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Source: Ursus, 2021(32e9) : 1-11

Published By: International Association for Bear Research and Management

URL: https://doi.org/10.2192/URSUS-D-20-00022.3

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Abstract: The rubbing of trees by bears is an example of scent-marking that has been studied only in a limited number of bear species in the world. Our study analyzes the marking behavior of the European brown bear (*Ursus arctos*), based on filming by remote cameras placed in front of 25 rub trees in the central Italian Alps during 2012 to 2014. We obtained 546 videos of bears from a sampling effort of 9,302 camera-days. The bears captured in the videos were classified according to age and sex, and type and duration of each behavior was recorded. The data allowed us to assess temporal patterns of rubbing behavior and differences within sex, age, and among individuals. Rubbing was performed significantly more by adult males, with a peak during the breeding season. Adult males also used a variety of positions to mark the trees as compared with the other sex–age classes. Rubbing also was observed during the nonbreeding season, but with lower frequency, whereas investigation of rub trees was performed by bears of all ages and sexes throughout the seasons. The only 3 female bears that rubbed the trees were recorded in autumn, outside the breeding season. The results showed that scent-marking triggered a response in individuals that subsequently passed by the same rub tree; in 62% of the cases, the second bear either rubbed or investigated the tree, regardless of the time since the passage of the first bear. Our results supported the hypothesis that tree-rubbing during the breeding season is a means of communication, as already documented for brown bears and American black bears (*U. americanus*) in North America, but the function of this display outside the breeding season remains unclear.

Key words: Alps, camera traps, chemical communication, Italy, remote videos, scent-marking, *Ursus arctos arctos*

DOI: 10.2192/URSUS-D-20-00022.3 ***Ursus 32:article e9 (2021)***

Many species scent-mark territories in order to establish and defend these territories from intruders (Alcock 2013). Studies of marking activity across various Carnivore families indicate that the main goal of leaving a scent mark is to prevent a confrontation between the territory owner and potential intruders, and to help locate mates (Peters and Mech 1975, Boitani and Powell 2012, Gittleman 2013, Allen et al. 2014). The receiver modifies its behavior based on the information received from the smell, and after inspecting it can decide how to use the information and move or signal back (Gittleman 2013). The deposition of scent marks in a conspicuous spot or along travel routes, which also is common in many species, increases the chances that the message could be detected by other individuals. However, scent-marking has also been found in nonterritorial species, such as those belonging to the *Ursidae* family, the meaning of which is less obvious and possibly linked to mating strategy and food defense strategy (Clapham et al. 2012, Seryodkin 2016).

The rubbing of trees by bears is an example of scent-marking, whereby the animal rubs the back or other body parts on the bark of a tree, sometimes leaving visible marks with its claws or teeth. This behavior has been recorded throughout the range of the brown bear (*Ur-*

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sus arctos; Green and Mattson 2003, Puchkovskiy et al. 2012, Sato et al. 2014), as well as other bears, such as the American black bear (*U. americanus;* Burt and Pelton 1983, Taylor et al. 2015), the Andean bear (*Tremarctos ornatus;* Filipczykova et al. 2017), and the giant panda (*Ailuropoda melanoleuca;* Kleiman 1983, Nie et al. 2012). Brown bears possess an anal sac that secretes a variety of chemical compounds that likely carry information about the individual's sex (Rosell et al. 2011), a feature that is similar to and well-documented in giant pandas (Kleiman 1983). Sergiel et al. (2017) investigated the existence of pedal glands in brown bears and documented that some of the compounds found in those glands were exclusive to males, reinforcing their role in chemical communication for the species.

The objects chosen for rubbing are usually live or dead trees, with a preference for conifers (Green and Mattson 2003, Clapham et al. 2013a), but rocks or artifacts such as power poles have also been recognized as rub sites (Karamanlidis et al. 2007). Most deciduous and broadleaf tree species tend to have smoother bark than conifers, so evidence of rubbing (e.g., hair deposition and smoothing of bark) on these trees is more easily missed, and hence is likely underrepresented, in studies of bear rubbing behavior.

Rub trees can be reused over time by different individuals and they are usually recognizable from the surrounding environment because of the size of the trunk (Puchkovskiy et al. 2012) or because they belong to a different species (Puchkovskiy 2009, Clapham et al. 2013a Kleiner et al. 2018). Rub sites are most often found in prominent locations along trails or forest roads (Green and Mattson 2003, Tattoni et al. 2015) that are used by the bears and other species to travel (Henderson et al. 2015, Tattoni et al. 2015). In North America, rub trees also occur away from trails (Kendall and McKelvey 2008). Comparison with marking behavior by other carnivores indicates that marking in locations that are conspicuous and elevated from the ground not only maximizes detectability, but also increases odor dispersal.

Indirect chemical communication among bears is the most plausible function of tree-marking for a solitary mammal that lives in a forested habitat where visual communication is limited (Puchkovskiy, 1998, Taylor et al. 2015, Sergiel et al. 2017). Field evidence from grizzly (*U. arctos;* Clapham et al. 2013a) and American black bears (Burt and Pelton 1983, Taylor et al. 2015) has shown that rubbing leaves a scent mark on trees and that this behavior is mainly performed by adult males during the breeding season. Clapham et al. (2014) observed that dominant male bears used more complex postures to deposit the scent compared with other sex–age classes, suggesting that the signaler is advertising its status to receivers (i.e., competitors and mates) in analogy to some bird species, where the more experienced males perform more complex vocal or motion displays. Systematic observations of the rubbing behavior of European brown bears in the wild are lacking, although rub trees have been used for collecting samples for genetic investigations (De Barba et al. 2010a, 2010b; Gervasi et al. 2012), population monitoring (Karamanlidis et al. 2007, Ciucci et al. 2015), and occupancy modeling (Tattoni et al. 2015).

In this study we focused on the behaviors European brown bears displayed at rub trees. To our best knowledge, this is the first study in Europe using videos from remote cameras to investigate marking activities in a population of brown bears. Based on the studies by Clapham et al. (2014) and Preston Taylor et al. (2015), we expected to observe the following: 1) a peak of tree-rubbing activity during the breeding season; 2) adult males rubbing more often than females and subadults; 3) adult males showing a more complex motion pattern while rubbing; and 4) an ethological response to the deposition of the scent

Materials and methods

Study area

The study area lies entirely within the province of Trento (46°04′00″N 11°07′00″E), Northern Italy, in a mountain environment with an elevation range of 500–2,000 m above sea level (a.s.l). Forest covers the majority of the area, with beech (*Fagus sylvatica*) and spruce (*Picea abies*) being the dominant species together with other submontane, montane, and subalpine vegetation associations, as well as bare rocks and glaciers (Ciolli et al. 2012).

Most of the study area belongs to the Adamello–Brenta Natural Park, the protected area in which the last 3 brown bears in the area survived until the 1990s. To preserve a population that also has an iconic value (Tattoni et al. 2017, Tattoni 2019), 10 brown bears were translocated from Slovenia between 1999 and 2002 (Mustoni et al. 2003). The reintroduction was successful, and the population increased to 50–54 individuals in 2015 (Groff et al. 2016) and to 80–100 in 2020 (Wildlife Service of the Province of Trento, unpublished data). The core area of the population is connected with the eastern DinaricPindos brown bear populations by 2 corridors (Preatoni and Tattoni 2006, Peters et al. 2015), which are used occasionally by dispersing males. Groff et al. (2016) identified ≥156 rub trees in the park area. These trees

occurred mostly in broad-leaved forests (beech), but also in coniferous (spruce and fir) and mixed forests, at altitudes between 650 and 1,700 m a.s.l., all situated along forest paths and hiking or game trails (Tattoni et al. 2015). Most of the rubbing sites selected by bears were living coniferous trees, even though the most common type of forest in the area is beech (Tiso 2011, this study).

Data collection

We used the database of videos collected by the Wildlife Service of the Province of Trento (PAT) in collaboration with MUSE – the Science Museum of Trento and the Adamello Brenta Nature Park. The camera-trap survey lasted 3 years (2012–2014) and was conducted during the bears' activity period (i.e., Apr–Nov; Groff et al. 2016), thus including the breeding season (from 15 May through 15 Jul; C. Groff, personal communication). The deployed sampling effort was 9,900 camera-days and the realized effort was 9,320 camera-days (see Tattoni et al. 2015 for description of the sampling procedures). We used UOVision UV572 IR+ camera traps (UOVision Technology, Shenzhen, China), equipped with an infrared flash for night recording. We set cameras to work in continuous mode over 24 hours to record, upon triggering, a 20-second video with date and time impressed in the images and checked them every 3 weeks for data download and battery replacement. No bait was used, to avoid any attractive or repulsive effect (Kendall et al. 2008).

We collected data from 25 rub trees in an area of approximately 600 km^2 (Tattoni et al. 2015), a rectangle of about 30 × 20 km encompassing the entire park and the surrounding area (Fig. 1), where most of the females' home ranges occurred according to Global Positioning System (GPS) telemetry analyses performed by Groff et al. (2014). The core area of the females is approximately 1,068 km^2 and has a density of 3.3 bears/100 km^2 (Groff et al. 2016).

The wildlife office also provided the GPS locations of 16 bears (10F, 6M) from 2006 to 2017 to calculate home ranges in the study area and analyze their overlap with the rub trees. Figure S1 (Supplemental material) shows the spatial distribution of the rub trees in relation to the home range of 16 collared bears; the rub trees were located within the home range of the females ($N = 10$) and most of the males (4 of 6). Females tended to stay within and near the park, where the most frequented rub trees also are found. All the rub trees equipped with remote cameras overlapped ≥3 home ranges, with a maximum of 7 home ranges and a mean of 5.1 ($N = 25$ trees and 16 bears).

Data classification

We screened downloaded videos for species identification and classification of behavior at the rub tree as described in Tattoni et al. (2015). Videos of bears recorded within an interval of 1 hour were considered as a single 'independent event,' sensu Kays and Slauson (2008). We standardized these 'independent' events for sampling effort by computing the camera-trapping rate (i.e., the no. of events/camera-days), and multiplied by 100 to decrease the number of decimals (e.g., Rovero et al. 2014, 2017).

Bears

We determined the number of individuals and sex of videoed bears and recorded these data in the database. The sex of the bear was visually determined when the genitals were visible in the videos, and we considered a female to be any adult bear with cubs; for tagged individuals, the sex was known. Single individual recognition was possible only for 12 individuals, 4 of them marked by ear tags or GPS collar, and 8 of them were later recognized by cross-referencing with the PAT's genetic database. Most individuals remained unknown.

We attributed a bear to a sex–age class followed the classification proposed by Clapham et al. (2014): AM was an adult male; AF was an adult female; CUB was a bear aged <1 year; JUV was a juvenile, nonreproductive bear aged <3–4 years; UND was undetermined, all those not clearly belonging to any of the previous classes.

Behaviors

We classified behaviors according to the following ethogram (Clapham et al. 2014, Tattoni et al. 2015, Taylor et al. 2015): (1) Investigate—the animal sniffed or stopped to inspect the tree; (2) Rub—the bear rubbed its back or other body parts on the tree; (3) Investigate and rub—rubbing followed an obvious investigation; (4) No response—the animal just passed by; and (5) Other marks—claw marking, urination, or defecation. We also recorded the duration of each behavior and the part of the body used to mark the tree in each session.

Different parts of the body are likely to leave a different scent, so we grouped the types of rubbings according to the body part used (Rosell et al. 2011). The "back" rubbing mode occurred when the animal was standing on its hind limbs and rubbed its back on the tree; in the "head" mode, the bear stood on its 4 limbs or sat near the tree and rubbed only its head; and the "flank" mode was the same as the previous, but the flank was used. We also considered combinations of these behavioral patterns regardless of the order in which they were performed, and

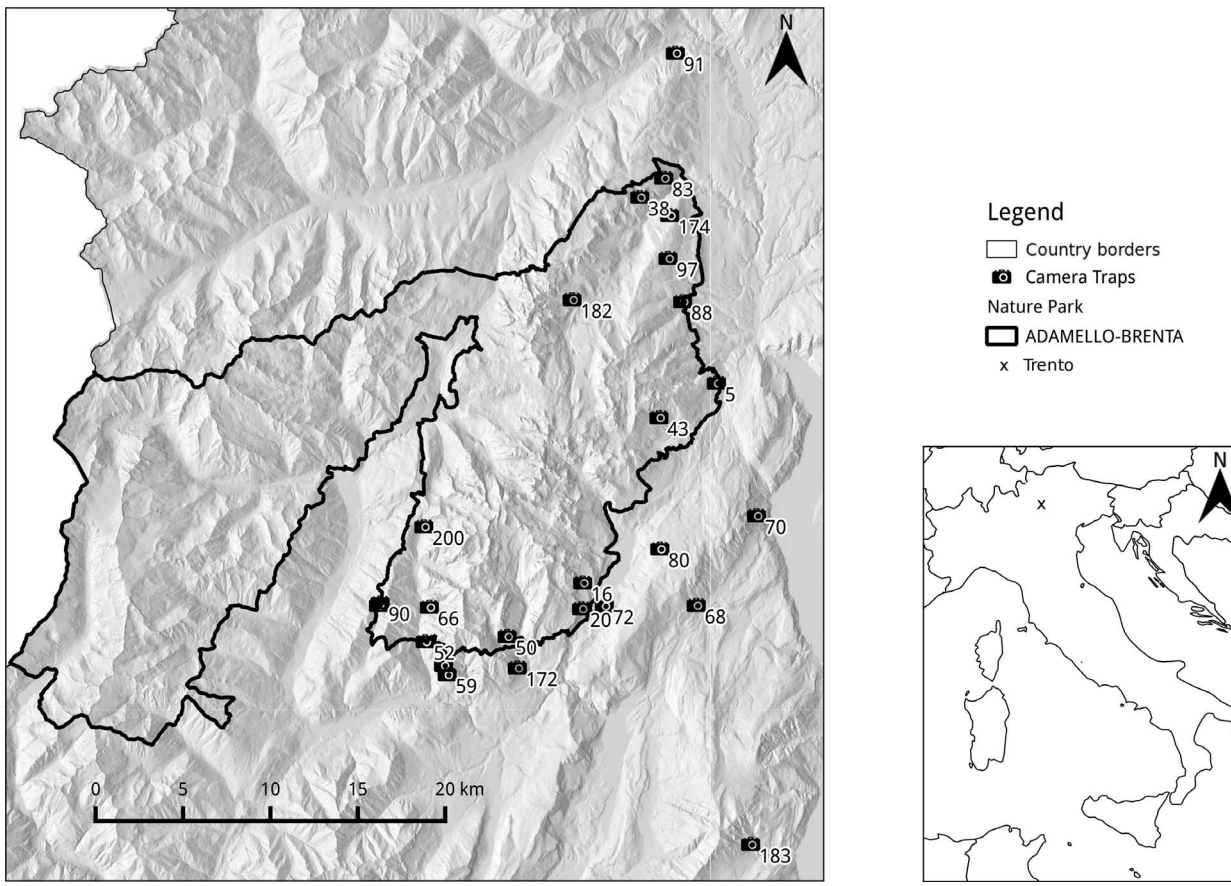

Fig. 1. The location of Adamello Brenta Nature Park within Italy, along with the location and ID of the remote cameras in the study area where we observed frequency of tree-marking behavior, according to sex–age classes, by European brown bear (*Ursus arctos*) during 2012 to 2014.

recorded them as "back and flank," "back and head," and "HBF" (head, back, and flank).

Behavioral sequences

To understand whether the act of marking triggered a response from the next bear that passed by the same rub tree, we analyzed the type of behavior exhibited, sex–age class, and the elapsed time between the initial rubbing event and the arrival of the second bear. We considered the first rubbing event occurring at a tree to be the starting point (time = 0). If a bear visited the tree within a maximum of 40 days, we recorded the pair and then considered the next rubbing event after the second event as a new starting point. If the subsequent visit occurred after 40 days, we considered it to be an independent event and the process restarted from the next rubbing event. Based on the presumed duration of scent mark in other species (Rosell and Sanda 2006, Vogt et al. 2014), we assumed that 2 sequential visits >40 days apart were independent. For this analysis, we grouped "rub" and "investigate and rub" together to limit the number of different combinations of behaviors. In the very few cases in which the second event occurred in a different season from the first, we used the season of the second event.

Statistical analysis

We built a Generalized Linear Mixed Model (GLMM) with rubbing as the binary response variable, a binomial error distribution, and a logit link function. We used the season (breeding or nonbreeding), the previous event (rub, or not rubbing), and age of the scent-mark (days) as fixed factors and the tree ID as a random factor. The first and last observations of each event for a given year for each rub tree were omitted, resulting in a final number of

Table 1. Behaviors at rub trees performed by different sex–age classes of European brown bears (*Ursus arctos*) in the Italian Alps during 2012 to 2014, as detected by remote cameras (AF = adult females, AM = adult males, JUV = juveniles, CUB = cubs, UND = undetermined, *N* = 546), as reported by Tattoni et al. (2015).

Behavior	AF	AM	JUV	CUB	UND	%
Investigate	14	62	30	6	81	35.3
Investigate and rub	3	62	4	0	7	13.9
Rub	0	35	0	0	3	7
No response	20	56	21	8	134	43.8

Table 2. Observed positions of the rubbing behavior of the European brown bears (*Ursus arctos*) in the Italian Alps during 2012 to 2014: adult males use a more diverse motion pattern compared with the other classes. Figures are the number of independent events (*N* = 115), last row is the percent of each behavior. AF = adult females, AM = adult males, JUV = juveniles, CUB = cubs, UND = undetermined, HBF = head, back, and flank.

Sex–age class	Back	Back + flank	Back + head	Flank	Head	HBF
AF	2	1	0	0	1	0
AM	74	2	3	3	0	1
CUB	0	0	0	0	0	0
JUV	8	0	1	0	1	0
UND	13	2	0	1	1	1
%	84.35	4.35	3.48	3.48	2.61	1.74

events of $N = 500$. We performed all data analyses using open source software: QGIS 3 R 3.4.4 (R Core Team 2018) and RStudio 1.0.136 (RStudio Team 2016). We ran the GLMMs using the packages 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017).

Results

Bear detections

The screening and classification of the 15,147 videos of animals, people, and motor vehicles and the construction of the database are described in Tattoni et al. (2015). The database contained 4,242 videos of people walking or various vehicles and records of 30 other species: 17 mammals including 5 domestic animals, 12 birds, and 1 amphibian (see table S1 from Tattoni et al. 2015 for the complete checklist). The database included 546 independent passages of brown bears: 106 in 2012, 211 in 2013, and 229 in 2014, with an average of 10.8 videos of bear per camera (range = 1–61). These represented 37 adult females, 215 adult males, 14 cubs, and 55 juveniles, leaving 255 undetermined cases.

Behaviors

The bears that rubbed the trees were mostly males, with undetermined animals rubbing 10 times, females 3 times, and no observations of cubs rubbing (Table 1). Bears of all ages and sexes investigated the trees, but the most common behavior was indifference (Fig. 2). The number of events recorded was similar between the breeding season (with 298 events) and the rest of the year (with 248 events; Fig. 3). The mean duration of the investigative behavior was 9 seconds (range = 1–40 sec) and the average duration for rubbing was 12 seconds (range = 1–150 sec). The duration of those 2 behaviors was tested for differences by sex–age classes and season, with no significant differences (sex–age: Pearson's Chi-squared = 99.77, 100 df, $P = 0.48$; season: Pearson's Chi-squared = 46.75, 56 df, $P = 0.13$), except for the longer investigation time in 2013 (Pearson's Chi-squared = 69.92, 50 df, $N = 546$, $P < 0.05$). The body part most commonly used for marking behavior was the back (97 occasions, $N = 115$), then "back and flank" (5); the other parts were rarely used (Table 2). Scratching bark with the claws was observed 5 times, always during a rubbing display—3 times by adult males and 2 by juveniles. In 2 instances, the bark was peeled off the trunk and licked. This behavior was rare, so we did not use this behavior in the analyses. Investigation of trees occurred throughout the period of activity and by both sexes (Figs. 3, 4).

Twelve individuals were identified. Four were identified by the presence of ear tags and/or GPS collars, and the others were identified by matching the information from the genetic profiling stored in the database—4 females (named BJ1, Daniza, F13, F16) and 8 males (named Gasper, JJ5, M2, M3, M6, MJ2G, MJ4, MJ5). In 3 cases, images of bears classified as undetermined proved to be males and in 2 cases a juvenile turned out to be an adult male (Table 3). Genetic analysis and images could not always be paired because of the time shift between video recording and hair collection. Individual determination was possible in 87 events for males and 8 events for females. Males generally used more rub trees than females. Although the females only used 1 or 2 rub trees (4–8% of the observed trees), a single male could interact with up to 10 different trees (42% of the trees). Despite the limitation of identifying only 12 bears, it was still possible to ascertain a pattern of individual variation in the rubbing activities, as well as in the space use.

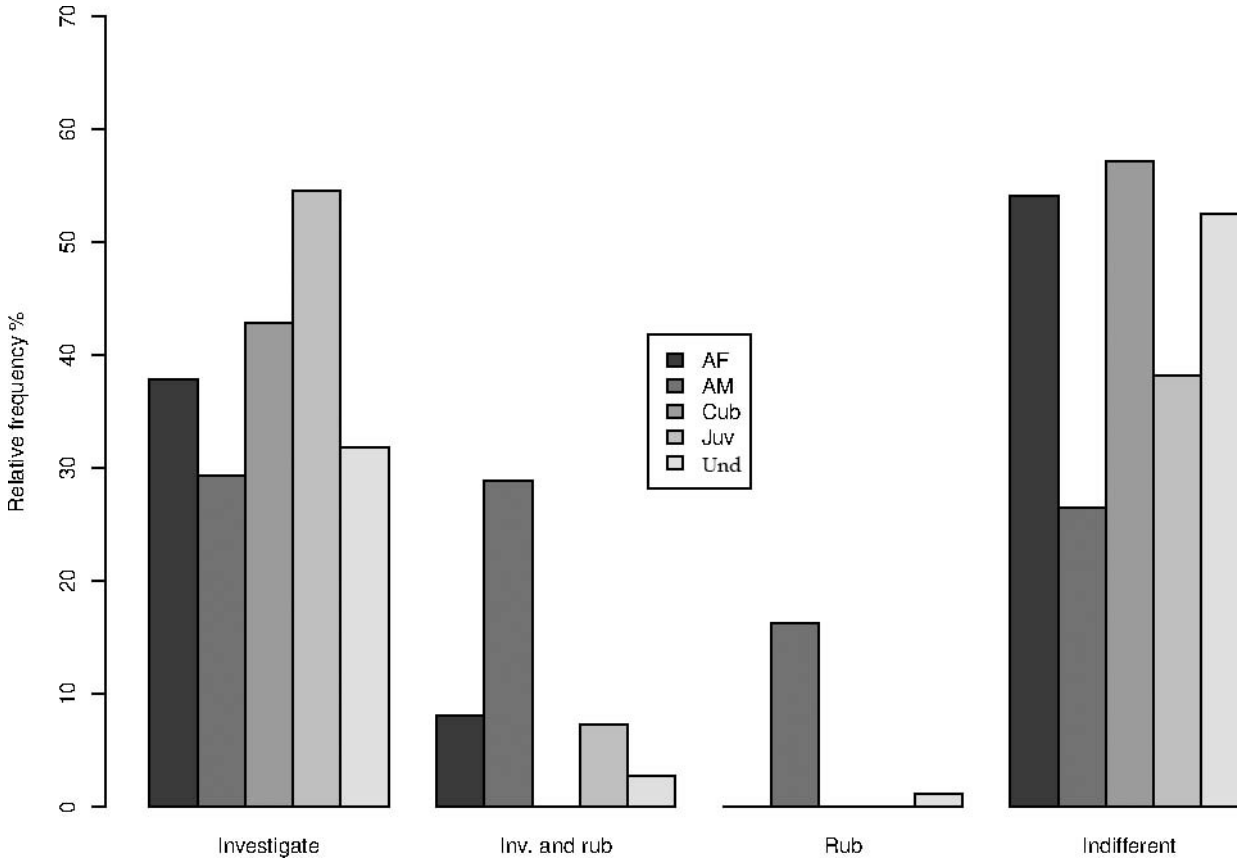

Fig. 2. Observed frequency for each tree-marking behavior, according to sex–age classes by European brown bear (*Ursus arctos*) in the Italian Alps during 2012 to 2014: observed difference in the rubbing behavior among sex–age groups is significant (Pearson's Chi-squared test <0.05). AF = adult females, AM = adult males, Cub = cubs, Juv = juveniles, Und = undetermined.

Table 3. Behavioral variability of 12 European brown bears (*Ursus arctos*) in the Italian Alps during 2012 to 2014: 4 females (BJ1, Daniza, F13, F16) and 8 males (Gasper, JJ5, M2, M3, M6, MJ2G, MJ4, MJ5). Figures are the number of independent events.

Bear name	Investigate	Investigate and rub	Rub	No response	Total
BJ1	1	1	0	1	3
Daniza	2	0	0	1	3
F13	0	1	0	0	1
F16	0	1	0	0	1
Gasper	3	10	3	5	21
JJ5	0	1	2	0	3
M2	5	1	0	0	6
M3	5	3	1	3	12
M6	11	7	4	10	32
MJ2G1	0	3	1	1	5
MJ4	0	3	1	0	4
MJ5	0	2	2	0	4

Behavioral sequences

Camera traps recorded 90 passages after an initial rubbing, with an average interval between passages of 9.1 days (SD = 1.07 days). The sequence was initiated by a male bear most (82%) of the times (Supplemental material, Table S1), with the second bear passing the same tree being another male 43% of the time or a bear of indeterminate sex 28% of the time. In about 17% of the cases, no bear passed by the tree during the 40-day threshold. The other second events were juveniles (7.8%), females (4.4%), or cubs (1%). The recorded sequences (Supplemental Table S1) suggested that marking triggered a reaction from the second bear of either rubbing or investigation 63% of the times (33% rub and 30% investigate). In the other 20% of the occasions, when a bear just passed by the tree, we could not tell if it smelled the scent but did not investigate it with an obvious display.

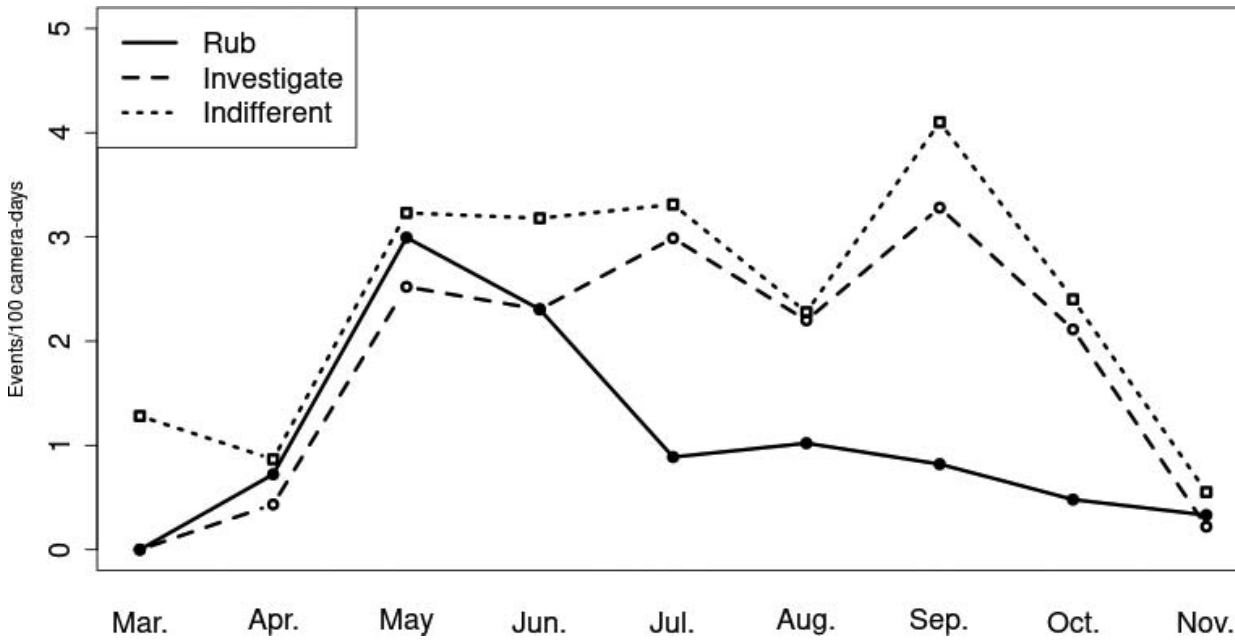

Fig. 3. Temporal pattern of observed behaviors by European brown bears (*Ursus arctos*) at rub trees in the Alps, as detected by remote cameras during 2012 to 2014.

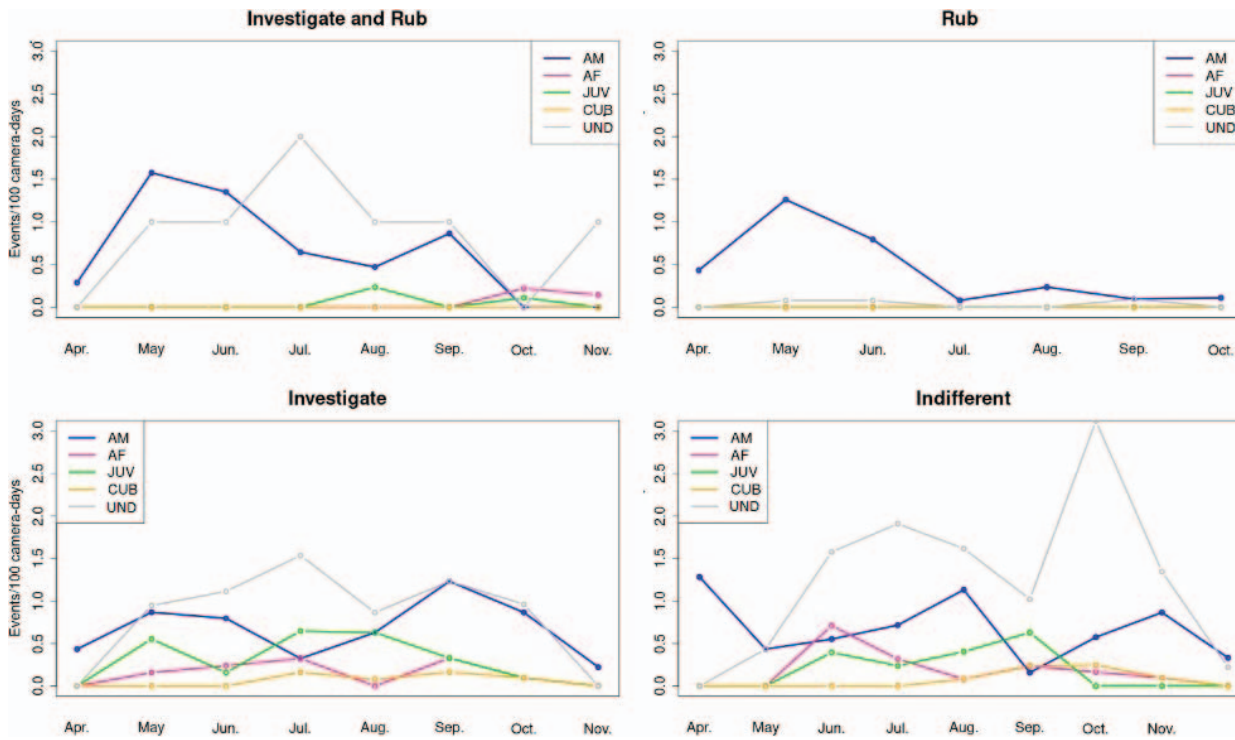

Fig. 4. Seasonal patterns in the behavior of the European brown bear (*Ursus arctos*) in the Italian Alps among sex–age classes, as detected by remote cameras during 2012 to 2014. AF = adult females, AM = adult males, JUV = juveniles, CUB = cubs, UND = undetermined.

Table 4. Generalized linear mixed model of the factors affecting the probability of a rubbing event for the European brown bear (*Ursus arctos*) in the Italian Alps during 2012 to 2014. Data ($N = 500$) were fitted to a binomial distribution. "Age of mark" is expressed in days and "rub" is a binary variable (0, 1) indicating whether the previous event was rubbing (1) or not (0). The ID of the rub tree was used as a random effect in the model (estimated variance component = 0.0232, SD = 0.1523). Effect size calculated with the MuMIn R2c = 0.133.

Model variable	Estimate	Lower CI 2.5%	Upper CI 97.5%	SE	*P*
Intercept	0.2172	0.1341	0.3011	0.0424	0.000
Season	− 0.0395	− 0.1034	− 0.3853	0.0351	0.122
Age of mark	− 0.0003	− 0.0036	0.0042	0.0020	0.686
Rub (previous event)	0.0971	0.0117	0.1868	0.0450	0.025

Multiple regression modeling

The only significant variable in the GLMM was that the brown bears were more likely to rub over an existing scent mark ($P = 0.025$; Table 4). The ID of the rub tree, which was a random effect in the model, also was significant, indicating a tree-dependent variability (Table 4). Male and female bears showed different patterns in their behaviors according to season (Fig. 4), with rubbing mainly displayed by males (Pearson's Chi-squared = 38.92, 3 df, $P < 0.01$). Females were indifferent most of the times (20); however, they investigated 14 times and rubbed 3 times, only after investigation and outside the breeding season (Fig. 4).

Discussion

Remote cameras allowed us to study the behavior of the European brown bear at rub trees and assess its temporal pattern and differences by sex, age, and individual. Our results support the hypothesis that tree-rubbing could be a means of communication, as already proposed for grizzlies and American black bears in North America (Kendall et al. 2008, Clapham et al. 2013a, Allen et al. 2014). Hair deposition at rub trees for genetic analysis tends to be biased toward males (De Barba et al. 2010a), which is known to limit interpretation and inference of the results for the whole population (Graves et al. 2011, Ciucci et al. 2015). However, Kendall et al. (2016) found similar detection rates for males and females during some sampling occasions. Despite the number of undetermined bears, the use of remote cameras permitted the identification of females, cubs, and individuals that normally did not leave their hairs in the bark. This partially overcame the sampling bias of the collection of hair in the rub trees.

Although rubbing was confirmed to be a typical adult male display, other sex–age classes did investigate, but with different temporal patterns according to sex–age classes. Males and subadults investigated the trees during the mating season, with a peak of activity in late May and the beginning of June; however, in our study, they also did it intensely in autumn, during hyperphagia preceding hibernation. Adult females checked the trees in 40% of their passages, but this behavior was performed throughout the year without a seasonal pattern. The undetermined bears inspected the trees with a pattern similar to those displayed by females; this group probably included several young bears of both sexes that might have been interested in knowing whether an adult male is in the area. During the mating season, adult males advertise their presence to other bears (Clapham et al. 2013b) and both sexes investigated the trees, which was consistent with the hypothesis that this display contains a message directed to both competitor males and possible mates. Investigation was performed by all bears, especially by juveniles that could be interested in avoiding direct competition with adult males, as well as by females with cubs as a possible way to protect their offspring from infanticide (Steyaert et al. 2013).

Although most bears just passed in front of the rub trees without showing a particular interest or action, the GLMM results showed that, after a bear rubbed a tree, the next passing bear rubbed or investigated more frequently, supporting the hypothesis that scent-marking performs a communication function and triggers a feedback reaction. The chemical signals left by males were likely to be of interest to all bears, even if only adult males send a message back. The age of the scent mark did not appear to influence the type of response from subsequent bears, but little is known about the environmental conditions that affect the time that a mark lasts. The significant effect of tree ID deserves further investigation in order to understand whether the bears' choice is influenced by the tree size or species. Clapham et al. (2011) demonstrated that, in grizzly bears, the frequency of marking varied in relation to food availability. The year 2013 was a mast year for the beech acorns (Dr. Chiara Azzetti, National Biodiversity Center, Peri, Italy, personal communication), and we can only speculate that the longer investigation could be

linked to the availability of food, or perhaps the scent had a different persistence in particularly dry and hot years.

Adult males showed a greater variety of motion patterns while rubbing. This supports the communication theory that dominant individuals have a greater "repertoire" of signals to describe their status, compared with younger and inexperienced bears that have more limited skills, as has been observed for other species (birds, whales; Alcock 2013). We observed a certain variety of displays in the undetermined category, suggesting that some adult males belonged to this class, as was verified by genetic detection. Video recording of the European brown bear showed that adult males, compared with other sex and age classes, have a more complex and diverse array of rubbing positions, using different body parts on the bark, analogous to the observations of American black bears reported by Preston Taylor et al. (2015). These results strengthen the assumption that rubbing is a means of communication. Clapham et al. (2014) reported that young grizzly bears had more simplistic marking-motion patterns than did dominant males. The function of rubbing by females and in autumn deserves further investigation. We observed scratching of the bark with the claws or teeth only occasionally, suggesting that this behavior was not as common in European brown bears as in American black bears (Green and Mattson 2003, Clapham et al. 2014).

In conclusion, our study on European brown bear behavior at rub trees supports the hypothesis of rubbing as a mean of social communication. Indeed, our results suggest that such social communication is linked to the mating season, but we believe that the communication system is likely to be in place throughout the year, with a different purpose than finding a mate. This is supported by the modeling results showing that the occurrence of a previous rub more significantly predicted the next rubbing event than did season. Rubbing and investigation were performed throughout the year with less intensity, suggesting that the communication among bears may be more complex than has been supposed and could be related to other factors, such as competition for food in autumn or food availability during a mast year (Clapham et al. 2013b), spatial use of the resources (Nevin and Gilbert 2005,) and even orientation (Green and Mattson 2003).

Acknowledgments

Data collection was supported by PAT (Provincia Autonoma di Trento) and MUSE – Museo delle Scienze (Trento, Italy) through a formal agreement between these 2 institutions. The University of Trento provided publication funding through DICAM research resources and EIT Climate-KIC Deep Demonstrations in Forging Resilience in Dolomites 2 project. We wish to thank E. Santoni for her help with sorting videos. We are grateful to the personnel from the Servizio Foreste e Fauna of Trento Province and from the Adamello–Brenta Natural Park for their valuable assistance with data collection. The authors would like to thank Editor-in-Chief J. Swenson and the reviewers for their commitment to improving this manuscript, and Associate Editor O.T. Nevin and copy editor T. Estabrook Boal for their support.

Literature cited

ALCOCK, J. 2013. Animal behavior: An evolutionary approach. 10th edition. Sinauer Associates Inc., Sunderland, Massachusetts, USA.

ALLEN, M.L., H.U. WITTMER, AND C.C. WILMERS. 2014. Puma communication behaviours: Understanding functional use and variation among sex and age classes. Behaviour 151: 819–840. http://dx.doi.org/10.1163/1568539X-00003173.

BATES, D., M. MAECHLER, B. BOLKER, AND S. WALKER. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48. doi:10.18637/jss.v067.i01.

BOITANI, L., AND R.A. POWELL, editors. 2012. Carnivore ecology and conservation: A handbook of techniques. Oxford University Press, New York, New York, USA.

BURT, T.L., AND M. PELTON. 1983. Black bears mark trees in the Smoky Mountains. Bears: International Conference on Bear Research and Management 5:45–53.

CIOLLI, M., C. TATTONI, AND F. FERRETTI. 2012. Understanding forest changes to support planning: A finescale Markov chain approach. Models of the Ecological Hierarchy: From Molecules to the Ecosphere 25:355–373. https://doi.org/10.1016/B978-0-444-59396-2.00021-3.

CIUCCI, P., V. GERVASI, L. BOITANI, J. BOULANGER, D. PAETKAU, R. PRIVE, AND E. TOSONI. 2015. Estimating abundance of the remnant Apennine brown bear population using multiple noninvasive genetic data sources. Journal of Mammalogy 96:206–220. DOI: 10.1093/jmammal/gyu029.

CLAPHAM, M., O.T. NEVIN, A.D. RAMSEY, AND F.T. ROSELL. 2012. A hypothetico-deductive approach to assessing the social function of chemical signalling in a non-territorial solitary carnivore. PLoS ONE 7:1–11. https://doi.org/10.1371/journal.pone.0035404.

———, ———, ———, AND ———. 2013a. The function of strategic tree selectivity in the chemical signalling of brown bears. Animal Behaviour 85:1351–1357.

———, ———, ———, AND ———.. 2013b. Food availability affects the scent marking frequencies of wild brown bears. Oral presentation. International Conference on Bear Research and Management 22, 15–20 Sep 2013, Provo, Utah, USA. https://core.ac.uk/download/pdf/146489668.pdf. Accessed 12 Feb 2021.

———, ———, ———, AND ———. 2014. Scent-marking investment and motor patterns are affected by the age and sex of wild brown bears. Animal Behaviour 94: 107–116.

DE BARBA, M., L.P. WAITS, E.O. GARTON, P. GENOVESI, E. RANDI, A. MUSTONI, AND C. GROFF. 2010a. The power of genetic monitoring for studying demography, ecology and genetics of a reintroduced brown bear population. Molecular Ecology 19:3938–3951.

———, ———, P. GENOVESI, E. RANDI, R. CHIRICHELLA, AND E. CETTO. 2010b. Comparing opportunistic and systematic sampling methods for non-invasive genetic monitoring of a small translocated brown bear population. Journal of Applied Ecology 47:172–181.

FILIPCZYKOVA, E., I.M.A. HEITKONIG, A. CASTELLANOS, W. HANTSON, AND S.M.J.G. STEYAERT. 2017. Marking behavior of Andean bears in an Ecuadorian cloud forest: A pilot study. Ursus 27:122–128. https://doi.org/10.2192/ursud-16-00002.1.

GERVASI, V., P. CIUCCI, J. BOULANGER, E. RANDI, AND L. BOITANI. 2012. A multiple data source approach to improve abundance estimates of small populations: The brown bear in the Apennines, Italy. Biological Conservation 152:10–20.

GITTLEMAN, J.L., editor. 2013. Carnivore behavior, ecology, and evolution. Springer Science + Business Media, Dordrecht, the Netherlands.

GRAVES, T.A., K.C. KENDALL, J.A. ROYLE, J.B. STETZ, AND A.C. MACLEOD. 2011. Linking landscape characteristics to local grizzly bear abundance using multiple detection methods in a hierarchical model. Animal Conservation 14:652–664.

GREEN, G.I., AND D.J. MATTSON. 2003. Tree rubbing by Yellowstone grizzly bears *Ursus arctos*. Wildlife Biology 9:1–9.

GROFF, C., F. ANGELI, D. ASSIN, N. BRAGALANTI, L. PEDROTTI, R. RIZZOLI, AND P. ZANGHELLINI. 2016. Rapporto orso 2015. Technical report. Servizio Foreste e fauna della Provincia Autonoma di Trento, Italy. [In Italian.] http://www.orso.provincia.tn.it/binary/pat\s\do5(o)rso/rapporto\s\do5(o)rso/Rapporto\s\do5(O)rso\s\do5(2)015.1457515432.pdf. Accessed 20 Jul 2019.

———, N. BRAGALANTI, R. RIZZOLI, AND P. ZANGHELLINI. 2015. RAPPORTO ORSO 2014. Technical report. Servizio Foreste e fauna della Provincia Autonoma di Trento, Italy. [In Italian.]

HENDERSON, M. J., M. HEBBLEWHITE, M.S. MITCHELL, J.B. STETZ, K.C. KENDALL, AND R.T. CARLSON. 2015. Modeling multi-scale resource selection for bear rubs in Northwestern Montana. Ursus 26:28–39.

KARAMANLIDIS, A.A., D. YOULATOS, S. SGARDELIS, AND Z. SCOURAS. 2007. Using sign at power poles to document presence of bears in Greece. Ursus 18:54–61.

KAYS, R.W., AND K.M. SLAUSON. Remote cameras. Pages 110–140 in R.A. Long, P. MacKay, W.J. Zielinski, and J.C. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, DC, USA.

KENDALL, K.C., A.C. MACLEOD, K.L. BOYD, J. BOULANGER, J.A. ROYLE, W.F. KASWORM, D. PAETKAU, M.F. PROCTOR, K. ANNIS, AND T.A. GRAVES. 2016. Density, distribution, and genetic structure of grizzly bears in the Cabinet-Yaak Ecosystem. Journal of Wildlife Management 80: 314–331.

———, AND K.S. MCKELVEY. 2008. Hair collection. Pages 135–176 in R.A. Long, P. MacKay, J.C. Ray, and W.J. Zielinski, editors. Noninvasive survey methods for North American Carnivores. Island Press, Washington, DC, USA.

———, J.B. STETZ, D.A. ROON, L.P. WAITS, J.B. BOULANGER, AND D. PAETKAU. 2008. Grizzly bear density in Glacier National Park, Montana. Journal of Wildlife Management 72:1693–1705.

KLEIMAN, D.G. 1983. Ethology and reproduction of captive giant pandas (*Ailuropoda melanoleuca*). Zeitschrift für Tierpsychologie 62:1–46.

KLEINER, J.D., R.C. VAN HORN, J.E. SWENSON, AND S.M.J.G. STEYAERT. 2018. Rub-tree selection by Andean bears in the Peruvian dry forest. Ursus 29:58–66.

KUZNETSOVA, A., P.B. BROCKHOFF, AND R.H.B. CHRISTENSEN. 2017. lmerTest Package: Tests in linear mixed effects models. Journal of Statistical Software 82:1–26. doi: 10.18637/jss.v082.i13.

MUSTONI, A., E. CARLINI, B. CHIARENZI, S. CHIOZZINI, E. LATTUADA, E. DUPRE, P. GENOVESI, L. PEDROTTI, D. MARTINOLI, A. PREATONI, L. WAUTERS, AND G. TOSI. 2003. Planning the brown bear *Ursus arctos* reintroduction in the Adamello Brenta natural park. A tool to establish a metapopulation in the central-eastern Alps. Hystrix: The Italian Journal of Mammalogy 14:3–27.

NEVIN, O.T., AND B.K. GILBERT. 2005. Perceived risk, displacement and refuging in brown bears: Positive impacts of ecotourism? Biological Conservation 121: 611–622.

NIE, Y., R.R. SWAISGOOD, Z. ZHANG, Y. HU, Y. MA, AND F. WEI. 2012. Giant panda scent-marking strategies in the wild: Role of season, sex and marking surface. Animal Behaviour 84:39–44.

PETERS, R., AND L. MECH. 1975. Scent-marking in wolves. Radio-tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well. American Scientist 63:628–37.

PETERS, W., M. HEBBLEWHITE, M. CAVEDON, L. PEDROTTI, A. MUSTONI, F. ZIBORDI, C. GROFF, M. ZANIN, AND F. CAGNACCI. 2015. Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps. Biological Conservation 186:123–133.

PREATONI, D., AND C. TATTONI. 2006. Action A.2 Analysis of possibilities of establishing a brown bear metapopulation. Final Report. LIFE CO-OP NATURE PROJECT: Principles for the establishment of an Alpine brown bear population LIFE2003NAT/CP/IT/000003, Adamello-Brenta Nature Park, 2006. https://www.google.com/url?

sa=t&rct=j&q=&esrc=s&source=web&cd=&ved=2ahUKEwigvdzx3-XuAhWJQc0KHaWVB4UQFjAAegQIAhAC&url=https%3A%2F%2Fwww.pnab.it%2Finfo%2Farea-download%2F%3Fupf%3Ddl%26id%3D7991&usg=AOvVaw3JmFouQwa4r6DMLshQZDUh. Accessed 12 Feb 2020.

PRESTON TAYLOR, A., M.S. GUNTHER, AND M.L. ALLEN. 2015. Black bear marking behaviour at rub trees during the breeding season in northern California. Behaviour 152:1097–1111.

PUCHKOVSKIY, S.V. 1998. The role of man in forming the communication system of the brown bear (*Ursus arctos* L.), and the problem of monitoring. Russian Journal of Ecology 29:344–348.

———. 2009. Selectivity of tree species as activity target of brown bear in taiga. Contemporary Problems of Ecology 2:260–268.

———, M.S. BUINOVSKAYA, D.K. VORONETSKAYA, AND G.V. NEUSTROEV. 2012. On the studies of marking behaviour of brown bear in terms of tree diameter selectivity. Contemporary Problems of Ecology 5:1995–4255.

R CORE TEAM. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 20 Jul 2019.

ROSELL, F., S.M. JOJOLA, K. INGDAL, B.A. LASSEN, J.E. SWENSON, J.M. ARNEMO, AND A. ZEDROSSER. 2011. Brown bears possess anal sacs and secretions may code for sex. Journal of Zoology 283:143–152.

———, AND J. SANDA. 2006. Potential risks of olfactory signaling: The effect of predators on scent marking by beavers. Behavioural Ecology 17:897–904.

ROVERO, F., E. MARTIN, M. ROSA, D. SPITALE, AND J.A. AHUMADA. 2014. Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. PLoS ONE 9 (7). doi:10.1371/journal.pone.0103300.

———, N. OWEN, T. JONES, E. CANTERI, A. IEMMA, AND C. TATTONI. 2017. Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. Biodiversity and Conservation 26:1103–1119. https://doi.org/10.1007/s10531-016-1288-2.

RSTUDIO TEAM. 2016. RStudio: Integrated development for R. RStudio, Inc., Boston, Massachusetts, USA. http://www.rstudio.com/. Accessed 20 Jul 2019.

SATO, Y., C. KAMIISHI, T. TOKAJI, M. MORI, S. KOIZUMI, K. KOBAYASHI, T. ITOH, W. SONOHARA, M.B. TAKADA, AND T. URATA. 2014. Selection of rub trees by brown bears (*Ursus arctos*) in Hokkaido, Japan. Acta Theriologica 59:129–137.

SERGIEL, A., J. NAVES, P. KUJAWSKI, R. MAŚLAK, E. SERWA, D. RAMOS, A. FERNANDEZ-GIL, E. REVILLA, T. ZWIJACZ-KOZICA, F. ZIĘBA, J. PAINER, AND N. SELVA. 2017. Histological, chemical and behavioural evidence of pedal communication in brown bears. Scientific Reports 7:1052. https://doi.org/10.1038/s41598-017-01136-1. Accessed 12 Feb 2021.

SERYODKIN, I.V. 2016. Behavior of brown bears during feeding in the Sikhote-Alin. Achievements in Life Science 10:38–47. https://doi.org/10.1016/j.als.2016.05.003.

STEYAERT, S.M.J.G., J. KINDBERG, J.E. SWENSON, AND A. ZEDROSSER. 2013. Male reproductive strategy explains spatiotemporal segregation in brown bears. Journal of Animal Ecology 82:836–845.

TATTONI, C. 2019. Nomen omen. Toponyms predict recolonization and extinction patterns for large carnivores. Nature Conservation 37:1–16. https://doi.org/10.3897/natureconservation.37.38279.

———, N. BRAGALANTI, C. GROFF, AND F. ROVERO. 2015. Patterns in the use of rub trees by the European brown bear. Hystrix: The Italian Journal of Mammalogy 26:118–124. http://dx.doi.org/10.4404/hystrix-26.2-11414.

———, G. GRILLI, AND M. CIOLLI. 2017. Advertising value of the brown bear in the Italian Alps. Ursus 27:110–121. doi: 10.2192/URSU-D-16-00011.1.

TAYLOR, A.P., M.L. ALLEN, AND M.S. GUNTHER. 2015. Black bear marking behaviour at rub trees during the breeding season in Northern California. Behaviour 152:1097–1111.

TISO, M. 2011. Rub trees: Testing a new method for genetic monitoring of brown bear (*Ursus arctos* L.) in Trentino. Master's thesis, Universita degli studi di Padova, Padua, Italy. [In Italian.]

VOGT, K., F. ZIMMERMANN, M. KOLLIKER, AND U. BREITENMOSER. 2014. Scent-marking behaviour and social dynamics in a wild population of European lynx *Lynx lynx*. Behavioural Processes 106:98–106.

Received: July 14, 2020
Accepted: November 17, 2020
Associate Editor: O.T. Nevin

Supplemental Material

Table S1. Sequences of visits by European brown bear (*Ursus arctos*) to the same rub tree in the Italian Alps. Number of events (*N*) are ordered by occurrence (%). None is reported in the case that no bear passed within 40 days after it was marked.

Fig. S1. The home ranges (HR: minimum convex polygon [MCP] from GPS data, *N* of bears = 16) of male and female brown bears (*Ursus arctos*) overlapped with the known rub trees in Trentino (Italy). Rub trees were located within the HR of all collared females (*N* = 10) and 4 males.