Brown bear communication hubs: Patterns and correlates of tree rubbing and pedal marking in a long term marking site

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ABSTRACT

Chemical communication is critical for many species of mammals. Male brown bears mark trees with the secretion of glands located in their back. The recent discovery of pedal glands and pedal-marking in a site used for tree-rubbing led us to hypothesize that both types of marking form part of a more complex communication system. We described the patterns of chemical communication used by different types of individuals, including their role as information providers or receivers, during five years in a long-term marking site. Using automatic video recording we registered a total of 285 bear-visits and 419 behaviours associated with chemical communication. Bears visited more frequently the site during the mating season, when communication behaviours were more frequent. A typical visit by male bears consisted in sniffing the depressions where animals pedal mark, performing pedal-marking, sniffing the tree, and, finally, rubbing against the trunk. Adult males almost completely capitalized pedal- and tree-marking (95% and 66% of the cases, respectively). Males pedal-marked and tree-rubbed in 81% and 48% of their visits and sniffed the pedal marks and the tree in 23% and 59%, respectively. Adult females never pedal marked and juveniles did at very low frequencies. Females rubbed against the tree in just 9% of their visits; they smelled the tree and the pedal

marks in 51% and 21% of their visits. All sex and age classes performed pedal and tree-sniffing. There were significant associations between behaviors indicating that different behaviors tend to occur during the same visit and are more likely if other individual had recently visited. These synergies inducing repeated marking of the site can promote the establishment of long-term marking sites. Marking sites defined by trees and the trails leading to them act as communication hubs that bears use to share and obtain important information at population level.

INTRODUCTION

Marking behaviour is critical in the mediation of chemical communication and social interactions in mammals (Potts & Penn 2002; Johansson & Jones, 2007). The chemical signals left in specific sites provide long-lasting messages in the absence of the signal provider (White, Swaisgood & Zhang, 2002; Scordato, Dubay & Drea, 2007). In carnivores, the function of scent marks has been associated with territorial defense (Wronski *et al*., 2006), intra-sexual competition (Gosling & Roberts, 2001) or the defense of trophic resources (Piñeiro & Barja, 2015). Scent marking is particularly relevant for solitary species ranging widely in large home ranges (Begg *et al*., 2003; Vogt *et al*., 2014). These species must rely on an effective communication system that maximizes the transfer of information at low cost in order to maintain their social organization by advertising to mates and competitors (Allen, Yovovich & Wilmers, 2016).

Urine and faeces are a relatively inexpensive means of scent marking used by many carnivore species at the expense of a relatively low efficiency in the transfer of information (Vogt *et al*., 2016). More specialised chemical compounds may provide detailed information on the individual, sex and reproductive status (Alberts, 1992). They are produced by specialised holocrine, apocrine and/or eccrine skin glands, often located in anal, subcaudal, interdigital, chin, and other areas. To be effective, their secretions should persist in the environment for long periods to maximise the probability of reaching potential receivers (Swaisgood *et al*., 2004). Additionally, individuals scent mark specific sites, such as territorial borders, and prominent locations that are often revisited by them and other individuals, such as dens, food sources or busy trails (Sillero-Zuburi & Macdonald, 1998; Revilla & Palomares, 2002; King *et al*.,2017). Chemical cues guide receiving individuals to investigate, ignore, counter and/or over-mark previous marks (Laidre & Johnstone, 2013). The presence of long-lasting marks of one or more individuals in a marking area may promote the synergy between different types of signals, potentially eliciting multiple communication-related behaviours (Sumpter & Brännström, 2008). These complexities make some particular types of marking sites especially important in the regulation of social behaviour. The repeated use by multiple individuals for long periods of time convert these marking sites in critical communication hubs at population level (King *et al*., 2017).

Ursids are non-territorial animals that move over large areas with low contact rates between individuals (Martin *et al*., 2013). In spite of this, they maintain a complex network of social interactions in which the information on the presence of other individuals is critical (Støen *et al*., 2005; Steyaert *et al*., 2012). Chemical communication plays a relevant role in the maintenance of the social organization of bears (Noyce & Grarshelis, 2014). They mark conspicuous objects such as trees, rocks or even poles, with the secretion of the sebaceous glands and possibly also apocrine glands located in the skin of their back (Tomiyasu *et al*., 2018), and, in some cases, also with claw and bite marks (Nie *et al*., 2012; Clapham *et al*., 2013; Taylor, Allen & Gunther, 2015). Bipedal back-rubbing against trees has been widely described as the most common marking behaviour of brown bears *Ursus arctos* across its Holarctic range, showing seasonal and sex-age variations in marking frequencies (Green & Mattson, 2003; Clapham *et al*., 2012, 2013; Sato *et al*., 2014; Seryodkin, 2014; Spassov *et al*., 2015; Tattoni *et al*., 2015). Additionally, pedal-marking has been recently reported as a relevant marking behaviour (Taylor *et al*., 2015; Sergiel *et al*., 2017). Typical deep marks left in the ground by bears possibly during pedal-marking were described long ago as leading towards bear trees (LeFranc *et al*., 1987). The presence of pedal scent glands in brown bears and their significance in communication have been also described (Sergiel *et al*., 2017). Nevertheless, pedal-marking remains to be characterised in terms of occurrence in relation with season, sex-age of the individual and other environmental correlates, as well as its connection with tree marking, given that they seem to simultaneously occur in the same marking sites (Clapham *et al*., 2014; Sergiel *et al*., 2017).

In this paper we hypothesise that pedal-marking and tree-rubbing are deeply linked, forming a more complex communication system than previously acknowledged. Additionally, we expect to find important differences in the use of marking sites by different types of individuals, depending or their main role as information providers or receivers. Specifically, we describe the chemical communication by brown bears in a long-term marking site in the Cantabrian Mountains, northern Spain. The site is known to be intensively used for pedal-marking and tree-rubbing by brown bears at least since 2002 (see Sergiel *et al*., 2017 for a basic description of pedal marking in this site). Specifically, we aimed at (1) assessing the frequency of main marking behaviours by bears of different age-sex classes across seasons; (2) identifying synergies among behaviours as well as among signal providers and receivers, and (3) determine the role of other factors, such as climatic variables, in the occurrence of marking behaviours. We finally discuss the significance of these communication hubs intensively used by bears for long periods of time.

MATERIALS & METHODS

Study site

The study was conducted in the western half of the Cantabrian Range (NW Spain), a mountain system inhabited by a population which currently holds around 230 individuals (Pérez *et al*., 2014). The study area is located in Fuentes del Narcea, Degaña e Ibias Natural Park (Cangas del Narcea, Asturias). Our study site is located in an area with high quality habitat for bears (Naves *et al*., 2003), including denning and mating areas, areas used by females with cubs, and also vegetation offering plenty of resources used during hyperphagia, when bears feed continuously in preparation for hibernation. In this area, there are multiple sites used by bears for chemical communication. These sites can be easily identified by the presence of a tree, pole or rock that is used for rubbing often in association with ground pedal marks in the way leading to the vertical structure that is marked. We selected one site for continuous monitoring based on the evidence of repeated use by bears for pedal-marking (Sergiel *et al.*, 2017). We do not provide the exact location of the site due to conservation reasons. First evidence of ground pedal-marking in this site was obtained in 2002 during an opportunistic observation by one of us (DR) of an adult male during the mating season. The site is characterized by an oak tree (*Quercus petraea*) heavily used by bears for rubbing, headed by conspicuous marks in the ground made by the bears´ feet during pedal-marking (a total of 48).

Sampling protocol

Data was collected in the selected site during long-term monitoring for conservation and management purposes by DR. Principado de Asturias–Consejería de Agroganadería y Recursos Autóctonos granted data access, and DR was authorised to participate by exp-no. 2016/033072, Principado de Asturias-Consejería de Hacienda y sector Público. An automatic camera (Bushnell Trophy digital camera trap #19466) was located between January 2012 and January 2016, when it was working almost continuously. Initially, between January 2012 and April 2012, the device was placed laterally in a low position from which the tree marked by bears was visible. Data obtained during these first four months were not used in analyses. The camera was later placed on a zenithal position at a height of six meters in the main trunk of the marked tree to obtain a standardized field of view and to reduce direct interference with bears and other animals. The camera was programmed to shoot videos of one-minute duration, with a 10 seconds lapse between videos. We considered a visit event as the group of videos recorded in the 20 minutes after the first evidence of a bear presence. This time window was selected after visual inspection of the plot of the cumulative proportion of videos sorted by the time to the next video (Fig. S1 in supplementary material). For comparative purposes we also used this time interval to define visit events for other species.

Individuals and communication behaviours

We classified the recorded individuals within the following sex-age categories: adult males, identified by the combination of large size and neck and head shape; adult females, when accompanied by cubs, or by their size, head and neck shapes and explicit behaviour in the presence of other bears, often with adult males in the mating season; cubs, bears in their first year or in their second year until May and always accompanied by their mother; juveniles, independent bears in their second year of life from June onwards and in their third year, clearly of smaller size than adults and usually accompanied by other siblings; and, undetermined sex-age class, which included the rest of the animals. In the case of adult males some bears were individualized by comparison with known animals observed in repeated sightings in other sites of the study area. These individuals were characterised by a combination of size, head shape, colour patterns and specially the pattern of permanent markings of light colour, usually in their necks. In other cases we were able to classify temporarily some individuals in an age-sex class or even identify them during shorter periods of time because they were associated with other bears in seasonal or yearly groups such as mating pairs, females with dependent cubs, and groups of independent juveniles. Females are more difficult to individualise on a permanent basis and we used the number of accompanying cubs to establish a minimum number of females visiting the site. We did not attempt to individualise other bears such as independent juveniles and cubs.

We classified the behaviours displayed by bears in the videos into the following types: Pedal-marking, performed by a walking bear with the particular gait of twisting their fore and hind feet on the ground in the specific depressions on the ground repeatedly used by the same and other individuals in previous visits; tree-rubbing, when a bear vigorously rubs its back, neck or shoulders against the trunk of the tree while standing on its hind feet; sniffing pedal marks, when an individual stops or slows its pace to sniff the pedal marks on the ground; tree-sniffing, when an individual sniffs the trunk of the rubbing tree; and, finally, other behaviours, usually walking in and out of the field of vision, apparently not related with chemical communication. In the videos recorded at the study site we did not detect any clear instance of scratching the tree (clawing; Taylor *et al*., 2015). For each visit event we counted how many times each type of behaviour was performed by each bear/bears in the available videos.

Analyses

First, we described the overall use of the site and the behaviours performed by the visiting bears over time and by age-sex classes. Then, we analysed which descriptors could have an effect on the observed patterns (Table 1). We hypothesized that the probability that a bear attended the marking site and performed one of the behaviours could be affected by the time elapsed since the previous visit by a bear, the season, and the age and sex class of the focal bear, and, in some analyses, by the weather conditions occurred between visit events affecting the duration of the chemical signals. We performed Generalized Linear Mixed Models (hereafter GLMMs) on the response variables (occurrence of the specific behaviours) using a binomial error distribution and year as a random factor. Models were run with the potential combination of biologically meaningful explanatory variables within each group of response variables. From the resulting models, we report only those within $\Delta AIC<2$. Analyses were performed in *R* vs3.3.3 (MuMIn library).

RESULTS

In total, the camera was active for 1174 days (April 2012 to December 2015), with an average temporal coverage of 83% of the potential days per month (Table S1, Supplementary Material). It registered 1029 videos with bear presence; representing 224 visits and a total of 285 bear visit events (a visit can include more than one individual, as is the case of females with cubs). Bears were the most common visitors (42%), with more than five visits per month on average (Fig 1).

The visitation rate of other species was considerably lower despite of being, more abundant in most cases (Fig 1). Among bears, adult male bears were the most frequent visitors with 132 bear visits (46% of total bear visits). The rest of the visits were performed by adult females in 57 cases (20 %), cubs in 44 (15 %), juveniles in 23 (8%) and bears of undetermined age or sex in 29 (10 %). Most visits occurred during spring and summer (Fig 2).

Communication behaviours

The typical sequence of a visit consists of a bear approaching the tree following the path where it can sniff the depressions where animals pedal mark, perform pedal-marking, stop at the tree, sniff it, and, finally, rub against the trunk (see video in Supplementary materials). This sequence can vary with different combinations of behaviours and in different orders, and some parts of the sequence can be repeated. In one occasion a male also rubbed against pedal marks. From a total of 482 recorded behaviours, the majority corresponded with some form of chemical communication (87%). Tree-sniffing was the most frequent (153 cases, 31%), followed by pedal marking (113, 23%), tree-rubbing (96, 20%), and finally, sniffing of pedal marks (58, 12%; Table S3 in supplementary materials). In 22% of the visits there was no apparent communication behaviour, although they could have occurred out of the field of view of the camera. The communication behaviours displayed by bears varied greatly among age and sex classes. Individuals identified as adult males almost completely capitalized pedal-marking (107 cases, 95%) and, to a lesser extent, tree-rubbing (63, 66%, Fig 3). Interestingly, adult females did not perform pedal-marking, while juveniles did it at very low frequency (Fig 3). Tree-rubbing was performed by all age and sex classes, but at higher frequencies by males (Fig 3). All sex and age classes performed pedal and tree-sniffing (Fig 3).

Males performed pedal-marking and tree-rubbing in 81% and 48% of their visits to the site, respectively; and both of them during the same visit in 43% of their visits. In general sniffing behaviours were performed less frequently. Males sniffed the pedal marks and the tree in 23% and 59% of their visits, respectively. They both pedal-marked and smelled the pedal marks in 20% of their visits and did both tree-rubbing and tree-sniffing in 35% of their visits. Adult females rubbed against the tree in just 9% of their visits, but they smelled the tree and the pedal marks in 51% and 21% of their visits. Juveniles, cubs and undetermined individuals showed interest in the tree, smelling it in 48%, 61% and 26% of their visits, while rubbing in 39%, 34% and 14% of the occasions, respectively. Juveniles and undetermined bears pedal-marked in 17% and 7% of their visits, respectively, smelling them in 48% and 26% of their visits. Cubs sniffed pedal marks in 61% of their visits but never marked. Communication behaviours occurred in most months except in January and February, but with higher frequencies in the mating season (spring, April-June), and later in the autumn during hyperphagia (Fig 3; Table S3 in supplementary material).

Several recognizable individuals attended the site repeatedly, some of them during all the study period. Four adult males visited the site between 10 and 35 times during the study, with up to 15 visits in one year (M1 to M4, Table S5 supplementary material). These males were frequent markers; for example, M2 and M3 monopolized most of the instances of pedal-marking (59 %, Table S6 supplementary material), while M2 was the bear that most frequently displayed tree-rubbing (43%, Table S6 in supplementary material). Additionally, there were other males visiting the site sporadically. These additional males corresponded with individual bears known from repeated observations near the study area (at least four additional males in 2012, five in 2013 and 2015 and seven in 2014). A minimum of one female visited the site in 2013 and 2015, two in 2014 and three in 2012.

Factors affecting communication behaviours

Bears visited more frequently the marking site during the mating season (Table 3; Table S7 in supplementary material). The probability that a bear visited the marking site in a given day was negatively associated with the time since a male bear last visited the site (the shorter the lapse, the higher the probability), and was also negatively associated with the time elapsed since the last visit of a bear performing pedal-marking, and displaying tree-rubbing (both tended to be performed by males, Fig 3; Table 3; Table S7 in supplementary material).

The probability that a bear sniffed the pedal marks during a visit was higher outside the mating season (Table 2). Also, the lower the average precipitation and the average temperature in the previous days, the higher the probability of sniffing the pedal marks (Table 3). Finally, it was negatively related to the time elapsed since a (male) bear previously performed pedal-marking at the site (or visited the site, Table 3; Table S7 in Supplementary Material). The probability of performing pedal-marking by male bears visiting the site was positively associated with tree-rubbing by the same individual and negatively with the time elapsed since the previous visit of a bear that pedal-marked the site (the shorter the time, the higher the probability to pedal mark, Table 3). The association of pedal-marking with the rest of the factors was weaker (Table S7 in Supplementary material).

Interestingly, the probability of sniffing the tree was higher the longer the time elapsed since the previous tree marking and negatively with the precipitation in that period (Table 3), and was not affected by the sex-age of the individual. In the case of tree-rubbing, the probability that a bear performed it during a visit was positively associated with tree-sniffing and pedal-marking by the same individual (Table 3) and with the time since the previous tree-rubbing (Table 3). Juveniles and adult males had a higher probability of tree-rubbing during their visits (Table 3; Table S7 in Supplementary Material).

DISCUSSION

In this work we show that the chemical communication behaviour of bears in tree-rubbing sites is more complex than previously acknowledged, being pedal-marking an integral part of the communication system. These marking sites form communication hubs where individual bears share and receive important information at population level. Tree-rubbing is a well-known scent-marking behaviour performed by bears (Green & Mattson, 2003; Clapham *et al.*, 2012; Sato *et* *al.*, 2014; Seryodkin, 2014; Tattoni *et al.*, 2015; Lamb *et al.*, 2017). Marking bears rub energetically their flanks and back against the tree to scent mark it with the secretions of the glands located in their back (Tomiyasu *et al.*, 2018). Bears also mark in the same way other types of objects, especially in areas where the availability of trees is low (Seryodkin 2014). Our results, in accordance with published information, show that tree rubbing can be performed by any type of individual at any moment, but it is clearly monopolised by adult males, especially during the mating season (Clapham *et al.*, 2012; Lamb *et al.*, 2017). Additionally, our results also indicate that the information is received by all types of individuals irrespectively of their age or sex.

Interestingly, tree marking does not occur in isolation. Pedal-marking by males occurs as part of the marking process in association with tree-rubbing. As it occurs with tree-rubbing, pedal-marking is performed by males with a higher frequency during the mating season, while all types of individuals acted as receivers of the information. The existence of deep footprint marks forming one or more trails in the ground leading towards trees has been known for a long time (eg., LeFranc *et al.*, 1987; Clapham *et al.*, 2013; Seryodkin 2014). Additionally, the typical behavioural sequence performed by males during pedal-marking have also been described with a variety of names, including bear dance, sumo walking, cowboy walk or stomping (Sergiel *et al.*, 2017), but were often interpreted as part of a stereotyped behaviour leading to marking the tree. The recent description of pedal glands in bears' feet and the concomitant pedal-marking (Sergiel *et al.*, 2017) and our results on the relationship between both pedal and tree marking offers new light in the interpretation of scent marking in bears.

The data used in our description has some shortcomings that need to be considered. We provide data from only one site, although for a very long period of nearly continuous monitoring. The area covered by the camera recorded only part of the area and, therefore, we may have missed behaviours, such as pedal-marking or sniffing when animals were out of the field of vision; or tree marking when the bears used other trees (there nearby trees also used for marking). Additionally, the zenithal position of the camera may have limited our capacity to detect other potential marking behaviours such as urination or more complex stereotyped behaviours associated with tree-rubbing (Clapham *et al.*, 2014). In spite of these limitations, our results provide important information on the role of chemical communication at marking sites by brown bears.

Sending and receiving information

The importance of chemical communication at the site varied as a function of the individuals, depending on their sex, age, and presumably other conditions such as dominance or breeding status. Nearly half of the visits to the marking site were done by animals identified as adult males. They were responsible of most pedal, and, to a lesser extent, tree-rubbing behaviours. Both behaviours were strongly associated when displayed by adult males. Some males visited the site very often while others were more sporadic. Interestingly, some marked in most of their visits while others mostly acted as information receivers. This may reflect a structure of dominance in the males sharing the area. Females, on the other hand, never pedal-marked and rarely rubbed the tree and so did the cubs accompanying their mothers. Young animals showed an intermediate pattern between males and females. Tree-rubbing was more frequently displayed by bears also sniffing the tree and performing pedal-marking and positively related with the time elapsed since a previous tree-rubbing, typically describing the behavioural sequence of visiting males. Male brown bears have seasonally enlarged sebaceous glands in their back and prominent eccrine, apocrine and sebaceous glands in their feet; glands that are more active during the mating season, in association with their testosterone levels (Sergiel *et al*., 2017; Tomiyasu *et al*., 2018). Therefore, males acted as main sources of chemical messages at the site, as has been shown in other study areas (Clapham *et al*., 2014; Lamb *et al*., 2017).

Sniffing behaviour, especially that of ground marks, is less evident and therefore more prone to be missed in videos. Nevertheless, all types of individuals showed interest on the chemical marks, acting as genuine information receivers. The probability of sniffing the marks during a visit was affected by weather conditions, with higher temperatures and precipitation in the previous days reducing the probability of sniffing ground marks, a pattern that was not associated with actual pedal-marking; and higher precipitation negatively affecting tree sniffing. The effects of precipitation and temperature on the volatility of the odorous molecules left by bears at the marking site are a plausible interpretation of these results. Interestingly, the probability of sniffing the tree was higher the longer the time elapsed since the previous visit, while it was the opposite for ground sniffing, suggesting a differential detectability between the chemical compounds secreted by pedal and back glands.

Why bears visit these sites

Bears use chemical marking to convey information from senders to receivers. Why they do this and which type of information is transferred is still a matter of discussion. The chemical profiles of pedal and shoulder secretions indicate that they contain information on at least the sex and reproductive status of the individual (Sergiel *et al*., 2017; Tomiyasu *et al*., 2018). Additionally, it would not be surprising if information on the actual individual is also provided, as seems to occur with secretions from anal sacs (Rosell *et al*., 2011; Jojola *et al*., 2012). In species that normally have a solitary non-territorial use of space, knowing how/who are the individuals with whom they can meet is very invaluable. Several non-exclusive hypotheses have been proposed to explain scent marking in brown bears: self-advertisement for mate attraction, communication of individual dominance, competitor assessment and infanticide avoidance, with different roles depending on bear density (Clapham *et al*., 2012; Lamb *et al*., 2017). Our results evidence a complex role of chemical communication in bears. Males are the main senders and also the main receivers, with some of them marking a lot while others tend to mostly receive information, indicating communication of individual dominance and the ability to assess male competitors. They mark all year around but with a main peak during the mating season and a secondary one during hyperfagia, both moments of intense competition. This pattern has been also found in rubbing trees, both natural and artificially created to collect bear hairs (i.e. tree hair traps) in different ecosystems (Green & Mattson 2003, Karamanlidis et al. 2010, Sato et al. 2014, Berezowska-Cnota et al. 2017, Lamb et al. 2017).

Females visit the site less often, but all year around, and when they do, they are especially interested in receiving information. Knowing which males are moving around and their social dominance is very relevant for females in their mate selection, since mating with the more dominant males that are present all year around would minimize the overall risk of infanticide of their litters. Additionally, females with cubs of the year may benefit from knowing if a new male enters the area (Bellemain *et al*., 2006). Although more rarely, females, juveniles and cubs also rub the trees, but it is unclear why they do it. In the case of juveniles learning by imitation may be the main reason (Clapham *et al*., 2014). Given that the sebaceous secretion in the shoulder of males is linked to testosterone levels, it can be expected that the secretion of females, cubs and juveniles is testimonial or simply lacking. If that is the case, their tree-rubbing may serve the purpose of masking their odour with that of adult males roaming in the area. The resulting increase in chemical similarity could help in reducing the risk of infanticide by scent-matching (Gosling & McKay, 1990). If this interpretation holds, tree-rubbing would have a scent-marking purpose only for males, helping females and cubs to obtain a chemical camouflage by scent-rubbing and transitionally being part of the learning process of juveniles. In summary, there is no single best hypothesis explaining the role of these communication hubs, being a complex combination of dominance, mate selection, competitor assessment, mate selection and infanticide avoidance the most plausible.

Brown bear communication hubs

Undoubtedly, sites like the one we monitored are important for bears at population level. Our results show that the tree and the trails leading to it form part of a communication hub that bears living in the area use to share and obtain information. Bears were the most frequent visitors of our site in spite of the easy accessibility and that bears are not the most common large mammal in the area. Bears choose specific trees in places with a good location for the passage of other individuals (Green & Mattson 2003; Sato *et al*., 2014). In these sites there is a clear synergy in the association between different communication behaviours, with marking behaviours triggering the subsequent marking and sniffing of later visitors (Berezowska-Cnota et al. 2017). Nevertheless, these sites are not uncommon. In the vicinity of our site there were other trees used repeatedly by bears for marking (see Supplementary video). Bears maintain a dense system of marking sites that allow for a complex communication network over large spatial scales. Although they are not easy to locate by humans, several authors report varying densities of marking sites depending on bear density, such as 0.26 sites/km^2 in the Italian Alps, 0.4 sites/km^2 in Hokkaido, Japan, 1.4 sites/km^2 in Russian Komi Republic, 20 sites/km^2 in the British Columbia, or the 27 sites/km^2 in the Valley of Geysers in Kamchatka Peninsula (Lloyd, 1979; Sato *et al*., 2014; Seryodkin, 2014; Tattoni *et al*., 2015). Many of these studies describe evidence of pedal-marking in the trails leading to the trees (eg., Clapman *et al*., 2013; Seryodkin, 2014).

CONCLUSIONS

We showed that pedal-marking and tree-rubbing are deeply associated in a complex chemical communication system. In our site, bears visited more frequently during the mating season. More dominant male bears typically sniff the depressions where animals pedal mark, perform pedal-marking, sniff the tree, and rubb against the trunk. Adult males almost completely capitalized pedal- and tree-marking. Adult females, on the other side, never pedal mark and juveniles rarely do so. Females act more as information receivers, rarely rubbing the tree. All sex and age classes performed pedal and tree-sniffing, thus obtaining information on previous visitors. Different behaviors tend to occur during the same visit and are more likely if other individual had recently visited, generating long-term marking sites as the one we described. These sites act as communication hubs that bears use to share and obtain important information on the animals present in a wide area at population level. The intense use of these sites and their number and density offer an idea of the importance of this communication system for this wide ranging, naturally scarce and non-social large carnivore, with a complex mating system.

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Figure 1. Total number of visits for the species recorded at the study site. Each visit defined by all videos of a species separated by less than 20 minutes to the nearest video (grey bars, right axis) and average number of visits per month (± standard deviation; black dots, left axis). Plotted data refer to the subperiod between April 2013 and December 2015 (Table A1 in Appendix A of Supplementary material). Wild boar *Sus scrofa*, chamois *Rupicapra pyrenaica*, roe deer *Capreolus capreolus*, red fox *Vulpes vulpes*, wildcat *Felis sylvestris*, common genet *Genetta genetta*, pine marten *Martes martes*, red squirrel *Sciurus vulgaris*, and wolf *Canis lupus*.

Figure 2. Monthly distribution of bear visits to the marking site. Measured as the average number of individual bear visits per day (left axis, indicating the fraction of those identified as males) and the sampling effort (right axis), measured as the fraction of the days that the camera was active every month (Table A1 in Appendix A of Supplementary material).

Figure 3. Frequency distributions of the different behaviours. Data by age-sex classes and per month (Tables A3 and A4 in Appendix A of Supplementary material).

Table 1(on next page)

Description of response and explanatory variables used in the analyses

All response variables were binary (occurrence in a given day for bear visit or visit for communication behaviours) and the variables listed were the ones explored in each model

Table 1. Description of response and explanatory variables used in the analyses. All response variables were binary (occurrence in a given day for bear visit or visit for communication behaviours) and the variables listed were the ones explored in each model.

Explanatory variables		Response variables				
label	**description**	*bear visit*	*sniff pedal marks†*	*pedal marking**	*sniff tree †*	*tree rubbing†*
Individual descriptors						
age_sex	age-sex class of the bear (Male, Female, Juvenile, Undetermined)		*X*		*X*	*X*
age_sex_t	age-sex class of the previous bear marking the tree (Male, Female, Juvenile, Undetermined)				*X*	
Temporal descriptors						
log_n_days	time to the previous bear visit (in days, logarithm)		*X*	*X*	*X*	*X*
log_n_days_m	time to the previous visit of a male (in days, logarithm)	*X*				
log_n_days_p	time to the previous bear visit that performed pedal marking (in days, logarithm)	*X*	*X*	*X*		
log_n_days_t	time to the previous bear visit that performed tree rubbing (in days, logarithm)	*X*			*X*	*X*
Weather descriptors						
m_P_p	average precipitation of the days elapsed since the previous bear visit that performed pedal marking (mm)		*X*			
m_P_t	average precipitation of days elapsed since the previous bear visit that performed tree marking (mm)				*X*	
m_T_p	average temperature of the days elapsed since the previous bear visit that performed pedal marking (º C)		*X*			
m_T_t	average Tempt of the days elapsed since the previous bear visit that performed tree rubbing (º C)				*X*	
Behavioural descriptors						
pedal_marking	pedal marking performed by the same bear visit					*X*
season	season: mating (April, May, June) vs no mating (other months)	*X*	*X*	*X*	*X*	*X*
sniff_pedal	sniff pedal marks performed by the same bear visit			*X*		
sniff_tree	sniff tree rubbing performed by the same bear visit					*X*
tree_rubbing	tree-rubbing performed by the same bear visit			*X*		

*only for males
†all bears except cubs

Table 2(on next page)

Number of behaviours displayed by different age and sex classes

Data recorded by the automatic camera at the marking site between 2012 and 2015.

Table 2. Number of behaviours displayed by different age and sex classes. Data recorded by the automatic camera at the marking site between 2012 and 2015.

	Age-Sex classes					
Behaviour	Males	Females	Cubs	Juveniles	undetermined	Total
Pedal-marking	107	0	0	4	2	113
Tree-rubbing	63	5	15	9	4	96
Sniffing pedal marks	30	12	3	9	4	58
Sniffing tree	78	29	27	11	8	153
Other	5	20	12	7	18	62
Total number of behaviours	283	66	57	40	36	482
Total number of visits	132	57	44	23	29	285

Table 3(on next page)

Estimates of the effect of the factors included in the best models

Models were GLMMs with binomial distribution and year as random factor (Table A7 in Appendix A of Supplementary material). The models on bear visits were run with all types of individuals, those on pedal marking only on males and the rest with all types of individuals except for cubs. See Table 1 for a description of the variables.

Table 3. Estimates of the effect of the factors included in the best models. Models were GLMMs with binomial distribution and year as random factor (Table A7 in Appendix A of Supplementary material). The models on bear visits were run with all types of individuals, those on pedal marking only on males and the rest with all types of individuals except for cubs. See Table 1 for a description of the variables.

model	**estimate**	**SE**	***p***
bear visit (all classes of individuals)			
(intercept)	1.139	0.280	<0.0001
log_ndays_m	-1.548	0.336	<0.0001
log_ndays_p	0.696	0.329	0.034
log_ndays_t	-1.186	0.294	<0.0001
season	-0.416	0.182	0.023
sniff pedal marks (all classes of individuals except cubs)			
(intercept)	-2.069	0.797	0.009
log_n_days_p	-0.725	0.389	0.062
m_P_p	-0.013	0.006	0.036
m_T_p	-0.011	0.005	0.013
season	2.046	0.546	<0.001
pedal marking (males)			
(intercept)	1.946	0.494	<0.0001
log_n_days_p	-1.255	0.477	0.009
tree_rubbing	1.315	0.527	0.013
sniff tree (all classes of individuals except cubs)			
(intercept)	-0.090	0.249	0.717
log_n_days_t	0.885	0.379	0.019
m_P_t	-0.011	0.005	0.047
tree rubbing (all classes of individuals except cubs)			
(intercept)	-3.611	0.651	<0.0001
log_n_days_t	0.857	0.461	0.063
sniff_tree	1.412	0.352	<0.0001
pedal_marking	1.293	0.502	0.010
age_sex			
Undetermined	0.378	0.771	0.624
Juvenile	1.790	0.753	0.018
Male	1.146	0.666	0.086

Figure 1

Total number of visits for the species recorded at the study site

Each visit defined by all videos of a species separated by less than 20 minutes to the nearest video (grey bars, right axis) and average number of visits per month (± standard deviation; black dots, left axis). Plotted data refer to the subperiod between April 2013 and December 2015 (Table A1 in Appendix A of Supplementary material). Wild boar *Sus scrofa*, chamois *Rupicapra pyrenaica*, roe deer *Capreolus capreolus*, red fox *Vulpes vulpes*, wildcat *Felis sylvestris*, common genet *Genetta genetta*, pine marten *Martes martes*, red squirrel *Sciurus vulgaris*, and wolf *Canis lupus*.

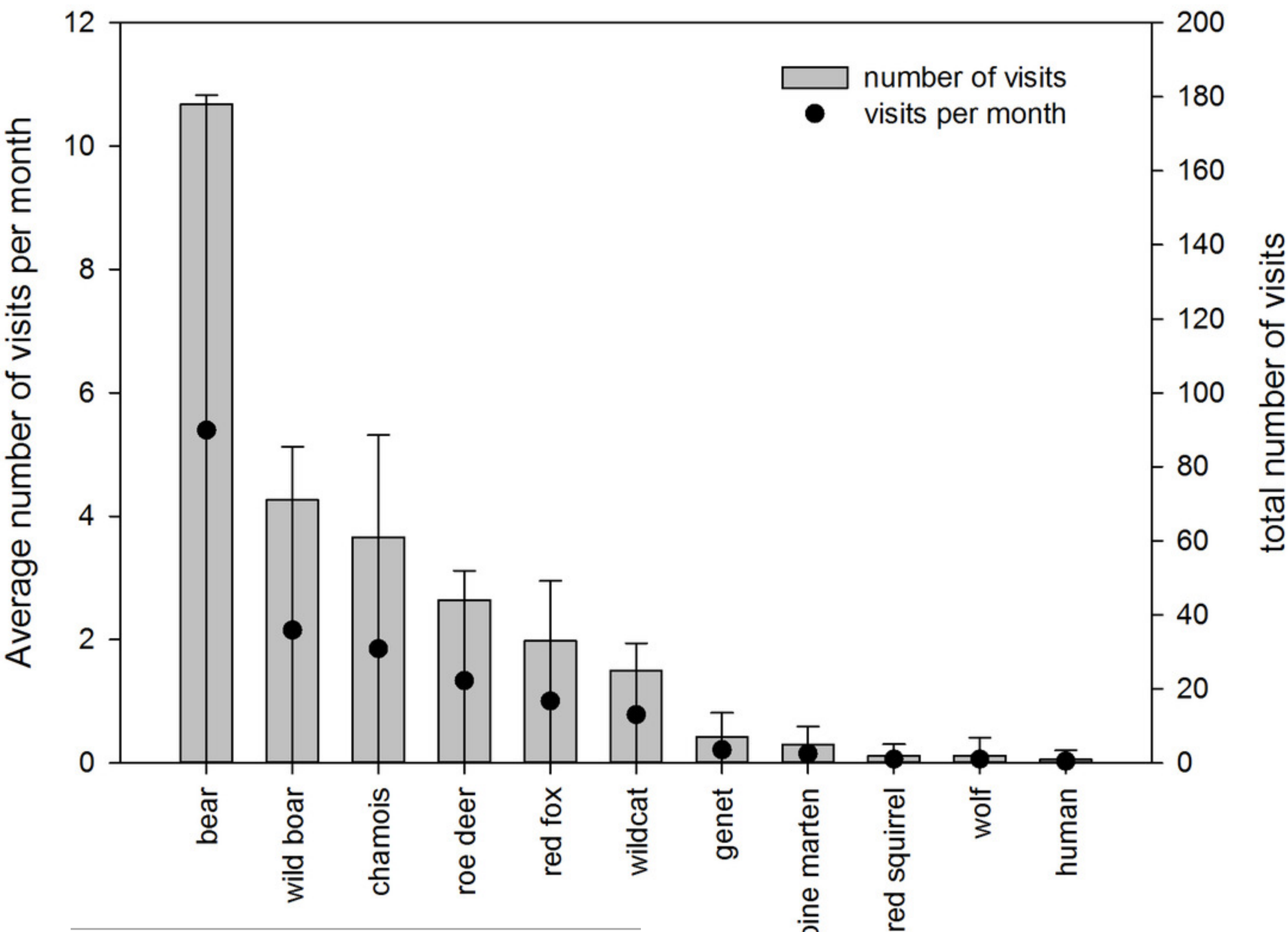

Figure 2

Monthly distribution of bear visits to the marking site

Measured as the average number of individual bear visits per day (left axis, indicating the fraction of those identified as males) and the sampling effort (right axis), measured as the fraction of the days that the camera was active every month (Table A1 in Appendix A of Supplementary material).

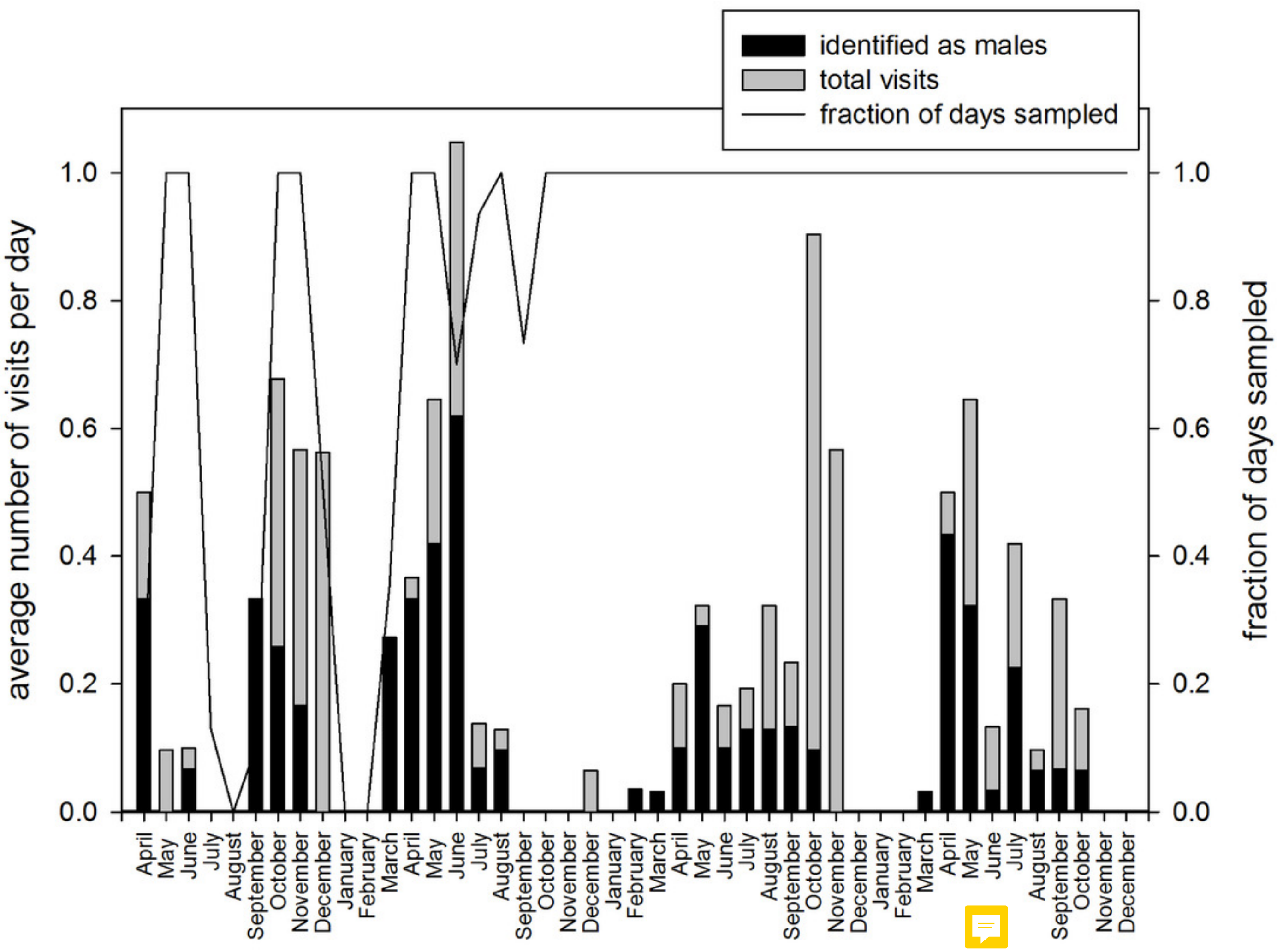

Figure 3

Frequency distributions of the different behaviours

Data by age-sex classes and per month (Tables A3 and A4 in Appendix A of Supplementary material).