Burgess *et al.*, 2007; Rovero *et al.*,



**Figure 2** Estimated species richness in Mwanihana (MW) and Uzungwa Scarp (US) forests (mean, 50% BCI and 95% BCI). Black dots are the number of observed species. Large-bodied mammals that were extirpated from Uzungwa Scarp by the early 1970s are shown in the red box. Drawings by J. Kingdon reproduced with permission. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



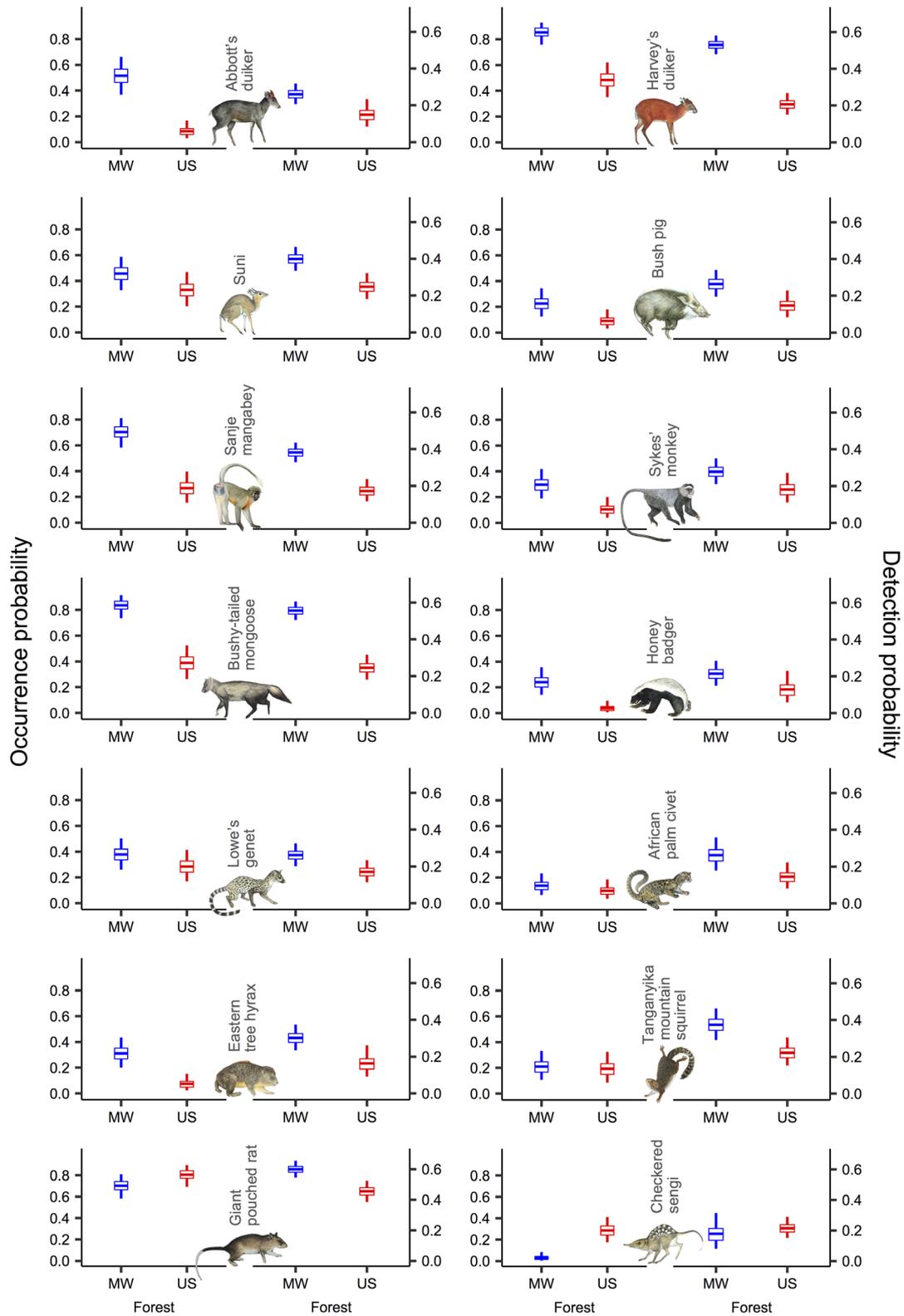
**Figure 3** Estimated number of species for each functional guild (a) in Mwanihana (MW) and Uzungwa Scarp (US) forests respectively (mean, 50% BCI and 95% BCI), and their proportions (b) in each community (mean, 50% BCI and 95% BCI), also shown with pie charts (c). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

2014a). Furthermore, such loss can have profound repercussions on tropical forest dynamics, including the composition, structure, regeneration and carbon storage potential of vegetation (Kurten, 2013; Osuri *et al.*, 2016). Our results confirm the absence of large-bodied mammals, including elephant *Loxodonta africana* and leopard *Panthera pardus* in Uzungwa Scarp, likely a result of intensive hunting for bushmeat trade since the 1970s (Rovero *et al.*, 2012). This supports the notion that larger mammals face higher extinction risk (Cardillo *et al.*, 2005; Ripple *et al.*, 2016). Much of the conservation effort in the tropics is focused on extending the area under official protection rather than on improving the enforcement of existing reserves (Harrison, 2011, e.g. Brooks *et al.*, 2004; Joppa *et al.*, 2008). Hunting is now the biggest threat to biodiversity in many parts of the tropics (Harrison, 2011), yet many of the mammal species threatened by hunting remain poorly studied and are in great need of basic biological and ecological research, including abundance estimations (Ripple *et al.*, 2016). Studies on the consequences of defaunation have also consistently indicated that the ecology of heavily hunted forests is severely disrupted (Fa & Brown, 2009; Harrison, 2011). Worldwide, Africa is considered one of the regions with the most species facing this threat (Ripple *et al.*, 2016). Tanzania is arguably mainland Africa's most important nation for conservation, as the country is losing habitat and natural resources rapidly (Caro & Davenport, 2016).

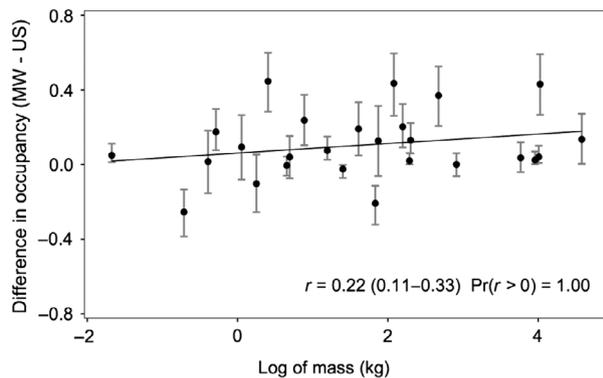
We documented a decrease in insectivores and carnivores in Uzungwa Scarp, the highly disturbed PA, as compared to Mwanihana, the PA with higher levels of protection. Carnivores are experiencing massive declines in their populations and geographic ranges globally (Ripple *et al.*, 2014); our

results for mammal insectivores match findings on birds, as insectivorous birds have also shown a disproportionate sensitivity to disturbance (Gray *et al.*, 2007). Global declines in insect abundance could also have been affecting insectivores (Sánchez-Bayo & Wyckhuys, 2019). The less pronounced differences we found for herbivores and omnivores may mirror their greater resilience and/or reflect compensatory dynamics within the community, with some species able to fill the ecological niche(s) of others (Wright, 2003). Medium-sized omnivores include many opportunistic species that have the ability to use a wide array of habitats and resources, thriving even after extensive human modification (Roemer, Gompper & Van Valkenburgh, 2009). However, this result is somewhat surprising for herbivores, given that they face unprecedented extinction rates at the global scale (Ripple *et al.*, 2015).

Our results at the species-specific level indicate that estimated occurrence probabilities were significantly lower in Uzungwa Scarp relative to Mwanihana for most species detected in both PAs. These differences are of particular conservation concern for endemic species, or species with narrow ranges, such as the Abbott's duiker and the Sanje mangabey. Yet, we found decreased occurrence probabilities in the disturbed forest even for generalist and widespread species, suggesting that failure to enforce protection is associated with changes in the whole mammal community (Robinson & Bennett, 2000). Occurrence estimates were higher in Uzungwa scarp only for the giant pouched rat and the checkered sengi, matching the results of a previous study (Hegerl *et al.*, 2015). However, this study lacked a standardized sampling design and temporal consistency in sampling effort between forests. Furthermore, the community



**Figure 4** Species-specific mean occurrence and detection probabilities, in Mwanihana (MW) and Uzungwa Scarp (US) forests respectively, for 14 forest-dwelling mammals that were detected in both areas (mean, 50% BCI and 95% BCI). Drawings by J. Kingdon reproduced with permission. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**Figure 5** Species-specific differences in estimated occurrence probabilities between Mwanihana (MW) and Uzungwa Scarp (US) forests (MW – US; mean and 95% BCI), for species detected in at least one forest, as a function of the log of average body mass (kg). The elephant was considered an outlier and excluded from this analysis. The estimated correlation coefficient, along with the probability of a positive correlation ( $\text{Pr}(r > 0)$ ) is reported.

composition analysis was based on raw detection rates. The giant pouched rat seems to be relatively unaffected by the level of human disturbance, potentially because this medium-sized omnivore is a generalist, adaptable species with a high reproductive rate (Engeman *et al.*, 2006). This can also be the result of low predation and reduced interspecific competition from depleted populations of other species, or even an effect of potential benefits to habitat created by disturbance. The much higher estimated occurrence probability for the checkered sengi in Uzungwa Scarp as compared to Mwanihana may be related to reduced interspecific competition with the endemic and narrow-ranged grey-faced sengi that is found in Mwanihana but not in Uzungwa Scarp (Rovero *et al.*, 2013). Similar biogeographic reason explains the non-detection of the blue duiker in Mwanihana. Our results also show marked differences in species-specific detection probabilities between forests, with a general trend of lower detection in Uzungwa Scarp as compared to Mwanihana. This may be an effect of the correlation structure between occurrence and detection in the model, suggesting that abundance for species may be lower in Uzungwa Scarp. However, it may also reflect different behaviors, as individuals may become more elusive with increasing disturbance (Rovero *et al.*, 2014b). To explore this result, we re-ran the model without the correlation structure. We found that the differences in species-specific detection probabilities between forests were still marked and significant, suggesting a behavioral response due to higher levels of anthropogenic disturbance in Uzungwa Scarp. Our results also provide evidence that hunting in Uzungwa Scarp is associated with a decrease in larger-bodied species, consistent with other research that has documented higher sensitivity of larger species to human disturbance (Cardillo *et al.*, 2005).

Across the study area hunting mainly targets duikers and other medium-sized forest mammals (Rovero *et al.*, 2010; Jones *et al.*, 2019). These include the relatively common Harvey's duiker *Cephalophus harveyi* and the poorly known,

endemic and IUCN-Endangered Abbott's duiker (IUCN 2016). Indeed both species have striking and significant differences in occurrence probability between Mwanihana and Uzungwa Scarp. Yet, being non-selective, snares used for hunting cause significant by-catch mortality on a variety of species (Lindsey *et al.*, 2011). Moreover, as the larger ungulates and bushpigs have decreased in Uzungwa Scarp, snaring tends to target smaller species. Detrimental effects of hunting on the abundance of arboreal primates, particularly the colobines, have also been documented (Rovero *et al.*, 2015; Cavada *et al.*, 2019).

The study design and analytical framework we used allowed us to simultaneously assess species richness, functional composition and species-specific occurrence across two different communities. Based on our results, differences in mammal communities strongly associate with the disproportionately greater hunting pressure in Uzungwa Scarp than Mwanihana. Logging and firewood collection may also affect mammal diversity and abundance and eventually lead to local extinction of some species through changes in the forest structure (Laurance *et al.*, 2006; Arroyo-Rodríguez & Dias, 2010; Rovero *et al.*, 2012). Nevertheless, in the disturbed forest, there is little spatial overlap between such activities: logging and firewood collection occur mainly toward the lower edge of the reserve (Hegerl *et al.*, 2015), whereas hunting occurs across the forest and especially in the interior zones. Since we placed camera traps evenly across both PAs, hunting is likely to be a more significant factor (Rovero *et al.*, 2012).

The upgrading of Uzungwa Scarp from forest reserve to nature reserve status in 2017 (the year right after our data collection) is a valuable step toward more efficient management, as it should bring boosted law enforcement to the PA. Protection should especially target areas adjacent to settlements, where direct disturbance is higher, and include the creation of buffer zones (Cavada *et al.*, 2019). Restoration of connectivity to reverse habitat isolation of Uzungwa Scarp will also help to address the long-term conservation of mammal communities, with wildlife corridors that maintain viability of isolated populations while ensuring ecosystem functionality (Rovero & Jones, 2012; Ruiz-Lopez *et al.*, 2016). Our study suggests that legal protection backed up by on ground protection plays a determinant role in maintaining diverse mammal communities in tropical forests. Protected areas are the cornerstone of efforts to conserve tropical biodiversity and final refuges for threatened species across the globe, but the future of biodiversity within them is closely tied to actual enforcement efficacy. This, in turn, is linked to adequate funding and capacity of PA management (Bruner *et al.*, 2001; Laurance *et al.*, 2012; Tranquilli *et al.*, 2014). Robust assessments on the status of wildlife populations remain fundamental to determine how effectively PAs are performing (Naughton-Treves, Holland & Brandon, 2005) and to design efficient and long-term conservation plans.

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## Conflict of interest

The authors declare that they have no conflict of interest.

## Data availability

The dataset generated and analyzed during the current study is available in the Figshare repository (<https://doi.org/10.6084/m9.figshare.7873454.v3>).

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## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** R and JAGS code for the multi-region community model.

**Appendix S2.** Checklist of the medium-to-large mammals detected by camera trapping in Mwanihana and/or Uzungwa Scarp.

**Appendix S3.** Summary of posterior parameter estimates from the multi-region community occupancy model.

# Co-occurrence of snow leopard *Panthera uncia*, Siberian ibex *Capra sibirica* and livestock: potential relationships and effects

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**Abstract** Understanding the impact of livestock on native wildlife is of increasing conservation relevance. For the Vulnerable snow leopard *Panthera uncia*, wild prey reduction, intensifying human–wildlife conflicts and retaliatory killings are severe threats potentially exacerbated by the presence of livestock. Elucidating patterns of co-occurrence of snow leopards, wild ungulate prey, and livestock, can be used to assess the compatibility of pastoralism with conservation. We used camera trapping to study the interactions of livestock, Siberian ibex *Capra sibirica* and snow leopards in a national park in the Altai mountains, Mongolia. We obtained 494 detections of wild mammals and 912 of domestic ungulates, dogs and humans. Snow leopards and Siberian ibex were recorded 14 and 33 times, respectively. Co-occurrence modelling showed that livestock had a higher estimated occupancy (0.65) than ibex, whose occupancy was lower in the presence of livestock (0.11) than in its absence (0.34–0.35 depending on scenarios modelled). Snow leopard occupancy did not appear to be affected by the presence of livestock or ibex but the robustness of such inference was limited by uncertainty around the estimates. Although our sampling at presumed snow leopard passing sites may have led to fewer ibex detections, results indicate that livestock may displace wild ungulates, but may not directly affect the occurrence of snow leopards. Snow leopards could still be threatened by livestock, as overstocking can trigger human–carnivore conflicts and hamper the conservation

of large carnivores. Further research is needed to assess the generality and strength of our results.

**Keywords** Altai mountains, camera trapping, human–wildlife conflict, Mongolia, occupancy, occurrence interactions, Siberian ibex, snow leopard

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## Introduction

The impact of livestock on native wildlife is a global conservation issue (Prins, 1992; Fleischner, 1994; Berger et al., 2013) that remains poorly understood despite much debate (e.g. Ekernas et al., 2017). High densities of livestock induce competitive exclusion, resulting in decline of wild herbivores (Bagchi et al., 2004; Madhusudan, 2004), and pastoralism affects large carnivores (Ogutu et al., 2005; Ripple et al., 2014). In areas such as Central Asia, where numbers of free-ranging livestock have increased exponentially (Berger et al., 2013), including within protected areas (Bagchi et al., 2004), the cascading threats to large carnivores such as snow leopard *Panthera uncia* and wolf *Canis lupus* are of concern. These include the intensification of human–carnivore conflict caused by depredation, leading to the retaliatory killing of carnivores, and the reduction of wild herbivore prey (Treves & Karanth, 2003; Mishra et al., 2010; Sharma et al., 2015). A recent study in Mongolia's Gobi steppe shows the complexity of the cascading effects of pastoralism on wildlife (Ekernas et al., 2017). Understanding the spatial interactions among large carnivores, wild herbivores and livestock is therefore of relevance for planning sustainable livestock grazing regimes and reducing threats.

Here we focus on co-occurrence patterns of snow leopards, one of their main wild prey, the Siberian ibex *Capra sibirica*, and domestic ungulates in a protected area in north-western Mongolia. Snow leopards have a vast but fragmented distribution across central Asia's mountain landscape, and their survival depends primarily on wild ungulates (Jackson et al., 2008; Snow Leopard Network, 2014). Globalization of the cashmere wool trade has increased livestock numbers across the snow leopard range, particularly in China and Mongolia, exposing this felid to intensified threats (Berger et al., 2013;

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Sharma et al., 2015). Prey reduction and human–wildlife conflicts resulting in the killing of snow leopards are the primary threats caused by livestock presence (Snow Leopard Network, 2014). Conflicts generated by depredation of livestock (Li et al., 2013; Chen et al., 2016), patterns of predation on livestock and wild prey (Johansson et al., 2015), and the impact of livestock on snow leopard prey (Bagchi et al., 2004) have been assessed. The impact of livestock on snow leopards, however, remains less understood. There is evidence of increased intensity in snow leopard site use with increasing livestock numbers, with a possible decrease beyond a threshold of livestock densities (Sharma et al., 2015). Greater predation on livestock by snow leopards has been reported in areas with lower abundance of wild prey (Bagchi & Mishra, 2006), although a review of 16 studies indicates that the proportions of wild ungulates and livestock in the diet of snow leopards are not correlated (Lovari et al., 2013).

We used camera trapping data and an occupancy framework (MacKenzie et al., 2002) to study the spatial interactions among snow leopards, ibex and livestock. The efficiency of camera trapping to detect snow leopards has been widely tested (Janečka et al., 2011) and recent studies show the potential of site occupancy modelling to study patterns in their distribution (Alexander et al., 2016a, b). We assess the usefulness of this approach to evaluate co-occurrence patterns of Siberian ibex, snow leopards and livestock by using an occupancy model that explicitly assesses co-occurrence (Waddle et al., 2010).

## Study area

We conducted the study in the Siilkhem National Park, Part B (centred on 49°49′21.42″N, 89°44′56.84″E; 1,400 km<sup>2</sup>), in the Altai Mountains, north-western Mongolia (Fig. 1), a steep, rocky and dry mountain environment up to 3,965 m altitude.

The study area is mainly grassland with sparse growth of shrubs on the slopes and larch *Larix sibirica* along valley bottoms. Traditional livestock husbandry is permitted in the limited use zones of national parks (Government of Mongolia, 1994), and most of the local people are pastoralists. There are large numbers of livestock: shepherds with dogs herd during the day along valleys and on accessible slopes, and livestock is housed in corrals at night. In the study district the number of goats increased from 21,937 in 1970 to 105,376 in 2015, with similar increases in other domestic animals (Mongolian Statistical Information Service, 2018).

## Methods

### Data collection

From March to June 2015 we used 49 camera traps across 513 km<sup>2</sup> (the minimum convex polygon around the camera-trap sites). We originally designed a regular grid of camera traps, with cells of 2 km<sup>2</sup> over the entire central and northern part of the Park, which, based on preliminary information, was considered suitable for snow leopards. Such spacing ensured that at least three camera traps sampled a snow leopard home range of c. 11–142 km<sup>2</sup> (Jackson, 1996; McCarthy et al., 2005). After taking into account the area's topography and presumed snow cover, we reduced the extent of the grid to survey valleys and slopes that we could reach, up to 3,200 m. We placed camera traps in each cell of this grid, on the nearest site to the centre of the grid cell suitable for snow leopard passage based on signs such as scrapes, scats, scratches on trees, scent markings and tracks. In the absence of such signs, we placed camera traps along probable snow leopard passing sites such as narrow valley bottoms and saddles along ridges. This was motivated by the fact that the snow leopard is the rarest

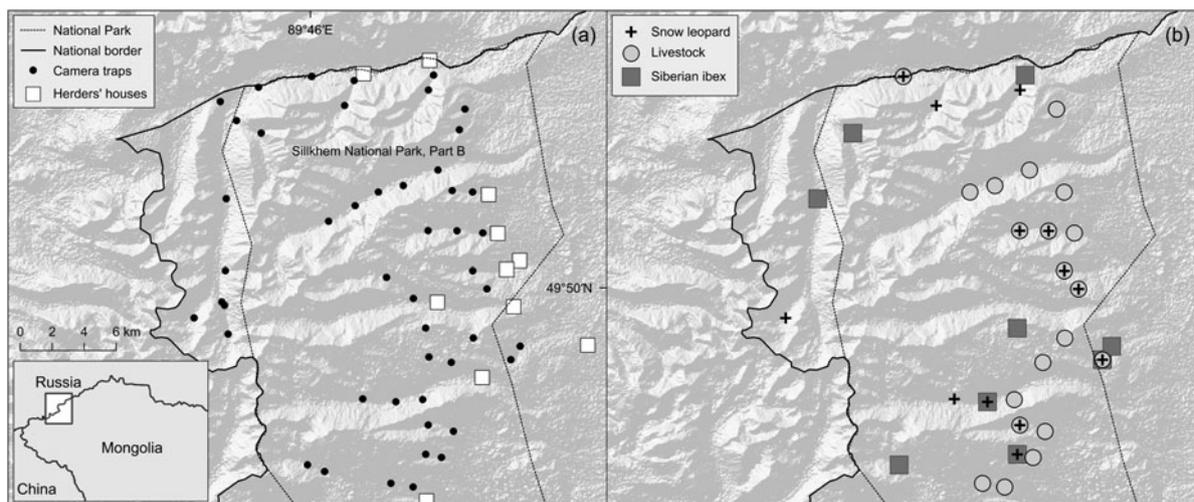


FIG. 1 The study area within Siilkhem National Park, Part B, north-western Mongolia: (a) locations of the 49 camera traps and herders' houses and camps; (b) sites where we detected livestock, Siberian ibex and snow leopards.

and most elusive of the species we wanted to detect. Sightings of ibex and livestock indicated that the sites were also suitable to capture their presence, although this design may have favoured the detection of snow leopards over ibex and livestock. The selected sites (Fig. 1) were at 2,219–3,126 m altitude.

For logistical reasons we used two grids: the first (26 sites) sampled from 17 March to 4 May and the second (23 sites) from 5 May to 29 June 2015. We used Xenon white flash digital camera traps (Cuddeback Ambush, Non Typical Inc., Green Bay, USA), which take colour images at day and night with a trigger time of 0.25 s. We set camera traps to work in continuous mode and fitted them in wooden bases on small rock piles c. 50 cm above the ground.

### Statistical analysis

We processed data in *R* (R Development Core Team, 2015), and first derived species' raw descriptors of captures: independent events (using a 15 min interval to separate subsequent images of the same species), relative abundance index (the ratio of events to sampling effort) and naïve occupancy (Rovero et al., 2014). For snow leopards, ibex and domestic ungulates we built matrices of detection/non-detection on daily occasions and used a model for estimating co-occurrence of interacting species developed by Waddle et al. (2010). Occurrence and detectability were modelled for a single dominant species and one or more subordinate species, where probabilities referred to subordinate species are conditional on presence of the dominant one. Given the limited number of snow leopard and ibex detections, we fitted models by contrasting two scenarios in which livestock occurrence was assumed independent of the other two species: livestock presence determines the occurrence of both snow leopard and ibex (scenario 1); livestock presence determines the occurrence of ibex and, in turn, ibex occurrence determines snow leopard occurrence (scenario 2). Sample sizes limited the number of environmental and human disturbance factors that we could use as model covariates. Thus, we considered (1) elevation at the camera trap site, derived from a Digital Elevation Model, as a proxy for the variation in habitat within the elevation range surveyed, and (2) distance of camera-trap sites to occupied herders' houses and camps (Fig. 1), as a proxy for anthropogenic disturbance.

Detailed model formulation and parameter constraints, and model fitting procedures, are reported in Supplementary Material 1. Livestock occurrence probability was modelled as a function of elevation and distance to herders' houses. We assumed ibex occurrence depends on the occurrence of livestock and distance to herders' houses. Livestock encounter probability was assumed to be constant and independent of occurrence of other species. Ibex

encounter probability was tested for an effect of distance to herders' houses and camps. Snow leopard encounter probability was a function of distance to herders' houses and camps, as we assumed these places may influence the elusiveness of snow leopards. Models were fitted using the Markov chain Monte Carlo framework, implemented in *JAGS* (Plummer, 2003), which we executed from *R* (see Supplementary Material 2 for model code and Supplementary Figs. 1 & 2 for the Bayesian learning plots of the posterior distributions).

### Results

Total sampling effort was 2,225 camera days (mean  $45.4 \pm$  SD 6.6 per camera) from the 49 camera traps set, yielding 494 detections of 12 species of wild mammals, 105 of people and 367 of livestock, primarily goats and sheep (188) and cattle/yaks (163). Livestock was detected at 21 locations (naïve occupancy = 0.43; Supplementary Table 1), with herds of sheep and goats numbering in their hundreds. We obtained 17 photographs of snow leopards representing 14 events at 13 locations (naïve occupancy = 0.27). By comparing individual coat patterns across events, we concluded that three individual leopards were detected, with all photographs allowing for identification. The sex of these individuals could not be determined from the photographs. We also recorded 33 events of Siberian ibex at nine locations (naïve occupancy = 0.18) (Fig. 1). The group size of ibex, as determined from camera trap images and opportunistic sightings, was 1–31. Detections did not show any marked pattern of temporal segregation: livestock and ibex were predominantly diurnal although ibex was occasionally detected in the first hours after dusk; snow leopards were active during 5.00–12.00 and the few detections did not reveal any peak of activity.

Occupancy modelling showed that for both scenarios livestock had a higher mean estimated occupancy (mean = 0.65; 95% credible interval 0.44–0.83; Table 1) than ibex, and ibex occupancy was negatively affected by the presence of livestock. The decrease in mean point estimate of ibex occupancy varied from 0.34 to 0.11 for scenario 1 and from 0.35 to 0.11 for scenario 2, in the absence and presence of livestock, respectively (Fig. 2, Table 1). In contrast, in the first scenario the mean point estimate of snow leopard occupancy was not affected by the presence of livestock (0.77 and 0.74 with and without livestock, respectively; Fig. 2), and similarly for detectability, which was 0.01 in the presence (95% credible interval 0.004–0.022) and absence (95% credible interval 0.003–0.021) of livestock (Table 1). Similarly, in the second scenario, the occupancy of snow leopard was not affected by the presence of ibex (mean = 0.80, 95% credible interval 0.340–0.996, and mean = 0.76, 95% credible interval 0.295–0.994, in the presence and

TABLE 1 Posterior parameter estimates (mean ± SD, and 95% credible interval quantiles, CRI) for occupancy ( $\psi$ ) and detection probability ( $p$ ) in the two scenarios (scenario 1: livestock presence determines the occurrence of both snow leopard *Panthera uncia* and ibex *Capra sibirica*; scenario 2: livestock presence determines the occurrence of ibex and, in turn, ibex occurrence determines snow leopard occurrence).

| Parameter*                  | Scenario 1     |               | Scenario 2     |               |
|-----------------------------|----------------|---------------|----------------|---------------|
|                             | Mean ± SD      | 95% CRI       | Mean ± SD      | 95% CRI       |
| <b>Occurrence</b>           |                |               |                |               |
| $\bar{\psi}^{LI}$           | 0.649 ± 0.100  | 0.443–0.830   | 0.648 ± 0.100  | 0.445–0.830   |
| $\bar{\psi}^{IB LI}$        | 0.105 ± 0.074  | 0.013–0.292   | 0.106 ± 0.074  | 0.013–0.292   |
| $\bar{\psi}^{IB \bar{L}}$   | 0.341 ± 0.123  | 0.156–0.646   | 0.346 ± 0.128  | 0.155–0.679   |
| $\bar{\psi}^{SL LI}$        | 0.771 ± 0.184  | 0.345–0.995   |                |               |
| $\bar{\psi}^{SL \bar{L}}$   | 0.736 ± 0.203  | 0.281–0.992   |                |               |
| $\bar{\psi}^{SL IB}$        |                |               | 0.796 ± 0.183  | 0.340–0.996   |
| $\bar{\psi}^{SL \bar{I}B}$  |                |               | 0.758 ± 0.197  | 0.295–0.994   |
| <b>Detectability</b>        |                |               |                |               |
| $\bar{p}^{LI}$              | 0.165 ± 0.012  | 0.142–0.189   | 0.165 ± 0.012  | 0.142–0.188   |
| $\bar{p}^{IB}$              | 0.057 ± 0.013  | 0.034–0.084   | 0.057 ± 0.013  | 0.004–0.016   |
| $\bar{p}^{SL}$              |                |               | 0.009 ± 0.003  | 0.004–0.016   |
| $\bar{p}^{SL LI}$           | 0.010 ± 0.005  | 0.004–0.022   |                |               |
| $\bar{p}^{SL \bar{L}}$      | 0.010 ± 0.005  | 0.003–0.021   |                |               |
| <b>Effect of covariates</b> |                |               |                |               |
| $\beta^{LI}_{elev}$         | -2.189 ± 0.721 | -3.777–-0.943 | -1.190 ± 0.718 | -3.768–-0.965 |
| $\beta^{LI}_{dist}$         | -0.850 ± 0.715 | -2.291–0.529  | -0.858 ± 0.711 | -2.311–0.510  |
| $\beta^{SL}_{elev}$         | -0.214 ± 1.670 | -3.258–3.553  | -0.311 ± 1.702 | -3.307–3.475  |
| $\beta^{SL}_{dist}$         | -0.279 ± 1.552 | -3.191–3.186  | -0.280 ± 1.630 | -3.288–3.157  |
| $\alpha^{dist}$             | -0.273 ± 0.448 | -1.174–0.578  | -0.350 ± 0.449 | -1.283–0.493  |
| $\beta^{IB}_{dist}$         | 0.569 ± 0.780  | -0.427–2.729  | 0.618 ± 0.840  | -0.408–2.953  |
| $\alpha^{IB}_{dist}$        | -0.158 ± 0.265 | -0.697–0.336  | -0.174 ± 0.269 | -0.711–0.328  |

\*The apex notation refers to the co-occurrence relationship modelled (e.g.  $\bar{\psi}^{IB|LI}$  is the intercept of ibex occupancy in the presence of livestock, and  $\bar{\psi}^{IB|\bar{L}}$  is the intercept of ibex occupancy in the absence of livestock; see Supplementary Material 1 for details). Coefficients  $\beta$  and  $\alpha$  quantify the effect of distance from human disturbance (dist) and elevation (elev) on the occurrence and detection probability, respectively. Estimates of the occurrence and detectability intercepts are given in the probability scale; coefficients  $\alpha$  and  $\beta$  are in the logit scale.

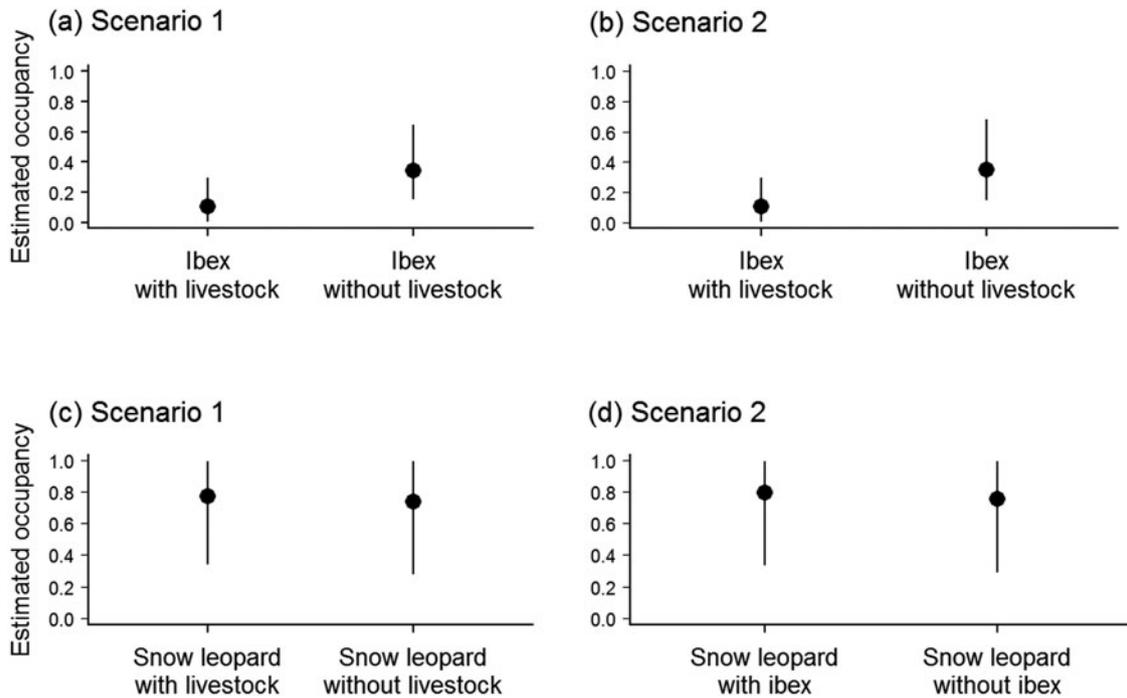


FIG. 2 Occupancy probability (mean and 95% credible interval) estimated from the modelling of co-occurrence patterns of (a) ibex depending on livestock, scenario 1; (b) ibex depending on livestock, scenario 2; (c) snow leopard depending on livestock, scenario 1; and (d) snow leopard depending on ibex, scenario 2.

absence of ibex, respectively). The only covariate with a significant impact (i.e. 95% credible interval did not encompass zero) was site elevation, which had a negative effect on the estimated occupancy of livestock in both scenarios (Table 1).

## Discussion

Our analysis suggests three patterns: (1) the occurrence of livestock may have a negative effect on the occurrence of ibex, with a difference in the mean point estimates despite some overlap in credible intervals; (2) livestock presence did not appear to affect the occurrence of snow leopards; (3) snow leopard occurrence did not seem to be affected by the presence of ibex. The small number of snow leopard and ibex detections limited the precision of our estimates, suggesting caution about the generality of the results. We acknowledge that the study design we used, primarily targeted at the snow leopard, may have resulted in an under-sampling bias for ibex and livestock. Additional data on herd numbers and movement patterns for livestock and ibex would be required to further assess these interactions.

Although the study area is a national park, our camera traps detected over 10 times more livestock compared to the only wild ungulate recorded, the Siberian ibex. Although we detected livestock at 43% of recording sites, our model estimated that livestock would occur at over two thirds of sites (mean estimated occupancy = 0.65). Data on temporal trends in the abundance of the ibex population will be required to assess whether the co-occurrence pattern we found reflects declining abundance of wild herbivores with increasing livestock densities, as suggested by studies in the Trans-Himalaya (Mishra et al., 2002; Bagchi et al., 2004).

There were 14 detections of three snow leopards at remote sites and larger valleys heavily used by livestock, and both snow leopards and livestock were detected at seven sites (Fig. 1). Beyond a threshold of livestock density, reduced wild prey populations and associated human disturbance may negatively influence the intensity of snow leopard habitat use (Sharma et al., 2015). In the Tost mountains, southern Mongolia, the snow leopard diet included more wild prey (73%) than livestock (27%; Johansson et al., 2015), despite livestock abundance being one order of magnitude higher. Data on retaliatory killings and predation pattern will be necessary to further examine how livestock affects snow leopards. Our discussions with local herders indicate that predation of free-ranging livestock occurs regularly, but this was attributed primarily to wolves. Predation in corrals was reported to occur sporadically, as in the Tost mountains (Johansson et al., 2015). Shepherds appeared aware that unlike wolves, snow leopards are protected, and their attitude towards snow leopards seemed more positive than towards wolves. We found skins of wolves in some herders' houses, but no evidence of snow leopard poaching.

These observations indicate that although livestock is widespread in Part B of Siilkhem National Park, and could have a negative impact on the occurrence of ibex, it may not have a significant impact on the occurrence of snow leopards, and there is no evidence of intense conflicts with local herders.

At a large scale there is generally a positive association between wild prey presence and site use by snow leopards (McCarthy et al., 2005; Alexander et al., 2016b) but at the local scale this pattern may not hold. In China site use by snow leopards was not strongly associated with the presence of bharal *Pseudois nayaur*, suggesting this pattern may be a result of the lack of spatial heterogeneity in bharal distribution, which were detected at all sites (Alexander et al., 2016a). We did not find a pattern of association, as the occurrence of snow leopards did not vary with the presence or absence of ibex. This result is compatible with the hypothesis that predator–prey occurrences may be decoupled (Ekernas et al., 2017), although the possible under-sampling of ibex may have masked the pattern of association.

In conclusion, our results support the potential of the occupancy framework for analysing snow leopard detection/non-detection data from camera traps (Alexander et al., 2016a). An improved evaluation of its application to model co-occurrence patterns will require greater sample sizes, and ideally site selection should not bias detection of a particular species. The added advantage of the model we used is that interactions among species are modelled explicitly, along with the effect of environmental covariates. The main constraint was the small number of detections of snow leopards and ibex. This limited the number of parameters and hence the co-occurrence interactions and covariate effects that we could model simultaneously.

The indication that livestock may negatively impact wild ungulates merits further research, as does the result that livestock may not directly affect the occurrence of the snow leopard. The negative effects that depletion of wild prey may have on large carnivores are well known, as is the potential resulting escalation of human–wildlife conflicts (Berger et al., 2013; Ekernas et al., 2017). Given that the study area is a national park, we suggest that ensuring protection of Siberian ibex and snow leopards in the Park requires a revision of the livestock grazing zone, and increased law enforcement, with emphasis on the creation and protection of livestock-free areas. Conservation efforts should concomitantly target livestock practices by engaging herders in the process of developing new grazing plans, as elaborated in the Snow Leopard Survival Strategy (Snow Leopard Network, 2014).

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### Author contributions

FR, CA and ST conceived and designed the study; FR, CA, FZ, RGH and CG collected the data; FR, ST and VO analysed the data. All authors, led by FR, contributed to the writing of the manuscript.

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## Biographical sketches

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