Mammalian Biology 87 (2017) 50–61

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original investigation

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

Valentina Oberosler[a,b,*], Claudio Groff[c], Aaron Iemma[d], Paolo Pedrini[d], Francesco Rovero[a]

[a] Tropical Biodiversity Section, MUSE—Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38122 Trento, Italy
[b] Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, via Ferrata 1, 27100 Pavia, Italy
[c] Servizio Foreste e Fauna, Provincia Autonoma di Trento, Via Trener 3, 38121 Trento, Italy
[d] Vertebrate Zoology Section, MUSE—Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38122 Trento, Italy

ARTICLE INFO

Article history:
Received 25 August 2016
Accepted 23 May 2017
Handled by Francesco Ferretti
Available online 27 May 2017

Keywords:
Camera traps
Activity pattern
Human impact
Detectability
Ursus arctos

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^2 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.

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

---

* Corresponding author at: MUSE—Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38122 Trento, Italy.
E-mail address: valentina.oberosler@muse.it (V. Oberosler).

http://dx.doi.org/10.1016/j.mambio.2017.05.005
1616-5047/

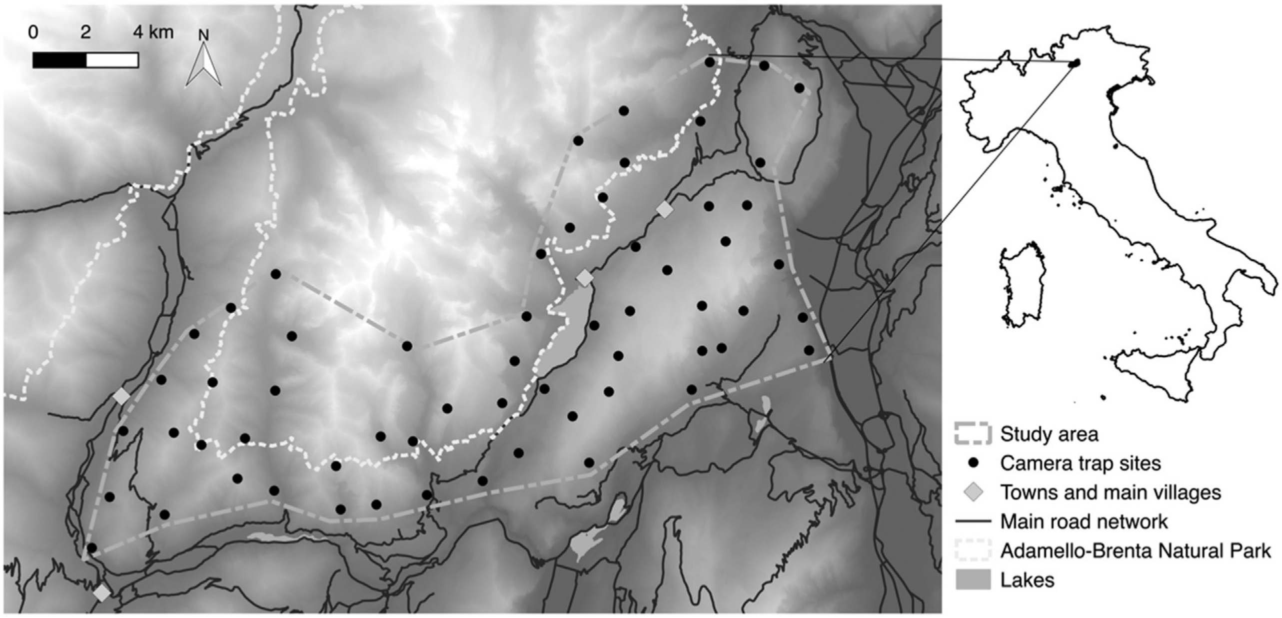

Fig. 1. Map of the study area (left) in western Trentino province, Northern Italy. The 60 camera trap locations are shown as black dots and the border of the Adamello-Brenta Natural Park is also shown. The background is a Digital Terrain Model, with brighter tones corresponding to higher elevation. The 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^2 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^2 (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 (ψ) respectively, as used in occupancy analysis, and the assumed relationship with p and ψ.

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 (ψ)	
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^2 instead of 2 km^2. 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 where 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, N1 = 18, N2 = 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 (ψ) 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 (ψ) 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 ψ
Vulpes vulpes	Red fox	Carnivora	Omnivore	562	28.41	0.621
Capreolus capreolus	Roe deer	Ungulates	Herbivore	302	15.27	0.793
Cervus elaphus	Red deer	Ungulates	Herbivore	208	10.52	0.638
Rupicapra rupicapra	Chamois	Ungulates	Herbivore	166	8.39	0.448
Lepus europaeus	Brown hare	Lagomorpha	Herbivore	114	5.76	0.293
Meles meles	Badger	Carnivora	Omnivore	64	3.24	0.328
Martes sp.	Marten	Carnivora	Carnivore	49	2.48	0.241
Ursus arctos	Brown bear	Carnivora	Omnivore	38	1.92	0.328
Sciurus vulgaris	Red squirrel	Rodentia	Rodent	8	0.40	0.086
Canis lupus	Wolf	Carnivora	Carnivore	1	0.05	0.017
Marmota marmota	Alpine marmot	Rodentia	Rodent	1	0.05	0.017
Mustela nivalis	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 ψ and p (i.e. $\psi(.)$, $p(.)$), for other models p and ψ 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 ΔAIC <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 Δ (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 Δ. Then, for each species, we used the Welch Two-Sample *t*-test to assess if the two generated distributions of Δ 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 ψ ranged from 0.29 to 0.83 and p ranged from

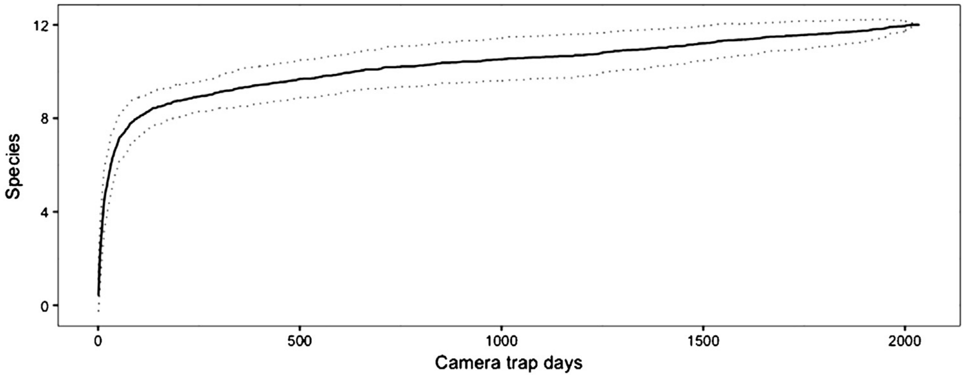

Fig. 2. Randomized species accumulation curve (solid line), with sampling effort for the community of medium-to-large mammals detected by camera trapping in the eastern Alps. Dotted lines indicate 95% confidence intervals.

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 ψ or p of all the others. Model selection indicated that no single model was demonstrably better (i.e. with ΔAIC 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 ψ 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 ψ. 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 ψ, 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 (ψ) 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 ψ and p from the final models at the 58 camera trap stations. Significant outcomes of the relationships between ψ 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 ψ	ψ	SE (ψ)	p	SE (p)	ψ (elevation)	ψ (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*]				
Martes 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

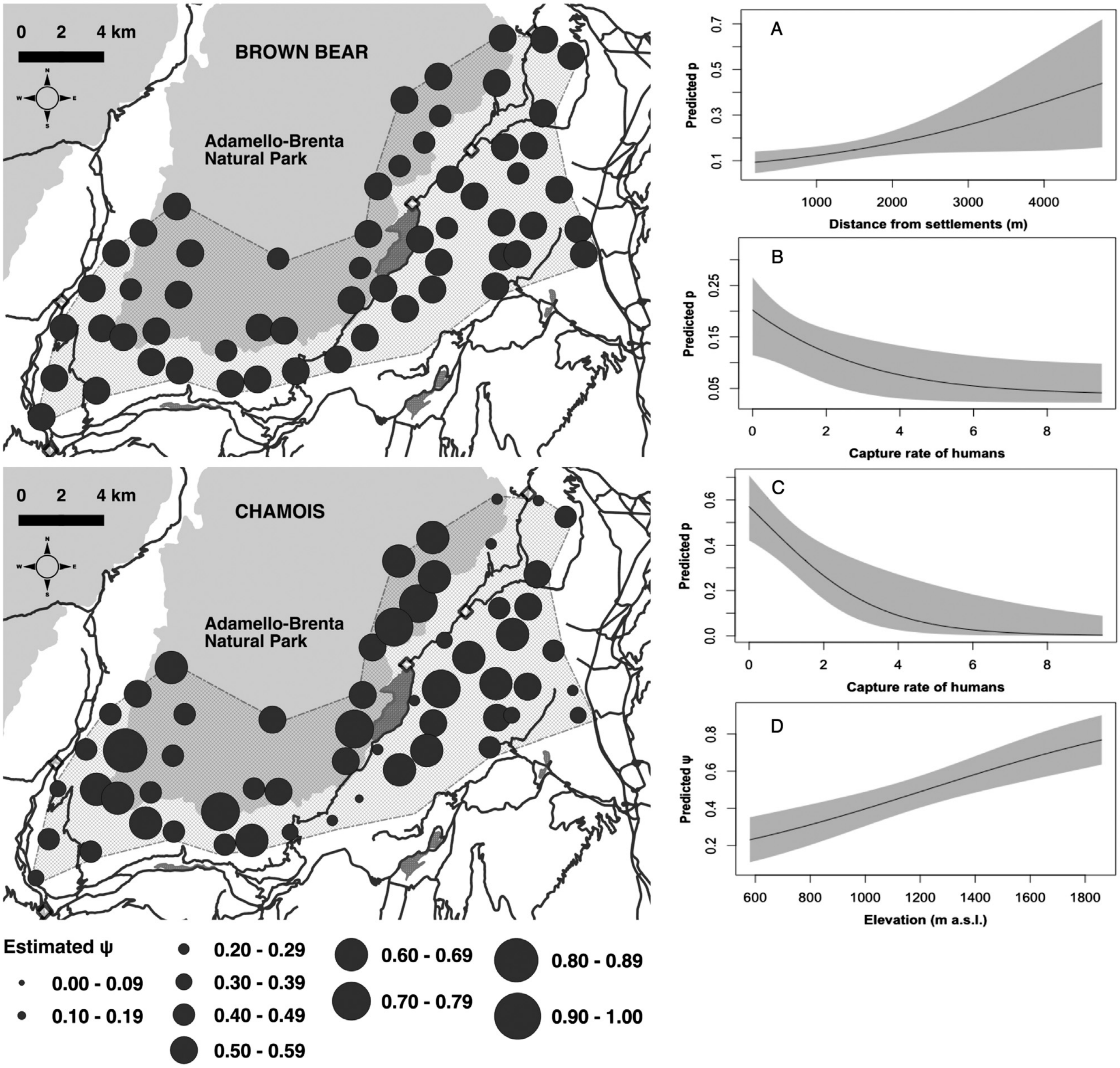

Fig. 3. Map of the distribution of the brown bear and chamois in the study area, eastern Alps, with locations of camera traps shown as dots of size proportional to their estimated occupancy. Charts show the influence of significant covariates on occupancy (ψ) or detectability (p).

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°, 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

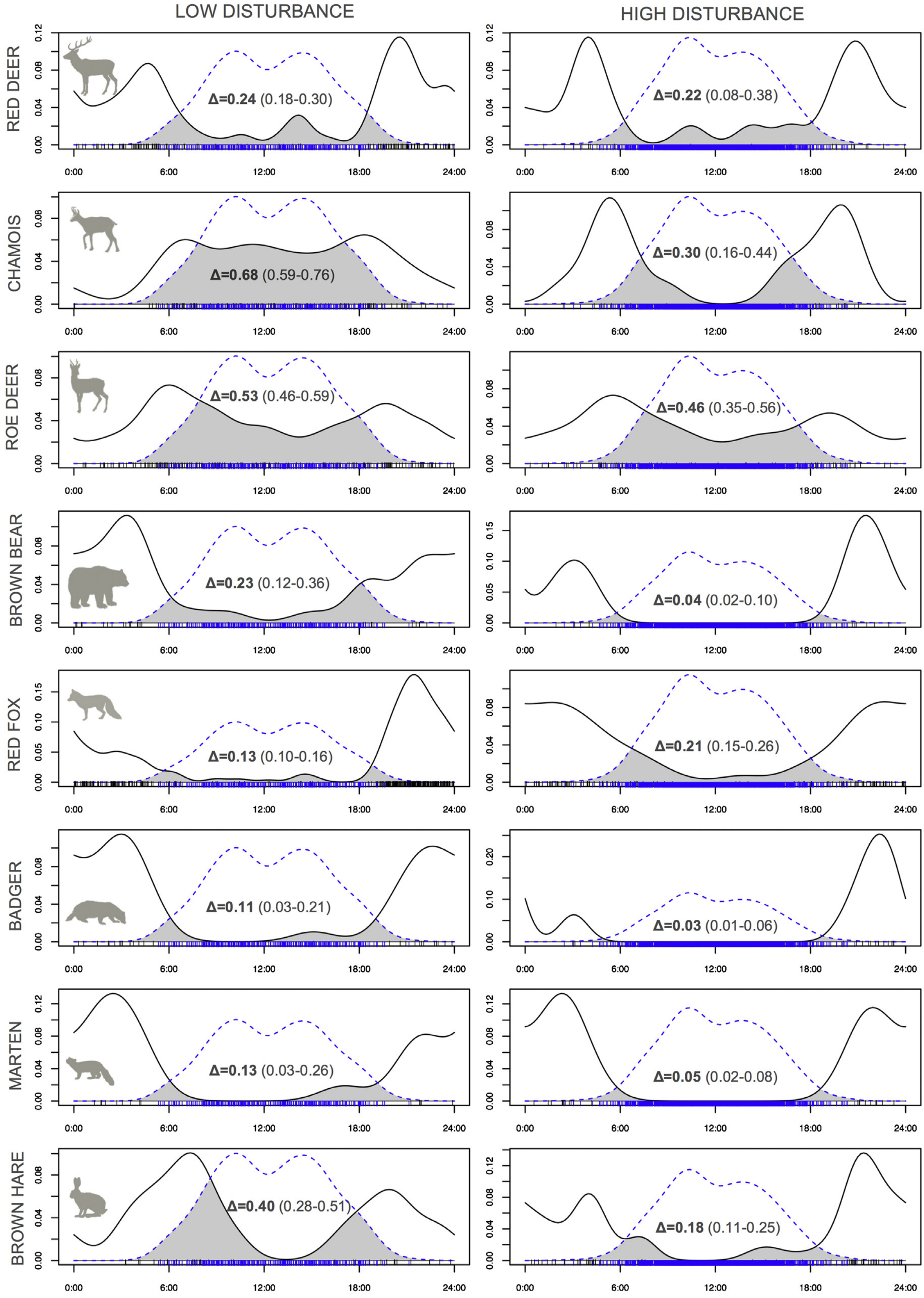

Fig. 4. Diel activity patterns (kernel density curves) for the eight most detected species in the study area, eastern Italian Alps. The overlap with human activity is shown for low and high disturbance levels. The activity pattern of people is shown as dotted lines. The coefficients of overlap (Δ) are 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).

Acknowledgements

We thank Patrick Jansen and an anonymous reviewer for constructive comments on an earlier version of the manuscript. We also thank the Forest and Wildlife Service of the Autonomous Province of Trento and the Adamello-Brenta Natural Park for the fruitful collaboration offered for the study. Funding came from the Autonomous Province of Trento through a formal agreement with MUSE-Museo delle Scienze. We are grateful to the following staff of these institutions and other people for their help in the field: Enrico Dorigatti, Riccardo Dorna, Renato Rizzoli, Simone Tenan, Massimo Vettorazzi, Gilberto Volcan, Matteo Zeni, Michele Zeni. Simone Tenan kindly provided advice during study design and analysis, and Natalia Bragalanti helped with mapping.

Appendix A. Top-ranked models for each species in the study area, the eastern Alps (the null model (ψ(.) p(.)) is also shown). Change in Akaike information criterion (ΔAIC) 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	ΔAIC	nPars	wi
Red deer	ψ (∼ve) p (∼mod+cab+homo+ve)	459.51	0.00	7	0.13
	ψ (.) p (∼mod+cab+homo+ve)	459.60	0.09	6	0.12
	ψ (∼el) p (∼mod+cab+homo+ve)	460.50	0.99	7	0.08
	ψ (∼homo+ve) p (∼mod+cab+homo+ve)	460.58	1.07	8	0.07
	ψ (∼el+ve) p (∼mod+cab+homo+ve)	460.93	1.42	8	0.06
	ψ (∼sl+ve) p (∼mod+cab+homo+ve)	460.94	1.43	8	0.06
	ψ (∼sl) p (∼mod+cab+homo+ve)	461.03	1.52	7	0.05
	ψ (.) p (.)	475.33	15.82		
Roe deer	ψ (∼sl) p (∼mod+tr+cab)	557.37	0.00	7	0.16
	ψ (.) p (∼mod+tr+cab)	558.24	0.87	6	0.09
	ψ (∼sl+homo) p (∼mod+tr+cab)	559.08	1.71	8	0.07
	ψ (∼sl+el) p (∼mod+tr+cab)	559.10	1.73	8	0.07
	ψ (∼sl+ve) p (∼mod+tr+cab)	559.24	1.87	8	0.06
	ψ (.) p (.)	564.85	7.48		
Chamois	ψ (∼sl+el) p (∼mod+homo)	339.91	0.00	6	0.16
	ψ (∼el) p (∼mod+homo)	340.59	0.69	5	0.12
	ψ (∼sl+el+homo) p (∼mod+homo)	341.56	1.65	7	0.07
	ψ (∼sl+el+el2) p (∼mod+homo)	341.66	1.75	7	0.07
	ψ (∼sl+el+ve) p (∼mod+homo)	341.89	1.98	7	0.06
	ψ (.) p (.)	348.99	9.08		
Brown bear	ψ (.) p (∼mod+cab+homo)	221.15	0.00	5	0.16
	ψ (.) p (.)	221.27	0.12	2	0.14
	ψ (∼el) p (∼mod+cab+homo)	222.21	1.06	6	0.10
	ψ (∼sl) p (∼mod+cab+homo)	222.43	1.28	6	0.08
	ψ (∼homo) p (∼mod+cab+homo)	223.04	1.89	6	0.06
	ψ (∼ve) p (∼mod+cab+homo)	223.07	1.92	6	0.06
Marten	ψ (∼homo) p (∼cab+homo)	198.47	0.00	5	0.17
	ψ (.) p (∼cab+homo)	199.14	0.67	4	0.11
	ψ (∼ve) p (∼cab+homo)	199.48	1.02	5	0.10
	ψ (∼homo+ve) p (∼cab+homo)	199.90	1.43	6	0.08
	ψ (∼el+homo) p (∼cab+homo)	200.17	1.71	6	0.07
	ψ (∼sl+homo) p (∼cab+homo)	200.26	1.80	6	0.07
	ψ (.) p (.)	204.08	5.61		
Red fox	ψ (∼el+homo) p (∼cab+ve)	454.24	0.00	6	0.26
	ψ (∼el+el2+homo) p (∼cab+ve)	455.94	1.70	7	0.11
	ψ (∼el+homo+ve) p (∼cab+ve)	455.97	1.74	7	0.10
	ψ (∼homo) p (∼cab+ve)	455.98	1.74	5	0.10
	ψ (∼sl+el+homo) p (∼cab+ve)	456.15	1.91	7	0.10
	ψ (.) p (.)	467.70	13.46		
Badger	ψ (∼el+ve) p (∼mod+cab+homo)	232.11	0.00	7	0.27
	ψ (∼sl+el+ve) p (∼mod+cab+homo)	233.56	1.45	8	0.13
	ψ (∼el+el2+ve) p (∼mod+cab+homo)	234.00	1.89	8	0.11
	ψ (∼el+homo+ve) p (∼mod+cab+homo)	234.07	1.96	8	0.10
	ψ (.) p (.)	259.11	27.00		
Brown hare	ψ (∼homo) p (∼mod+tr+cab+homo)	224.48	0.00	8	0.27
	ψ (∼homo+ve) p (∼mod+tr+cab+homo)	225.37	0.89	9	0.17
	ψ (∼sl+homo) p (∼mod+tr+cab+homo)	226.46	1.98	9	0.10
	ψ (∼el +homo) p (∼mod+tr+cab+homo)	226.47	1.99	9	0.10
	ψ (.) p (.)	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; ψ 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	ψ (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		
	ψ(el)	−0.464 (0.497)	0.3511	0.12	1		
	ψ(sl)	−0.365 (0.465)	0.4320	0.10	1		
	ψ(homo)	−0.272 (0.704)	0.6988	0.08	1		
	ψ(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		
	ψ(ve)	−0.482 (0.412)	0.24146	0.47	4		
	ψ(el)	−0.346 (0.371)	0.35156	0.21	2		
	ψ(sl)	−0.263 (0.349)	0.45076	0.18	2		
	ψ(homo)	1.068 (1.260)	0.39643	0.09	1		
Roe deer	ψ(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		
	ψ(homo)	−0.196 (0.340)	0.565100	0.11	1		
	ψ(el)	−0.230 (0.448)	0.608631	0.11	1		
	ψ(ve)	0.160 (0.477)	0.736725	0.10	1		
Chamois	ψ(sl)	0.568 (0.396)	0.15110	0.68	4	0.51 (0.13)	0.36 (0.06)
	ψ(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		
	ψ(homo)	−0.359 (0.582)	0.53699	0.12	1		
	ψ(el2)	0.162 (0.330)	0.62338	0.11	1		
	ψ(ve)	0.037 (0.294)	0.90009	0.10	1		
Red fox	ψ(el)	−0.630 (0.336)	0.06114	0.78	4	0.62 (0.11)	0.54 (0.04)
	ψ(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		
	ψ(el2)	−0.176 (0.322)	0.58378	0.13	1		
	ψ(ve)	0.186 (0.385)	0.62949	0.13	1		
	ψ(sl)	−0.089 (0.302)	0.76677	0.12	1		
Badger	ψ(el)	−1.058 (0.512)	0.0388	1.00	4	0.54 (0.14)	0.18 (0.05)
	ψ(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		
	ψ(sl)	−0.397 (0.552)	0.4724	0.18	1		
	ψ(el2)	0.175 (0.519)	0.7359	0.15	1		
	ψ(homo)	−0.132 (0.636)	0.8353	0.14	1		
Brown hare	ψ(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		
	ψ(ve)	−2.153 (2.712)	0.4275	0.22	1		
	ψ(sl)	−0.883 (1.713)	0.8877	0.13	1		
	ψ(el)	0.447 (1.601)	0.9440	0.13	1		
Marten	ψ(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		
	ψ(ve)	0.327 (0.327)	0.31721	0.28	2		
	ψ(el)	−0.211 (0.386)	0.58568	0.10	1		
	ψ(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 (ψ) for each species at each camera trap station (58 sites)

Site	Predicted ψ							
	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

References

Anderwald, P., Haller, R.M., Filli, F., 2016. Heterogeneity in primary productivity influences competitive interactions between red deer and alpine chamois. PLoS One 11 (1), e0146458.

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., Jenni-Eiermann, S., 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. Proc. R. Soc. Lond. B: Biol. Sci. 274 (1614), 1219–1224.

Aublet, J.F., Festa-Bianchet, M., Bergero, D., Bassano, B., 2009. Temperature constraints on foraging behaviour of male Alpine ibex (Capra ibex) in summer. Oecologia 159 (1), 237–247.

Baker, W.L., 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landsc. Ecol. 7 (3), 181–194.

Bartoń, K., 2015. MuMIn: Multi-Model Inference, Available at: http://cran.r-project.org/package=MuMIn.

Blumstein, D.T., Fernandez-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. J. Appl. Ecol. 42 (5), 943–953.

Boitani, L., Lovari, S., Vigna Taglianti, A., 2003. Fauna d'Italia. Calderini, pp. 1–434.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference. A Practical Information-Theoretic Approach, 2nd ed. Springer, New York.

Červinka, J., Drahníková, L., Kreisinger, J., Šálek, M., 2014. Effect of habitat characteristics on mesocarnivore occurrence in urban environment in the Central Europe. Urban Ecosyst. 17 (4), 893–909.

Corlatti, L., Lorenzini, R., Lovari, S., 2011. The conservation of the chamois *Rupicapra* spp. Mammal Rev. 41 (2), 163–174.

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L., 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos. Trans. R. Soc. B 366, 2642–2651, http://dx.doi.org/10.1098/rstb.2011.0120.

Crooks, K.R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conserv. Biol. 16 (2), 488–502.

Elsasser, H., Messerli, P., 2001. The vulnerability of the snow industry in the Swiss Alps. Mt. Res. Dev. 21, 335–339.

Fegraus, E., MacCarthy, J., 2016. Camera trap data management and interoperability. In: Rovero, F., Zimmermann, F. (Eds.), Camera Trapping for Wildlife Research. Pelagic Publishing, Exeter, UK (pp. 33–42).

Fernandez-Juricic, E., Tellería, J.L., 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. Bird Study 47 (1), 13–21, http://dx.doi.org/10.1080/00063650009461156.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.

Fiske, I., Chandler, R., 2015. Overview of Unmarked: An R Package for the Analysis of Data from Unmarked Animals.

GRASS Development Team, 2015. Geographic Resources Analysis Support System (GRASS GIS) Software, Version 7.0. Open Source Geospatial Foundation http://grass.osgeo.org.

George, S.L., Crooks, K.R., 2006. Recreation and large mammal activity in an urban nature reserve. Biol. Conserv. 133 (1), 107–117.

Gibeau, M.L., Clevenger, A.P., Herrero, S., Wierzchowski, J., 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. Biol. Conserv. 103 (2), 227–236.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.

Groff, C., Bragalanti, N., Rizzoli, R., Zanghellini, P., 2015. Rapporto Orso del Servizio Foreste e fauna della Provincia Autonoma di Trento.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6 (3), 324–337.

Jansen, P.A., Ahumada, J., Fegraus, E., O'Brien, T., 2014. TEAM: a standardised camera-trap survey to monitor terrestrial vertebrate communities in tropical forests. In: Meek, P.D., Ballard, A.G., Banks, P.B., Claridge, A.W., Fleming, P.J.S., Sanderson, J.G., Swann, D.E. (Eds.), Camera Trapping: Wildlife Research and Management. CSIRO Publishing, Melbourne, Australia (Pp. 263–270).

Kaczensky, P., Huber, D., Knauer, F., Roth, H., Wagner, A., Kusak, J., 2006. Activity patterns of brown bears (Ursus arctos) in Slovenia and Croatia. J. Zool. 269 (4), 474–485.

Kays, R., Parsons, A.W., 2014. Mammals in and around suburban yards, and the attraction of chicken coops. Urban Ecosyst. 17 (3), 691–705.

Kays, R., Parsons, A.W., Baker, M.C., Kalies, E.L., Forrester, T., Costello, R., Rota, C.T., Millspaugh, J.J., McShea, W.J., 2016. Does hunting or hiking affect wildlife communities in protected areas? J. Appl. Ecol. 54 (1), 242–252.

Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLoS One 11 (12), e0167259.

Lassen, P., Savoia, S., 2005. Ecoregion Conservation Plan for the Alps. WWF European Alpine Programme, Bellinzona.

Lovari, S., Ferretti, F., Corazza, M., Minder, I., Troiani, N., Ferrari, C., Saddi, A., 2014. Unexpected consequences of reintroductions: competition between reintroduced red deer and Apennine chamois. Anim. Conserv. 17 (4), 359–370.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8), 2248–2255.

MacKenzie, D.I., 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press.

Mackenzie, D.I., Nichols, J.D., 2004. Occupancy as a surrogate for abundance 'estimation. Anim. Biodivers. Conserv. 27, 461–467.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405 (6783), 243–253.

Mazerolle, M.J., 2012. AICcmodavg: Model Selection and Multi- Model Inference Based on (Q)AIC(c). R Package Version 1.26, http://CRAN.R-project.org/package¼AICcmodavg (Accessed 1 January 2013).

Meredith, M., Ridout, M., 2016. Overview of the Overlap Package.

Moe, T.F., Kindberg, J., Jansson, I., Swenson, J.E., 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). Can. J. Zool. 85 (4), 518–525.

O'Brien, T.G., Baillie, J.E.M., Krueger, L., Cuke, M., 2010. The wildlife picture index: monitoring top trophic levels. Anim. Conserv. 13, 335–343.

Olson, D.M., Dinerstein, E., 2002. The global 200: priority ecoregions for global conservation. Ann. Mo. Bot. Gard., 199–224.

Peters, W., Hebblewhite, M., Cavedon, M., Pedrotti, L., Mustoni, A., Zibordi, F., Cagnacci, F., 2015. Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps. Biol. Conserv. 186, 123–133.

Preatoni, D., Mustoni, A., Martinoli, A., Carlini, E., Chiarenzi, B., Chiozzini, S., Tosi, G., 2005. Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. Acta Oecol. 28 (3), 189–197.

Preisler, H.K., Ager, A.A., Wisdom, M.J., 2006. Statistical methods for analysing responses of wildlife to human disturbance. J. Appl. Ecol. 43 (1), 164–172.

QGIS Development Team, 2013. QGIS Geographic Information System, Available at: http://qgis.osgeo.org.

R Development Core Team, 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org.

Ražen, N., Brugnoli, A., Castagna, C., Groff, C., Kaczensky, P., Kljun, F., Majić, A., 2015. Long-distance dispersal connects Dinaric-Balkan and Alpine grey wolf (Canis lupus) populations. Eur. J. Wildl. Res., 1–6.

Reed, S.E., Merenlender, A.M., 2008. Quiet, nonconsumptive recreation reduces protected area effectiveness. Conserv. Lett. 1 (3), 146–154.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14 (3), 322–337.

Rogala, J., Hebblewhite, M., Whittington, J., White, C., Coleshill, J., Musiani, M., 2011. Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. Ecol. Soc. 16 (3).

Rovero, F., Spitale, D., 2016. Species-level occupancy analysis. In: Rovero, F., Zimmermann, F. (Eds.), Camera Trapping for Wildlife Research. Pelagic Publishing, Exeter, UK (pp. 68–94).

Rovero, F., Martin, E., Rosa, M., Ahumada, J.A., Spitale, D., 2014. Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. PLoS One 9 (7), e103300.

Rovero, F., Ahumada, J., 2017. The Tropical Ecology, Assessment and Monitoring (TEAM) Network: An early warning system for tropical rain forests. Sci. Total Environ. 574, 914–923.

Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141 (9), 2159–2173.

Sutherland, W.J., 2007. Future directions in disturbance research. Ibis 149 (s1), 120–124.

Swenson, J.E., 1999. Does hunting affect the behavior of brown bears in Eurasia? Ursus 11, 157–162.

TEAM Network, 2011. Terrestrial Vertebrate Protocol Implementation Manual, v. 3.1. Tropical Ecology, Assessment and Monitoring Network, Center for Applied Biodiversity Science. Conservation International, Arlington, VA, USA.

Tattoni, C., Bragalanti, N., Groff, C., Rovero, F., 2015. Patterns in the use of rub trees by the Eurasian Brown Bear. Hystrix Ital. J. Mammal. 26 (2).

Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. Ecol. Appl. 13 (4), 951–963.

Thiel, D., Menoni, E., Brenot, J.F., Jenni, L., 2007. Effects of recreation and hunting on flushing distance of capercaillie. J. Wildl. Manage. 71, 1784–1792.

Tobler, M.W., Carrillo-Percastegui, S.E., Powell, G., 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. J. Trop. Ecol. 25 (03), 261–270.

Zedrosser, A., Dahle, B., Swenson, J.E., Gerstl, N., 2001. Status and management of the brown bear in Europe. Ursus 12, 9–20.

Zimmermann, F., Foresti, D., Rovero, F., 2016. Behavioural studies. In: Rovero, F., Zimmermann, F. (Eds.), Camera Trapping for Wildlife Research. Pelagic Publishing, Exeter, UK (pp. 142–167).

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R.