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Research Article

Patterns in the use of rub trees by the Eurasian Brown Bear

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Abstract

The behaviour of marking trees by the brown bear occurs throughout the range of presence of the species. It has recently been recognised as a mean of intra-specific chemical communication, besides the likely function of ecto-parasite removal, and evidence from grizzlies showed that scent marking of trees is mainly performed by adult males during the breeding season. However, detailed studies on this behaviour in the Euroasian brown bear are lacking. We conducted a three year study on a wild bear population of 50 individuals in the Eastern Italian Alps, using camera traps. We aimed to assess the use of trees by bears' age and sex classes, its temporal variation, and to determine key habitat and human disturbance drivers of the intensity of use of rub trees. Camera trapping yielded more than 500 videos of bears from more than 9000 camera trapping days, age and sex classes were identified in 59% of the videos. Results showed that rubbing was mainly performed by adult males, with females and sub-adults that only occasionally rubbed. Rubbing was performed more during the breeding season, confirming that the main function of this behaviour is associated to males' breeding strategy. Olfactory investigation was performed by bears of all ages and sexes, indicating the importance of scent marking at rub trees for intra-specific communication. We used the camera trapping event rate as a raw index of intensity of usage of rub trees and found it to be affected by aspect, type of roads and passage of motor vehicles at the sites, while the passage of people did not affect it. We also estimated bear occupancy and detectability and found that the latter was influenced by trail type and distance from roads and buildings. Our study provides a first contribution to the use of rub trees by brown bears in the Alps.

Introduction

The behaviour of marking trees by the brown bear (Ursus arctos) is known to occur throughout the range of occurrence of the species (Green and Mattson, 2003; Puchkovskiy, 2009; Karamanlidis et al., 2010; Clapham et al., 2013; Sato et al., 2014) but only relatively recently it has been recognised as a mean of inter-specific chemical communication and not only a way to remove ectoparasites (Green and Mattson, 2003; Clapham et al., 2014). Studies in North America show that rubbing is performed more by adult males of both brown (Ursus arctos horribilis) and black bears (Ursus americanus), especially during the mating season, supporting the function of rubbing for chemical signalling to competitors to reduce aggressive encounters with other males and increasing the chances of finding a partner (Burt and Pelton, 1983; Green and Mattson, 2003; Clapham et al., 2013, 2014). The importance of rubbing behaviour in bears' biology has triggered genetic studies based on the analysis of hairs trapped in the tree bark (or in ad-hoc placed barbed wire poles), allowing to assess population structure in brown bear populations (De Barba et al., 2010a,b; Gervasi et al., 2012; Groff et al., 2015), or as additional records of presence for modelling abundance, population trends and density (Kendall et al., 2008; Stets et al., 2010; Sawaya et al., 2012; Ciucci et al., 2015). Rub trees are usually found at conspicuous locations, recognisable from the surrounding trees either by size or by being different species (Green and Mattson, 2003; Puchkovskiy et al., 2012; Clapham et al., 2013), with

coniferous trees being apparently preferred possibly because the duration of the scent leaved by bears is enhanced by the resins of the bark (Green and Mattson, 2003). These trees are often located along travel routes and some authors claim that they may be used as landmarks (Green and Mattson, 2003). Rub trees are considered also places of inter-specific communication, as markings from different species have been recorded at the same trees (McTavish and Gibeau, 2010).

Knowledge on tree rubbing by the Eurasian brown bear remains poorly investigated, with the only cases of a study in Greece, where only electric power poles were targeted as rubbing sites (Karamanlidis et al., 2007, 2010; Gohier, 2011), and in central Italy where the sub species U. a. marsicanus was targeted (Ciucci et al., 2015). Here, we provide a contribution to fill this gap by studying behavioural patterns and spatio-temporal variations in the use of rub trees in the brown bear population in Trento Province, NE Italy, the only population in the Italian Alps. We used camera traps set in front of rub trees to systematically detect passing bears over a period of three years. A few studies on grizzly bears (U. a. horribilis) and black bears (U. americanus) in North America have used camera trapping to monitor rub trees, allowing to determine differences in spatio-temporal patterns by age and sex classes, as well as to identify different motion patterns in the rubbing behaviour (Clapham et al., 2014; Talor et al., 2015). Camera trapping has emerged as a prime tool for a range of applications to wildlife research over the last decade (O'Connell et al., 2011; Rovero et al., 2013; Burton et al., 2015) but to our knowledge, this is the first study of the Eurasian brown bear (Ursus arctos arctos) using systematic camera trapping. Our specific objectives were to (1) study temporal

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variation, within the bears' activity season, in the use of rub trees; (2) assess the differences in the use of rub trees by sex/age classes; (3) determine habitat and human disturbance factors affecting the choice of rub trees by bears; and (4) determine factors affecting the detectability of brown bears at rub trees by camera trapping.

Methods

Study area and target species

The study area was the western part of Trento Province, Italy (lat. $46^{\circ}10'$ N, long. $10^{\circ}45'$ E, Fig. 1) and it encompassed the Adamello-Brenta Natural Park to the west, the adjacent Paganella mountain to the East and Monte Bondone to the South. The area is mainly covered by beech (*Fagus sylvatica*) and fir (*Picea abies*) forests with other submontane, montane and subalpine vegetation associations as well as bare rocks and glaciers. The elevation range known to be preferred by bears in southern Europe (i.e. 500-2000 m a.s.l.) is well represented in the study area (Clevenger et al., 1992; Dupré et al., 1998; Preatoni et al., 2005). The average human population density is $86/\text{km}^2$ with local and seasonal variation due to high winter and summer tourism.

The Eurasian brown bear (U.a.a.arctos) was historically widespread in the area, but in the 1990 the species was on the brink of extinction with only three males left. The present population is the result of the releases of 10 animals translocated from Slovenia from 1999 to 2002 (Mustoni et al., 2003; Preatoni et al., 2005). The area supports a stable presence for the species (Figure 1) (Tosi et al., 2015) and it is potentially connected with the eastern Dinaric-Pindos populations by two corridors (Preatoni and Tattoni, 2006; Peters et al., 2015) occasionally used by dispersing individuals. The brown bear population living in the area amounts to 45–50 individuals as estimated from the genetic identifications (Groff et al., 2015) and it is considered to have been stable in the area over the investigation period (Groff et al., 2014, 2015).

Data collection

Selection of rub trees

Our camera trapping study targeted each year 20 rub trees from a total set of 156 that have been monitored by the Wildlife Service of the Province of Trento (PAT) and other partners since 2011. All rub trees were mounted with barbed wire to collect samples of hairs to be later genetically analysed, barbed wire is not believed to be an attractive for bears who already used the tree before nor a repulsive (Kendall et al., 2008). The trees are found mainly in broad leave forests (beech) but also in coniferous (spruce and fir) and mixed forests, at an elevation range of 650–1700 m a.s.l. and are located along forest roads or trails. Most of the sites selected by the bears for rubbing were living trees belonging to the coniferous family of Pinacea, even if the most common forest type at that range is beech (*Fagus sylvatica*) (Tiso, 2011). All of the 156 known rub trees lay on roads or trails despite capillary exploration of the area by the park wardens (C. Groff, *pers. comm.*).

We selected rub trees for camera trap sampling using a criterion which was random but constrained by the locations of the pool of rub trees known in the area. Hence, to ensure a representative coverage of the core area of the population (600 km²; Groff et al., 2015), we divided the area into four quadrants and selected five rub trees in each, ensuring that the distance between adjacent trees was greater than 3 km. This selection resulted in targeted rub trees (density of 0.05/km²) located in places where elevation, slope, aspect, distance from roads and buildings did not have a significant difference from the whole sample (Wilcoxon rank sum test and Chi-square for categorical variables).

Camera Trapping

Camera traps were set to function continuously throughout the activity season of brown bears, i.e. from April to November 2012, 2013, 2014. Each year, 20 camera traps were placed in front of known rub trees with a total of 24 trees surveyed over the three years, of which 15 remained the same: 5 sites needed to be discarded due to thefts of the camera traps. We used UV565HD digital camera traps equipped with an infrared LED flash for video recording, that were set to work with no delay between consecutive triggers and in continuous across the 24 hours.

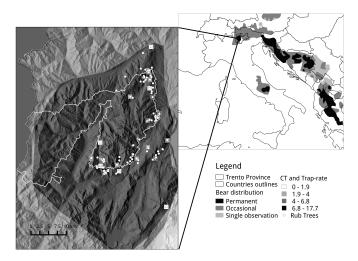


Figure 1 – Study area where rub trees where monitored by camera trapping during 2012–2014: distribution of the brown bear (*Ursus arctos*) in the Italian Peninsula and Dinaric-Pindo ranges (modified from "The distribution area of the Brown bear in Europe 2006-2011" available at KORA/LCIE websites (LCIE, 2013; KORA, 2013), right map. Location of the rub trees and the camera traps (CT) in the study area, left map (camera trapping rate is pooled for the tree years; white outline is the Adamello Brenta Natural Park).

Camera traps recorded a 20 second video at each trigger, with date and time impressed on the video file. Camera traps were fixed to a tree facing the rub-tree, at the height of about 2 meters and at an average distance of 4 meters. The camera traps were checked every three weeks for card (4 GB SD memory cards) and battery replacement. Camera trap sites were located on trails used by hunters (12), the remaining were equally parted among hiking trails, (i.e. mantained by the local Alpine Club) and forestry roads of type A, i.e. where vehicle passage is allowed with severe restrictions.

Environmental covariates

GIS data for the study area were obtained from publicly-available repositories and processed to derive potential covariates for the whole set of rub trees locations. The following digital maps were used in softwares GRASS GIS 6.4 (GRASS Development Team, 2012) and QGIS 2.1 (QGIS Development Team, 2015).

- Land cover, road network and building vector maps and Digital Elevation Model (DEM) raster at 10 m spatial resolution were downloaded from the PAT Geoportal (http://www.territorio.provincia.tn. it):
- 2. Vector map of forest types (Odasso, 2002);
- 3. Vector map of mountain trails was available at SAT website (SAT, 2014)

In addition, elevation, slope and aspect of the sites were derived from DEM while we measured the following distances as potential proxies of disturbance: distance from houses, distance from forestry roads, from paved roads and from trails. Forest types and land cover were reclassified in fewer classes in order to simplify categorical data interpretation.

After processing, the list of environmental covariates used in the models was the following: (1) elevation of the rub tree (in m a.s.l.); (2) slope expressed in degrees; (3) aspect: 8 classes North, West, East, South, NE, NW, SE, SW; (4) d_viapri: distance (m) from main road (paved) network; (5) d_build: distance (m) from single buildings, including mountain huts; (6) d_viafor: distance (m) from main forest road network (unpaved); (7) d_sat: distance (m) from hiking trails; (8) land cover: 7 land use categories (coniferous, broadleaf, mixed broadleaf, urban, pastures, bushland, water) (9) forest types: 8 forest category based on dominant tree species (beech, pine, fir, dwarf pine, larch ash/hornbeam, spruce forest and no forest); (10) trail type: 4 categories SE (hiking trails), SC (hunter trails); forestry roads of type A (used for logging), forestry roads of type B (restricted access). Different trail types have different usage by people: SE are popular trails where people pass daily in the tourist season, including with bicycles and motor bikes; SC are used only occasionally by hunters and mushrooms pickers. Forestry road of type A are only used for logging oper-

Table 1 – Summary of the survey effort and results of monitoring brown bears (*Ursus arctos arctos*) at rub trees in the eastern Alps using camera trapping set at 20 rub trees each year, See text for details. Last column reports the cumulative trap rate for the whole duration of the survey.

	Events			Camera days			Trap rate			
	2012	2013	2014	2012	2013	2014	2012	2013	2014	Total
Mean	5.58	10.55	11.45	155.32	181.55	165.90	4.04	5.55	6.24	4.90
Standard Deviation	4.75	11.16	15.44	50.51	53.60	63.95	3.64	5.04	6.52	4.79
Range	17	41	64	154	170	243	14.02	18.64	25.71	17.19
Minimum	1	0	0	41	63	0	0.52	0.00	0.63	0.52
Maximum	18	41	64	195	233	243	14.55	18.64	26.34	17.71
Sum	106	211	229	2951	3631	3318	76.76	111.01	118.52	117.70

ations and only occasionally used by people. Given the location of rub trees exclusive along trails and roads, we did not place camera traps off-trails; while we acknowledge that this may be a limit to generalize our results for habitat use by the bears, we could compare different intensity of usage among different types of trails/roads.

Data analysis

Single video sequences of individual bears were concatenated to derive complete events of passing bears (or other species), which were then screened for species identification and for classifying the rubbing behaviour. Results Data were stored in a relational database in Microsof Access 2000 format. The accounting of "independent events" (Rovero et al., 2014) was done by setting an arbitrary interval of one hour between videos of the same species. Individual events were later standardized in order to avoid biases due to different sampling efforts among sites. Trap rate is the relative frequency of capture for each species and it is computed as number events/camera days \times 100 (e.g. Rovero et al., 2014).

Videos of bears were classified for behaviour, number of individuals and sex. Bear sex could be determined only when postures exposed the genitals or when the cubs passed with their mother. The sexes are very similar, adult males tend to be bigger in size, but it was rarely possible to appreciate the proportion in a picture unless males and females were seen together. The lack of natural marks on the coat prevents individual recognition except for the four bears that were marked by ear tags or GPS collar. Age/sex classes were arranged as in Clapham et al. (2014) as follows: AM Adult Males, AF Adult Females, CUB bears aged less than 1 year, JUV non reproductive young bears aged less than 3–4 years, IND all those not clearly belonging to any of the previous.

The behaviours were classified in five categories: (1)"Indifferent"; (2)"Investigate": when the animal sniff or stop to inspect the tree; (3)"Rub": when the animal scratched its back or other body parts on the tree; (4)"Investigate and rub": when rubbing followed an obvious investigation; (5)"Mark": active marking of the tree by scratching with claws, biting for bears and also urination and defecation by other mammals

Covariance in the presence of different species, including humans, was computed using Peterson's pairwise correlation test, comparing the observations at each rub tree, we included only records for medium-to-large mammals, hence excluding birds and small mammals (basically *Apodemus* sp. and squirrels), as well a domestic animals being out of the interest of this study.

The analysis study of the environmental correlates of the use of rub trees was conducted using two complementary analysis (1) multivariate regression of the camera trapping rate at the rub trees and (2) occupancy analysis. The aim of the first analysis was to determine the

environmental drivers affecting the location and intensity of use of rub trees by bears. We used GLM negative binomial, with backward stepwise variable selection (available in the MASS R package Venables and Ripley, 2002); we selected the best models on the basis of minimizing AIC (Burnham and Anderson, 2002). The aim of the occupancy analysis, instead, was mainly to estimate detectability (see details below) and how it varied across sites, especially in relation to disturbance factors. Covariates were first checked for collinearity and outliers according to the protocol suggested by (Zuur et al., 2010). All statistical analysis were conducted using R (R Development Core Team, 2011; R Studio, 2015).

We modelled occupancy with covariates using the analytical framework developed by MacKenzie et al. (2003, 2006) to estimate the probability of occurrence (ψ) and detection (p) of the brown bear at the rub trees locations. Detection probability is defined as the likelihood of detecting a species at a site providing for the possibility that it may be present but can go undetected. We pooled data for the 3 years under the assumption that occupancy and detectability would not change significantly in a population considered stable (Groff et al., 2015) and also because we aimed to determine the effect of covariates that did not change in time. We therefore applied a single-season occupancy model (MacKenzie et al., 2003).

The data for the occupancy analysis were compiled as required by the unmarked R package (Fiske and Chandler, 2011) resulting in a matrix of 24 rows, one for each site, and 30 columns of sampling occasions. We considered a sampling occasion a week, thus we split our events on a weekly basis. Events were attributed to a week from mid April to mid-November; sites were considered occupied (1) if a bear was recorded there in any year. We tested the influence of a number of covariates on occupancy and detectability. Even though we were primarily interested in modelling detectability (knowing that bears occur across the sampled area), we also modelled occupancy (ψ) using the following sub-set of covariates of habitat and disturbance: elevation, slope, aspect, distance from buildings and roads. Instead, the following covariates, that we assumed of potential influence on the detection process, were used to model detection probability (p): distance from buildings and roads, type of road on which the rub tree is located (forest road SFA, hunters trail SC or mountain tail SE), camera trapping rate of both people and vehicles. Covariates were standardized prior to the analysis. Competing models were ranked by AIC (Akaike, 1973), and when we did not find a single, best model, those with delta AIC less than 4 were averaged with the function available in the R package MuMIn (Bartón, 2015).

Table 2 - Number of events of rubbing behaviour by age/sex classes, performed by the brown bear (Ursus arctos arctos) in the eastern Alps as detected by camera trapping.

Behaviour	Adult Females	Adult Males	Cubs	Indeterminate	Sub-adults
Investigate	14	62	6	81	30
Invest. and rub	3	62	0	7	4
Rub	0	35	0	3	0
Indifferent	20	56	8	134	21

Results

Of the 24 camera traps that we set overall, 5 were stolen and a few malfunctioned, realizing a sampling effort of 9302 camera days over the three years. This yielded 15147 videos of animals, people and motor vehicles, as reported in Table S1. The events were 11088, whereof 546 independent passages were of brown bears: 106 in the year 2012, 211 in 2013, and 229 in 2014, respectively (Tab. 1), with an average of 10.8 videos of bear per camera trap (range 1–61).

Cumulative camera trapping rate for brown bear ranged from 0.5 to 1.7 with an average of 4.9 (Tab. 1). In addition to bears, we recorded human presence through 84 videos of cars, 46 videos of motorbikes and quads, and 4112 videos of people either walking or riding a bicycle; we also recorded 21 species of other medium-to-large mammals (Tab. S1).

Rubbing behaviour

Only adult bears could be attributed to a sex class, as young males and young females are similar. We recorded 37 events of females, 215 of males and the remaining 294 events were of undetermined sex; among these, we identified 14 cubs and 55 sub-adults. Table 2 reports the observed behaviours according to sex/age classification. Bears who rubbed the trees were predominantly males (N=97), while in 10 cases they were undetermined, 4 were sub-adults, 3 were females while cubs (N=14) were never recorded rubbing. Rub tree investigation (35% of events) was performed by bears of all ages and sexes, however the most frequent behaviour was indifference (44% of events). The events recorded during the breeding season (May-July) were 298, while they were 248 during the rest of the year. The number of all individual events and the number of rubbings had a peak in the month of June, in correspondence with the mating season for the bear in the area. "Rubbing" and "Investigate and rubbing" were significantly more frequent during the breeding season (Pearson's Chi-squared test p<0.01; Tab. 2, Fig. 2), while investigation of the trees occurred throughout the period of activity and by both sexes (Fig. 3). Females passing by camera traps showed to be indifferent most of the times (20 events), they did investigate (14) and rubbed (3 events after investigation and only during the non breeding season).

The occurrence and behaviour of other species of medium-large mammals at rub trees showed that about 5% of the 1873 events of carnivores were of animals marking the trees, as well as a single event of chamoix among the 3919 of ungulates. Correlations in the events of bear and other mammals were tested using pairwise correlations: this was significant between brown bear and fox (r=0.7), brown bear and badger (r=0.5) and brown bear and martens (r=0.5). When carnivores other than bear were pooled, the correlation with bear increased (r=0.7),

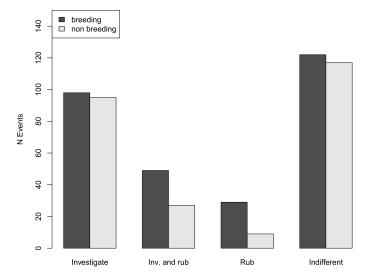


Figure 2 – Number of events for each behaviour performed by brown bears (*Ursus arctos arctos)* during the breeding and the non breeding season of a three year survey in the Italian Alps. The differences in rubbing frequency among seasons are significant (χ^2 test; p<0.01).

while the correlation with ungulates was not significant (r=0.4). No pairwise correlation was found between events of bears and of motor vehicles nor between events of bears and of people.

Covariates of the use of rub trees and bears' detectability

The relationship between cumulative camera trapping rate and spatial covariates showed that key drivers were aspect (especially southern and north east) and the location on a forestry road; the frequency of passing vehicles had a negative effect on bear's camera trapping rate while the frequency of passing people did not affect it (Tab. 3), according to a GLM model that explained 72.8% of deviance (which is a remarkably high proportion).

Occupancy analysis showed that estimated occupancy of the null model (i.e. no covariate effect) resulted almost equal to one (ψ =0.99, SE=1), while detection probability was 0.37 (SE=0.52). Out of 170 occupancy models with different combinations of the covariates 5 were selected based on delta AIC < 4 (see Appendix A for full results). Model averaging showed that occupancy was not affected by any of the covariates (Tab. 4), which is not surprising being the study sites in the core area of the population and given the fact that we pooled data for 3 years resulting in bears detected at nearly all sites (ψ =0.99 for the null model). Interestingly, however, detection probability was influenced by several human-related factors (Tab. 4, Fig. 5), with the most influential covariates (i.e. retained in all of the 5 best models) being distance from the main road network (negative effect) and trail type (significant preference for forestry roads). The best models also retained the frequency of passing vehicles as significantly and positively affecting detectability, a result in apparent contrast with the above mentioned results of negative effect of vehicles on bears' camera trapping rate.

Discussion

Our study provides new insights on the behaviour and spatio-temporal patterns of use of rub trees by Eurasian brown bears and shows that camera trapping is a critical tool to reveal aspects not derivable through other methods such as hair trapping. The use of camera trapping at rub trees allowed the sampling of bears belonging to different age/sex classes, hence overcoming the known male-bias of hair sampling which makes this techniques unsuited for collecting representative samples of the population (Graver et al., 2011). We found that adult males were the main performers of rubbing while females and sub-adults rubbed the trees only occasionally as observed also in the Marsican brown bear population (Ciucci et al., 2015). Adult males advertised their presence to other bears more intensely during the mating season, as observed in grizzlies by Clapham et al. (2013), supporting the hypothesis that they are communicating competitive abilities to other males. Scent marking by females occurred only three times, all of which in autumn, suggesting that female bears displayed this behaviour outside the breeding season as seen in the grizzlies (Clapham et al., 2014). The rubbing behaviour by males was performed also outside the breeding season, even though at lower intensity, suggesting a potential benefit for the

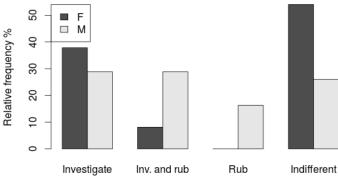


Figure 3 – Relative frequency of behaviours between brown bear (*Ursus arctos arctos*) sexes, as recorded in the Italian Alps by camera trapping. The differences in rubbing frequency among seasons is significant (χ^2 test; p<0.01).

Table 3 – Results of the GLM negative binomial regression where the dependent variable is the trap rate of brown bears (*Ursus arctos arctos*) from the 24 camera monitored sites in the Italian Alps. Legend for variables: slope is expressed in degrees; aspect: 8 classes North, West, East, South, NE, NW, SE, SW; trail type: SE (hiking trails), SFA forestry roads of type A (used for logging), motor_tr: trap rate for motor vehicles, men_tr: trap rate for people.

Coefficients							Confider	ice interval
Covariates	Estimate	Std. Error z	z value	$p(> \mathbf{z})$	<i>p</i> <0.05	Odds Ratio	2.50%	97.50%
aspect NE	1.411	0.306	4.614	0.000	*	4.100	2.268	7.556
aspect NW	-0.776	0.511	-1.519	0.129		0.460	0.155	1.194
aspect W	0.014	0.436	0.031	0.975		1.014	0.410	2.312
aspect SW	1.670	0.399	4.185	0.000	*	5.314	2.393	11.556
aspect S	-1.447	0.852	-1.697	0.090		0.235	0.032	1.049
aspect SE	0.926	0.439	2.111	0.035	*	2.524	1.047	5.938
slope	0.043	0.015	2.850	0.004	*	1.044	1.014	1.077
trail SE	0.090	0.425	0.213	0.831		1.095	0.450	2.428
trail SFA	1.275	0.442	2.887	0.004	*	3.579	1.513	8.653
motor_tr	-0.216	0.065	-3.308	0.001	*	0.806	0.701	0.909
men_tr	0.007	0.002	2.709	0.007	*	1.007	1.002	1.012

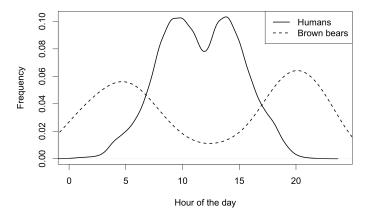


Figure 4 – Hourly activity patterns of people and brown bears (*Ursus arctos arctos*) as detected by camera trapping in the Italian Alps.

signalling bears that is still to be understood (Clapham et al., 2013). In our study, the inspection of rub trees was performed by bears of all ages and sexes suggesting that the message sent by males is directed to both competitors and possible partners, confirming the importance on rub-trees for intra specific communication.

The results of the analysis of spatial drivers of rub trees use, as indexed by camera trapping rate, are overall not of straightforward interpretation: aspect, trail type and road network are apparently key variables. Results revealed a clear difference in the daily activity patterns of bear and people (Fig. 4), a likely explanation to why the passage of people, which was intense along popular hiking trails, did not seem to affect the bears. A temporal shift in daily and seasonal activity has been observed elsewhere in bears as a response to human activity and the development of tourist resorts (Ordiz et al., 2011, 2013), especially in human dominated landscape (Martin et al., 2010). The results suggests that large trails and forestry roads may be preferred movement routes by bears in our study area, matching results for other populations (Kendall et al., 2008; Stets et al., 2010; Graver et al., 2011; Sawaya et

al., 2012; Clapham et al., 2013), while the effect of paved roads or high intensity logging routes proved to disturb the species elsewhere (Ordiz et al., 2014). The passage of motor vehicles had instead a negative influence on bears' camera trapping rate, indicating that vehicles are of clear disturbance to bears irrespectively of the time patterns of these events. While these results provide insights into rub trees use, we recommend caution in interpretation given the known limits of camera trap rate as a raw index of relative abundance that does not account for imperfect detection (e.g. Rovero et al., 2014).

On the contrary, estimation of occupancy and detectability provides for an unbiased metric (MacKenzie et al., 2006) and in our study it was of particular value to determine potential factors affecting bears' detection process, that may in turn be indicative of site-specific habitat features and/or behavioural responses to disturbance. Hence, decreasing bear detectability with increasing distance from roads indicate that proximity to road per se does not induce any avoidance or increased shyness, as it may have been expected for the species (e.g. Rovero et al., 2014). This is concordant with a comparable pattern of increased detectability with the camera trapping rate of people passing at camera sites. In contrast, increased detectability with distance from building may indicate greater bears' shyness in proximity of a direct and permanent source of disturbance. The positive and significant effect of the frequency of passing vehicles on detectability is, instead, of difficult interpretation and it is only apparently in contrast with the result highlighted above that vehicles negative affects the camera trapping rate of bears. Indeed while camera trapping rate can be used as an index of abundance, detectability is related to the observation process, hence the two metrics may not be concordant. However, in this specific case, the effect on detectability of vehicles may be spurious and possibly related to the fact that most trafficked forestry roads are sites where bear detection is theoretically higher; model results indeed indicate that the effect of hiking trails versus forestry road is higher, negative and significant (Fig. 5). These results overall shed lights on the adaptability of the target bear population to live in a highly settled area and humanmodified habitat. Even though human presence is high in the study area and rub-trees are located on mountain trails and forestry roads that can be intensively used, man-bear interactions remains rare but are of increasing concern as the bear population abundance increases in size.

Table 4 – Results of occupancy (ψ) and detection probability (p) estimation and modelling with covariates for brown bears (U. a. arctos) in the Eastern Alps. Model averaging was applied to the five models with delta AIC < 4. Full model details are reported in Table AI. Asterisks mark the significant covariates. No covariate of ψ was significantly retained.

Model-averaged coefficients	Estimate	Std. Error	z value	$p(> \mathbf{z})$	<i>p</i> <0.05
p(distance from roads)	-0.449	0.153	2.942	0.0033	*
p(trail type: hiking trail)	-1.066	0.236	4.523	< 0.0001	*
p(trail type: forest road A)	-0.547	0.312	1.751	0.0799	
p(vehicles' trapping rate)	0.299	0.127	2.350	0.0188	*
p(distance from buildings)	0.237	0.118	2.010	0.0445	*
p(humans' trapping rate)	0.254	0.124	2.041	0.0412	*

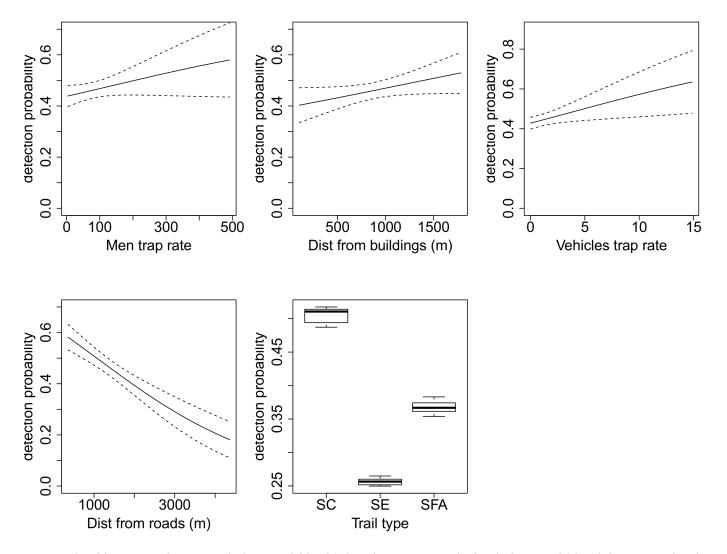


Figure 5 - Effect of the environmental covariates on the detection probability of the brown bear (U. a. arctos) in the Alps. The detection probability is higher on game trails (trail type SC) rather than on forest roads (SFA) and hiking trails (SE). See text for further details

Our study allowed for a number of other species to be detected, and among these we obtained the first records of wolves and wild boar dispersing into the study area. This study confirms the suitability of bear rub trees as privileged sites for camera trapping, as shown elsewhere (Steenweg et al., 2013). Rub trees are believed to play a role also for inter-specific communication due especially to their peculiar location and to the scent mark they diffuse in the nearby. The data collected in this work proved that rub trees are certainly located in places of transit for many species, however our results do not support a primary function for inter-specific communication.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 List of species and vehicles recorded by camera trapping and number of individual events per year.

Appendix A Occupancy model selection.