Brown bear communication hubs: patterns and correlates of tree rubbing and pedal marking at a long-term marking site

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ABSTRACT

Chemical communication is important for many species of mammals. Male brown bears, *Ursus arctos*, mark trees with a secretion from glands located on their back. The recent discovery of pedal glands and pedal-marking at a site used for tree-rubbing led us to hypothesize that both types of marking form part of a more complex communication system. We describe the patterns of chemical communication used by different age and sex classes, including differences in the roles of these classes as information providers or receivers over four years at a long-term marking site. Using video recordings from a camera trap, we registered a total of 285 bear-visits and 419 behavioral events associated with chemical communication. Bears visited the site more frequently during the mating season, during which communication behaviors were more frequent. A typical visit by male bears consisted of sniffing the depressions where animals pedal mark, performing pedal-marking, sniffing the tree, and, finally, rubbing against the trunk of the tree. Adult males performed most 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% of visits, respectively. Adult females never pedal marked, and juveniles did so at very low frequencies. Females rubbed against the tree in just 9% of their visits; they sniffed the

39 tree and the pedal marks in 51% and 21% of their visits, respectively. All sex and age classes
40 performed pedal- and tree-sniffing. There were significant associations between behaviors
41 indicating that different behaviors tended to occur during the same visit and were more likely if
42 another individual had recently visited. These associations leading to repeated marking of the site
43 can promote the establishment of long-term marking sites. Marking sites defined by trees and the
44 trails leading to them seem to act as communication hubs that brown bears use to share and obtain
45 important information at population level.
46

47 **INTRODUCTION**

48 Marking behavior is essential in the mediation of chemical communication and social interactions
49 in mammals (Potts & Penn 2002; Johansson & Jones, 2007). The chemical signals left at specific
50 sites provide long-lasting messages in the absence of the signal provider (White, Swaisgood &
51 Zhang, 2002; Scordato, Dubay & Drea, 2007). In carnivores, the function of scent marks has been
52 associated with territorial defense (Wronski *et al*., 2006), intra-sexual competition (Gosling &
53 Roberts, 2001), and the defense of trophic resources (Piñeiro & Barja, 2015). Scent marking is
54 particularly important for solitary species ranging widely in large home ranges (Begg *et al*., 2003;
55 Vogt *et al*., 2014). These species must rely on an effective communication system that maximizes
56 the transfer of information at low cost in order to maintain their social organization by advertising
57 to mates and competitors (Allen, Yovovich & Wilmers, 2016).
58   Urine and feces are a relatively inexpensive means of scent marking used by many
59 carnivore species at the expense of relatively low efficiency in the transfer of information (Vogt
60 *et al*., 2016). More specialized chemical compounds may provide detailed information on the
61 individual, including their sex and reproductive status (Alberts, 1992). They are produced by
62 specialized holocrine, apocrine and/or eccrine skin glands, often located in the anal, subcaudal,
63 interdigital skin, and chin areas, among others. To be effective, their secretions should persist in
64 the environment for long periods to maximize the probability of reaching potential receivers
65 (Swaisgood *et al*., 2004). Additionally, individuals scent mark specific sites, such as territorial
66 borders, and prominent locations that are often revisited by them and other individuals, including
67 dens, food sources and busy trails (Sillero-Zuburi & Macdonald, 1998; Revilla & Palomares, 2002;
68 King *et al*., 2017). Chemical cues guide receiving individuals to investigate, ignore, counter and/or
69 over-mark previous marks (Laidre & Johnstone, 2013). The presence of long-lasting marks of
70 multiple individuals in a marking area may promote the synergy between different types of signals,
71 potentially eliciting several communication-related behaviors (Sumpter & Brännström, 2008).
72 These complexities make some particular types of marking sites especially important in the
73 regulation of social behavior. The repeated use by multiple individuals for long periods of time
74 convert these marking sites into communication hubs at a population level (King *et al*., 2017).
75   Ursids are non-territorial animals that move over large areas with low contact rates between
76 individuals (Martin *et al*., 2013). In spite of this, they maintain a complex network of social
77 interactions in which information on the presence of other individuals is critical (Støen *et al*., 2005;
78 Steyaert *et al*., 2012). Chemical communication plays an important role in the maintenance of bear

79 social organization (Noyce & Grarshelis, 2014). Brown bears *Ursus arctos* mark conspicuous
80 objects such as trees, rocks or even poles, with secretions from the sebaceous glands and possibly
81 also the apocrine glands located in the skin of their back (Tomiyasu *et al.*, 2018), and, in some
82 cases, with claw and bite marks as well (Nie *et al.*, 2012; Clapham *et al.*, 2013; Taylor, Allen &
83 Gunther, 2015).
84   Bipedal back-rubbing against trees has been widely described as the most common
85 marking behavior of brown bears across its Holarctic range, showing seasonal and sex and age
86 variations in marking frequency (Green & Mattson, 2003; Clapham *et al.*, 2012, 2013; Sato *et al.*,
87 2014; Seryodkin, 2014; Spassov *et al.*, 2015; Tattoni *et al.*, 2015). Additionally, pedal-marking
88 has recently been reported as an important marking behavior (Taylor *et al.*, 2015; Sergiel *et al.*,
89 2017). Typical deep marks left in the ground by brown bears, possibly during pedal-marking, were
90 described long ago as leading towards bear trees (LeFranc *et al.*, 1987). The presence of pedal
91 scent glands in brown bears and their significance in communication have also been recently
92 described (Sergiel *et al.*, 2017). Nevertheless, pedal-marking has yet to be characterized in terms
93 of its phenology, the sex and age class of the individuals and other environmental correlates, as
94 well as its connection with tree marking, given that they seem to simultaneously occur at the same
95 sites (Clapham *et al.*, 2014; Sergiel *et al.*, 2017).
96   In this paper we hypothesize that pedal-marking and tree-rubbing are deeply linked in
97 brown bears, forming a more complex communication system than previously recognized. We
98 expect to find differences in the use of marking sites by different sex and age classes of individuals,
99 depending on their primary role as either information providers or receivers. Specifically, we made
100 use of a multi-year dataset on chemical communication by brown bears at a marking site in a well-
101 known population living in the Cantabrian Mountains, northern Spain. The site is known to have
102 been intensively used for pedal-marking and tree-rubbing by bears since 2002, when it was already
103 well stablished, and has therefore been used by more than a generation (see Sergiel *et al.*, 2017 for
104 a basic description of pedal marking at this site). Specifically, we aimed at (1) assessing the
105 frequency of main marking behaviors by brown bears of different age and sex classes; (2)
106 identifying associations among behaviors as well as among signal providers (the ones marking)
107 and receivers (the ones sniffing the marks), and (3) determine the role of other factors, such as
108 climatic variables, in the occurrence of marking behaviors. Finally, we discuss the significance of
109 these communication hubs intensively used by brown bears for long periods of time.
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111

112 **MATERIALS & METHODS**
113 **Study site**
114 The study was conducted in the western half of the Cantabrian Range (NW Spain), a mountain
115 system inhabited by a brown bear population which currently numbers around 230 individuals,
116 with a density of 1.6 individuals/100 km^2 (Pérez *et al.*, 2014). The study area is located in Fuentes
117 del Narcea, Degaña e Ibias Natural Park (Cangas del Narcea, Asturias). Our study site is located
118 in an area with high quality habitat for brown bears (Naves *et al.*, 2003), including denning and

119 mating areas, areas used by females with cubs, and also vegetation offering plenty of resources
120 used during hyperphagia, when bears feed continuously in preparation for hibernation.
121   In this area, there are multiple sites used by brown bears for chemical communication.
122 These sites can be easily identified by the presence of a tree, pole or rock that is used for rubbing,
123 often in association with a series of pedal marking tracks leading to the vertical structure that is
124 marked. We selected one site for continuous monitoring on the basis of the evidence of repeated
125 use by brown bears for pedal-marking for more than a decade (Sergiel *et al.*, 2017). As the
126 Cantabrian brown bear population is threatened, we do not provide the exact location of the site
127 due to conservation concerns. The first evidence of ground pedal-marking at this site was obtained
128 in 2002 during an opportunistic observation by one of the authors (DR) of an adult male during
129 the mating season. The site is characterized by an oak tree (*Quercus petraea*) heavily used by
130 brown bears for rubbing, and by conspicuous marks in the ground made by the bears' repeated use
131 of the same spots for pedal-marking (a total of 48 marks made by bears' feet are evident to the
132 human eye).
133
134 **Sampling protocol**
135 Data were collected by DR at the selected site during long-term monitoring for conservation and
136 management. The Principado de Asturias–Consejería de Agroganadería y Recursos Autóctonos
137 granted data access, and DR was authorised to participate by exp-no. 2016/033072, Principado de
138 Asturias-Consejería de Hacienda y sector Público. An automatic camera trap (Bushnell Trophy
139 digital camera trap #19466 with motion triggered day/night recording) was set up between January
140 2012 and January 2016, during which time it was working almost continuously. Initially, between
141 January 2012 and April 2012, the device was placed laterally in a low position from which the tree
142 marked by brown bears was visible. Data obtained during these first four months were not used in
143 the analyses. After this initial sampling, the camera trap was mounted in a zenith position (directly
144 above the site) at a height of six meters on the main trunk of the marked tree to obtain a
145 standardized field of view and to reduce direct interference with bears and other animals. The field
146 of view of the camera trap covered an area of about 100 m^2. The camera trap was programmed to
147 shoot one-minute videos, with a 10-second interval between consecutive videos. We considered a
148 visit event as the group of videos that are not more than 20 minutes apart. This time window was
149 selected following visual inspection of the plot of the cumulative proportion of videos sorted by
150 the time to the next video (Fig. S1). For comparative purposes, we also used a 20-minute time
151 interval to define visit events for other species. Note that a visit can include more than one
152 individual bear, as occurs in the case of females with cubs or males and females moving together
153 during the mating season. The weather data were obtained from the nearby automatic station of
154 Leitariegos, belonging to the Spanish Agencia Estatal de Meteorología (AEMET).
155
156 **Individuals and communication behaviors**
157 In the Cantabrian Mountains, the steep slopes and low forest cover make it relatively easy to
158 observe brown bears, especially during spring and summer. Individuals present in valleys are

detected by scanning the area with spotting scopes from vantage points. This method is used to obtain annual counts of the number of females with cubs of the year and as a long-term method to census this population (Wiegand *et al.*, 1998). As a result, some of the individuals moving in the study area are known, especially when they have some identifying marks, and are thus easily distinguished from other individuals. The professional technicians doing those censuses are experts in recognizing the sex and age of individuals by specific traits under good observation conditions. We classified the recorded individuals into the following sex and age categories: 1) adult males, identified by the combination of large size, and neck and head shape; 2) adult females, when accompanied by cubs, or identified by their size, head and neck shapes, and explicit behavior in the presence of other individuals, often adult males in the mating season; 3) cubs, individuals in their first year or in their second year until May and always accompanied by their mother; 4) juveniles, independent individuals in their second year of life from June onwards and in their third year, clearly smaller in size than adults and usually accompanied by siblings; and, 5) undetermined sex and age class, which included the remaining individuals.

In the case of adult males, some individuals were identified by comparison with known animals observed in repeated sightings at other sites in the study area. These individuals were characterized by a combination of body size, head shape, coat color patterns and especially the very characteristic light-colored permanent markings, normally present on their necks (see description of individualized bears in Supplementary Material). The Cantabrian brown bear population is characterized by its small size and the large variability shown by individuals in coat color and the common presence of markings especially on their necks (Clevenger & Purroy 1991). In other cases, we were able to temporarily classify some individuals in an age and 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 repeatedly seen in the area. Females are more difficult to identify individually on a permanent basis. We used the number of accompanying cubs to establish a minimum number of females visiting the site each year. We did not attempt to identify other types of individuals such as independent juveniles and cubs.

We classified the behaviors displayed by brown bears in the videos into the following types: 1) sniffing pedal marks, when an individual stops or slows its pace and puts its nose to the pedal marks on the ground; 2) pedal-marking, performed by a walking bear with the particular gait of twisting its fore and hind feet on the ground in specific depressions repeatedly used by that individual and other bears during previous visits; 3) tree-sniffing, when an individual calmly puts its nose to the trunk of the rubbing tree; 4) tree-rubbing, when a bear vigorously rubs its back, neck or shoulders against the trunk of the tree while standing on its hind legs; and, 5) other behaviors, in which a bear usually walks in and out of the field of vision. 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 determined if each type of behavior was performed (presence/absence of the behavior, not the number of times) by each bear in the available sequence of videos.

199 **Analyses**
200 First, we described the overall use of the site and the behaviors performed by the visiting brown
201 bears over time and by age and sex classes. Then, we analyzed which variables were associated
202 with the observed patterns (Table 1). We hypothesized that the probability that bears visited the
203 marking site in a given day and performed one of the behaviors in each visit was affected by not
204 only the time elapsed since the previous visit by a bear, but also the season, distinguishing between
205 mating season (April, May and June) and non-mating season (other months), as well as the age
206 and sex class of the focal individuals, and, in the analyses where it made biological sense, by the
207 weather conditions that occurred between visit events affecting the duration of the chemical
208 signals. We performed Generalized Linear Mixed Models (GLMMs) on the response variables
209 (occurrence of the specific behaviors) using a binomial error distribution and year as a random
210 factor. As some individuals were repeatedly observed, there could be some pseudoreplication
211 problem. Solving this issue is not easy as a fraction of the observations correspond to unknown
212 animals. Nevertheless, and in order to check if pseudoreplication was an issue, we repeated the
213 analyses of the selected models adding individual ID as an additional random factor (unidentified
214 individuals were grouped under a single individual label; results are shown in the supplementary
215 materials). Models were run with the potential combination of biologically meaningful explanatory
216 variables within each group of response variables (Table 1). To reduce the effect of
217 multicolinearity, when two predictors were correlated, we selected the one with a stronger
218 association with the dependent variable. From the resulting models, we report and interpret only
219 those within ΔAIC<2. We computed the marginal and conditional R^2 for each selected model
220 (Nakagawa & Schielzeth 2013). For inference we used a cut-off level of P<0.10. Analyses were
221 performed in R vs3.3.3 with lme4 (v1.1-19; Bates et al. 2015) and MuMIn (v1.43.6; Bartoń 2019)
222 packages.
223
224

225 **RESULTS**
226 In total, the camera trap was active for 1,174 days (April 2012 to December 2015), with an average
227 temporal coverage of 83% of the possible days per month (Fig 1, Table S1). It registered 329
228 videos with bear presence; representing 224 visit events and a total of 285 bear-visit events (note
229 that more than one individual can be present during the same visit event). Brown bears were the
230 most common visitors (42%), with more than five visits per month on average (Fig S2, Table S2).
231 The visitation rate of other species was considerably lower despite being more abundant in most
232 cases (Fig S2). Among brown bears, adult males were the most frequent visitors with 132 bear
233 visits (46% of total bear visits, Table 2). The rest of the visits were performed by adult females in
234 57 cases (20%), cubs in 44 (15%), juveniles in 23 (8%) and individuals of undetermined age and
235 sex in 29 (10%; Table 2). The visits followed a bimodal diel pattern with maxima around dawn
236 and dusk (Kaczensky et al. 2006) but occurred also throughout the day and into the night (24-h
237 rhythm, Fig S3). Bears visited the marking site more frequently during the mating season (April-
238 June; Fig 1, on average 26.3% of the days sampled per month had bears visiting the site during the

239 mating season, versus 14.1% during the rest of the year excluding the hibernation period (January
240 and February); Table 3; Table S3). The probability that the site was visited by bears on a given
241 day was negatively associated with the time since the last visit of a male (the shorter the lapse, the
242 higher the probability; Table 3; Table S3).
243
Communication behaviors
244
245 The typical sequence of a visit consists of a bear approaching the tree following the path where it
246 can sniff the depressions in which animals pedal mark, performing pedal-marking itself, stopping
247 at the tree, sniffing it, and, finally, rubbing against the trunk (see video in Supplementary
248 materials). This sequence can vary with different combinations of behaviors and in different
249 orders, and some parts of the sequence can be repeated. On one occasion, a male also rubbed its
250 body against pedal marks. There was no apparent communication behavior in 22% of the visits,
251 although some could have occurred out of the field of view of the camera trap.
252   Out of a total of 482 recorded behaviors, the majority corresponded with some form of
253 chemical communication (87%). Communication behaviors occurred in most months except
254 January and February (hibernation period; Table S4). Sniffing of pedal marks was less frequent
255 (58, 12%) than pedal-marking (113, 23%); while tree-sniffing (153 cases, 31%) was more frequent
256 than tree-rubbing (96, 20%; Table S4).
257   The communication behaviors displayed by bears varied greatly among age and sex
258 classes. All sex and age classes performed pedal- and tree-sniffing. Individuals identified as adult
259 males performed most of the pedal-marking (107 cases, 95%) and, to a lesser extent, tree-rubbing
260 (63 cases, 66%, Fig 2). Interestingly, adult females did not perform pedal-marking, while juveniles
261 did so at very low frequency (Fig 2). Tree-rubbing was performed by all age and sex classes, but
262 at higher frequencies by males (Fig 2).
263   Males and females sniffed the pedal marks in 23% and 21% of their visits, respectively;
264 while cubs, juveniles and undetermined bears did so in 61%, 48% and 26% of their visits,
265 respectively. The probability that a bear sniffed the pedal marks during a visit was higher outside
266 the mating season (Table 3). Also, the lower the average precipitation and the average temperature
267 in the preceding days, the higher the probability of sniffing the pedal marks (Table 3, Tables S3,
268 S8). Finally, the probability of sniffing the pedal marks tended to be negatively related to the time
269 elapsed since the last time a bear performed pedal-marking at the site (Table 3; Tables S3, S8).
270   Males performed pedal-marking in 81% of their visits to the site. They both pedal-marked
271 and sniffed the pedal marks in 20% of their visits. Juveniles and undetermined bears performed
272 pedal-marking in 17% and 7% of their visits, respectively, while females and cubs never pedal
273 marked. The probability of performing pedal-marking by male bears visiting the site was positively
274 associated with tree-rubbing by the same individual and negatively with the time elapsed since the
275 previous visit of a bear that pedal-marked at the site (the shorter the time, the higher the probability
276 of pedal-marking, Table 3; Tables S3, S8). The association of pedal-marking probability with the
277 remaining factors was weaker (Table S3).

278   Males sniffed the tree in 59% of their visits, while adult females did so in 51% of their
279   visits. Cubs, juveniles, and undetermined individuals showed interest in the tree, sniffing it in 61%,
280   48%, and 26% of their visits, respectively. Interestingly, the probability of sniffing the tree by a
281   visiting bear was higher the longer the time elapsed since the previous tree-marking event and
282   negatively related to the precipitation during that period (Table 3; Tables S3, S8), and was not
283   affected by the sex or age class of the individual. Nevertheless, the model was not very explanatory
284   (Table 3).

285   Males performed tree-rubbing in 48% of their visits. They engaged in both pedal-marking
286   and tree-rubbing during the same visit on 43% of their visits and tree-rubbing and tree-sniffing in
287   35% of their visits. Adult females rubbed against the tree in just 9% of their visits. Juveniles, cubs
288   and undetermined individuals tree-rubbed on 39%, 34% and 14% of occasions, respectively. Adult
289   males and juveniles had higher probabilities of tree-rubbing during their visits than females (Table
290   3; Table S3, S8). The probability that a bear performed tree-rubbing during a visit was positively
291   associated with tree-sniffing and pedal-marking by the same individual (Table 3; Tables S3, S8),
292   and tended to be positively associated with the time since the previous tree-rubbing event (Table
293   3; Tables S3, S8).

294   Several recognizable individuals visited the site repeatedly (Supplementary Material),
295   some of them throughout the study period. Four adult males visited the site between 10 and 35
296   times during the study, with up to 15 visits in one year (M1 to M4, Table S6). These males were
297   frequent markers; for example, M2 and M3 were responsible for most of the instances of pedal-
298   marking (59%, Table S7), while M2 was the bear that most frequently displayed tree-rubbing
299   behavior (43%, Table S7). Additionally, other males visited the site sporadically (Table S9). These
300   additional males were known individuals that were repeatedly observed near the study site (at least
301   four additional males in 2012, five in 2013 and 2015, and seven in 2014). A minimum of one
302   female visited the site in 2013 and 2015, two in 2014 and three in 2012. The minimum number of
303   different individual bears visiting the site per year ranged between 11 in 2013 and 18 in 2015
304   (Table S9).

305

306   **DISCUSSION**

307   In this work we show that the chemical communication behavior of brown bears at tree-rubbing
308   sites is more complex than previously recognized, with pedal-marking being an integral part of
309   this communication system. These marking sites form communication hubs where multiple
310   individuals share and receive important information at the population level (Sergiel *et al.* 2018).
311   Tree-rubbing is a well-known scent-marking behavior performed by bears (Green & Mattson,
312   2003; Clapham *et al.*, 2012; Sato *et al.*, 2014; Seryodkin, 2014; Tattoni *et al.*, 2015; Lamb *et al.*,
313   2017). Brown bears vigorously rub their flanks and back against the tree to scent mark it with
314   secretions from the glands located on their back (Tomiyasu *et al.*, 2018). They also mark other
315   types of objects in the same way, especially in areas where the availability of trees is low
316   (Seryodkin 2014). Our results, in accordance with published information, show that tree rubbing
317   can be performed by any class of individual at any time, but it is clearly monopolized by adult

318   males, especially during the mating season (see also Clapham *et al*., 2012; Lamb *et al*., 2017).
319   Additionally, our results indicate that the information is received by all types of individuals
320   irrespective of their age or sex.
321   Interestingly, tree-marking does not occur in isolation. Pedal-marking by males occurs as
322   part of the marking process in association with tree-rubbing. As with tree-rubbing, pedal-marking
323   is performed by males with a higher frequency during the mating season, while all classes of
324   individuals act as receivers of the information. The existence of deep footprint marks forming one
325   or more trails in the ground leading towards trees has been known for a long time, though not
326   examined in detail (e.g., LeFranc *et al*., 1987; Clapham *et al*., 2013; Seryodkin 2014).
327   Additionally, the typical behavioral sequence performed by males during pedal-marking has also
328   been described with a variety of names, including bear dance, sumo walking, cowboy walk or
329   stomping (Sergiel *et al*., 2017), but has been often interpreted as part of a stereotyped behavior
330   leading to marking the tree and not a marking in itself. The recent description of pedal glands in
331   the feet of bears and the concomitant pedal-marking (Sergiel *et al*., 2017) together with our results
332   on the relationship between both pedal- and tree-marking provide new insights into scent-marking
333   system in brown bears.
334   The data used in our description have some shortcomings that need to be considered. We
335   provide data from only one site, although for a long period of nearly continuous monitoring. The
336   area covered by the camera trap recorded only part of the area and, therefore, we may have missed
337   behaviors, such as pedal-marking or sniffing when animals were out of the field of view; or tree-
338   marking when the bears used other trees (there were nearby trees also used for marking). We could
339   only detect sniffing behaviors when they were apparent in the videos, whereas bears have a very
340   efficient olfactory system that might allow them to detect markings with little effort. Additionally,
341   the zenith position of the camera trap may have limited our capacity to detect other potential
342   marking behaviors such as urination or more complex stereotyped behaviors associated with tree-
343   rubbing (Clapham *et al*., 2014). Despite these limitations, we believe that our results are relevant
344   to the interpretation of chemical communication at marking sites by brown bears.
345

346   **Sending and receiving information**
347   The importance of chemical communication at the site varied as a function of the individuals,
348   depending on their sex, age, and presumably other conditions such as dominance or breeding
349   status. Nearly half of the visits to the marking site were made by animals identified as adult males.
350   They were responsible for most pedal-marking, and, to a lesser extent, tree-rubbing behaviors.
351   Both behaviors were strongly associated when performed by adult males. Some males visited the
352   site very often while others were more sporadic. Interestingly, some males marked in most of their
353   visits while others mostly acted as information receivers. This may reflect a structure of dominance
354   in the males sharing the area. Females, on the other hand, never pedal-marked and rarely rubbed
355   the tree, and neither did the cubs accompanying their mothers. Young animals (of unknown sex)
356   showed an intermediate pattern between males and females. Tree-rubbing was more frequently
357   displayed by bears which also sniffed the tree and performed pedal-marking and positively related

358   with the time elapsed since a previous tree-rubbing event, typically describing the behavioral
359   sequence of visiting males. Male brown bears have seasonally enlarged sebaceous glands on their
360   back and prominent eccrine, apocrine and sebaceous glands in their feet; glands that are more
361   active during the mating season, in association with their increased testosterone levels (Sergiel *et*
362   *al.*, 2017; Tomiyasu *et al.*, 2018). Therefore, males acted as main sources of chemical messages at
363   the site, as has been shown in other study areas (Clapham *et al.*, 2014; Lamb *et al.*, 2017).
364   Sniffing behavior, especially that of ground marks, is less obvious and therefore more
365   likely to go unnoticed in videos. Nevertheless, all types of individuals showed interest in the
366   chemical marks, acting as genuine information receivers. The probability of sniffing the marks
367   during a visit was affected by weather conditions, with higher temperatures and precipitation in
368   the preceding days reducing the probability of sniffing ground marks, a pattern that was not
369   associated with actual pedal-marking, and higher precipitation negatively affecting tree-sniffing.
370   The diluting effects of precipitation and temperature on the volatility of the odorous molecules left
371   by bears at the marking site are a possible interpretation of these results. Interestingly, the
372   probability of sniffing the tree was higher the longer the time elapsed since the previous visit, while
373   it was the opposite for ground sniffing, suggesting a differential detectability between the chemical
374   compounds secreted by pedal and back glands and among different substrates.
375
376 Why brown bears visit these sites
377   Brown bears use chemical marking to convey information from senders to receivers. Why they do
378   this and what type of information is transferred is still a matter of discussion. The chemical profiles
379   of pedal and shoulder secretions indicate that they contain information on at least the sex and
380   reproductive status of the individual (Sergiel *et al.*, 2017; Tomiyasu *et al.*, 2018). Additionally, it
381   would not be surprising if information on the actual individual is also provided, as seems to occur
382   with secretions from anal sacs (Rosell *et al.*, 2011; Jojola *et al.*, 2012). In species that normally
383   exhibit a solitary non-territorial use of space, knowing the individuals whom they may encounter
384   is quite valuable. Several non-exclusive hypotheses have been proposed to explain scent-marking
385   in brown bears: self-advertisement for mate attraction, communication of individual dominance,
386   competitor assessment and infanticide avoidance, with different roles depending on bear density
387   (Clapham *et al.*, 2012; Lamb *et al.*, 2017). Our results show that chemical communication in brown
388   bears is complex. Males are the main senders and also the main receivers, with some of them
389   marking a lot while others tend to mostly receive information, indicating communication of
390   individual dominance and the ability to assess male competitors. Male bears mark all year round
391   but with a main peak during the mating season, a period of intense competition. This pattern has
392   also been found at rubbing trees, both natural and artificially created to collect bear hairs (i.e. tree
393   hair traps), in different ecosystems (Green & Mattson 2003, Karamanlidis et al. 2010, Sato et al.
394   2014, Berezowska-Cnota et al. 2017, Lamb et al. 2017).
395   Females seem to visit the site less often, but all year round, and when they do, they are
396   especially interested in receiving information. Knowing which males are moving around and their
397   social dominance is very important for females in mate selection, since mating with the more

398   dominant males that are present all year round would minimize the overall risk of infanticide to
399   their litters. Additionally, females with cubs of the year may benefit from knowing if a new male
400   enters the area (Bellemain *et al.*, 2006). Although more rarely, females, juveniles and cubs also
401   rub trees, but it is unclear why they do it. In the case of juveniles learning by imitation may be the
402   main reason (Clapham *et al.*, 2014). Given that the sebaceous secretion in the shoulder of males is
403   linked to testosterone levels, the secretion of females, cubs and juveniles can be expected to be
404   testimonial or simply non-existent. If that is the case, their tree-rubbing may serve the purpose of
405   masking their odor with that of adult males roaming the area. The resulting increase in chemical
406   similarity could help to reduce the risk of infanticide by scent-matching (Gosling & McKay, 1990).
407   If this interpretation is correct, tree-rubbing would have a scent-marking purpose only for males,
408   while helping females and cubs to obtain a chemical camouflage by scent-rubbing as well as
409   transitionally being part of the learning process of juveniles. In summary, there is no single best
410   hypothesis to explain the role of these communication hubs, with the most plausible being a
411   complex combination of dominance, mate selection, competitor assessment, mate selection and
412   infanticide avoidance.

413

414   **Brown bear communication hubs**
415   Undoubtedly, sites like the one we monitored are important for brown bears at the population level.
416   Our results show that the tree and the trails leading to it form a communication hub that most bears
417   living in the area use to share and obtain information. Bears were the most frequent visitors to our
418   site despite the easy accessibility and the fact that bears are not the most common large mammal.
419   Bears choose specific trees in places that are well situated for the passage of other individuals
420   (Green & Mattson 2003; Sato *et al.*, 2014). At these sites there is an association between different
421   communication behaviors, with marking behaviors triggering the subsequent sniffing and marking
422   of later visitors (Berezowska-Cnota et al. 2017). Nevertheless, these sites are not uncommon. In
423   the vicinity of our site there were other trees used repeatedly by bears for marking (see
424   Supplementary video). Brown bears maintain a dense system of marking sites that allow for a
425   complex communication network over large spatial scales. Although they are not easy for humans
426   to locate, several authors report varying densities of marking sites depending on bear density,
427   including 0.26 sites/km^2 in the Italian Alps, 0.4 sites/km^2 in Hokkaido, Japan, 1.4 sites/km^2 in the
428   Russian Komi Republic, 20 sites/km^2 in British Columbia, and 27 sites/km^2 in the Valley of
429   Geysers on Kamchatka Peninsula (Lloyd, 1979; Sato *et al.*, 2014; Seryodkin, 2014; Tattoni *et al.*,
430   2015). Many of these studies describe trails evidencing pedal-marking (e.g., Clapman *et al.*, 2013;
431   Seryodkin, 2014). There are open questions that remain to be answered, such as the heterogeneity
432   in the use of the multiple marking sites available to brown bears within their home ranges or the
433   variability in marking intensity within and across populations.

434

435   **CONCLUSIONS**
436   We showed that pedal-marking and tree-rubbing are strongly associated in a complex chemical
437   communication system. At our site, bears visited more frequently during the mating season.

438 More dominant male bears typically sniffed the depressions where animals pedal marked,
439 performed pedal-marking, sniffed the tree, and rubbed against the trunk. Adult males
440 monopolized pedal- and tree-marking. Adult females, on the other hand, never pedal marked,
441 and juveniles rarely did so. Females acted more as information receivers, rarely rubbing the tree.
442 All sex and age classes performed pedal- and tree-sniffing, thus obtaining information on
443 previous visitors. Different behaviors tended to occur during the same visit and were more likely
444 if another individual had recently visited, generating long-term marking sites. These sites act as
445 communication hubs that brown bears use to share and obtain important information on the
446 animals present over a wide area at the population level. The intensive use of these sites and their
447 number and density provide an idea of the importance of this communication system for this
448 wide ranging, non-social large carnivore, with a complex mating system.
449
450

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455

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601   **Figure 1. Monthly distribution of brown bear visits to the marking site.** The average number
602   of individual visits per day of sampling (left axis, indicating the total number and those identified
603   as males) and the sampling effort (right axis), measured as the proportion of days that the camera
604   trap was active every month (x-axis) between April 2012 and December 2015. See Table S1 in
605   Supplementary material for numerical data.
606
607   **Figure 2. Proportion of the different behaviors.** Proportion of all observed behaviors
608   performed by age and sex classes (panels A and B) and per month (panels C and D). Proportions
609   were calculated as the number of observations within each class divided by the total number of
610   observations of all behaviors in all size classes. Data in Tables S4 and S5.
611
612
613

Description of response and explanatory variables used in the analyses

All response variables were binary: occurrence of visit or visits in a given day for *day visit* or occurrence within a visit for communication behaviors. The variables listed were the ones explored in each model (marked with *X*). Not all combinations were explored due to biological sense (weather variables were used only for sniffing behaviors because weather can affect the amount of time that marks last, or due to the most common logical sequence of events, from sniff pedal marks into tree rubbing), or to the structure of the data (*day visit* has no individual descriptors as in a given day more than one individual can occur; *pedal marking* can only be analysed for males because they were the only ones using this marking).

1 **Table 1. Description of response and explanatory variables used in the analyses**. All response variables were binary: occurrence
2 of visit or visits in a given day for *day visit* or occurrence within a visit for communication behaviors. The variables listed were the
3 ones explored in each model (marked with *X*). Not all combinations were explored due to biological sense (weather variables were
4 used only for sniffing behaviors because weather can affect the amount of time that marks last, or due to the most common logical
5 sequence of events, from sniff pedal marks into tree rubbing), or to the structure of the data (*day visit* has no individual descriptors as
6 in a given day more than one individual can occur; *pedal marking* can only be analysed for males because they were the only ones
7 using this marking).

Explanatory variables		Response variables				
Label	**Description**	*day visit*	*sniff pedal marks†*	*pedal marking**	*sniff tree †*	*tree rubbing†*
Individual variables						
age_sex	age-sex class of the bear (Male, Female, Juvenile, Undetermined)		X		X	X
age_sex_tree	age-sex class of the previous bear marking the tree (Male, Female, Juvenile, Undetermined)				X	
Temporal variables						
days	time since the previous visit of a bear (in days, common logarithm)		X	X	X	X
days_male	time since the previous visit of a male (in days, common logarithm)	X				
days_pedal	time since the previous visit of a bear pedal marking (in days, common logarithm)	X	X	X		
days_tree	time since the previous visit of a bear rubbing the tree (in days, common logarithm)	X			X	X
Weather variables						
Prec_pedal	average precipitation of the days elapsed since the previous bear visit that performed pedal marking (mm)		X			
Prec_tree	average precipitation of days elapsed since the previous bear visit that performed tree marking (mm)				X	
Temp_pedal	average temperature of the days elapsed since the previous bear visit that performed pedal marking (º C)		X			
Temp_tree	average temperature of the days elapsed since the previous bear visit that performed tree rubbing (º C)				X	

Behavioral variables

pedal_marking	pedal marking performed by the same bear visit					X
season	season: mating (April, May, June) vs non-mating (other months)	X	X	X	X	X
sniff_pedal	sniff pedal marks during the bear visit			X		
sniff_tree	sniff tree during the bear visit					X
tree_rubbing	tree-rubbing during the same bear visit			X		

8   *only for males
9   †all bears except cubs

Number of behaviours displayed by different age and sex classes

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

1 **Table 2. Number of behaviors displayed by different age and sex classes**. Data recorded by
2 the camera trap at the marking site between 2012 and 2015.

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

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

Models were GLMMs with binomial distribution and year as random factor (Table S7 in Supplementary material). The models on pedal marking were run only on males and the rest with all types of individuals except for cubs. Note that, for the *tree rubbing* model, the estimates of the *age_sex* parameters correspond with the comparison of those classes with females, which is the reference class (as defined by the intercept of the model). See Table 1 for a description of the variables.

1 **Table 3. Estimates of the effect of the factors included in the best models.** Models were
2 GLMMs with binomial distribution and year as random factor (Table S7 in Supplementary
3 material). The models on pedal marking were run only on males and the rest with all types of
4 individuals except for cubs. Note that, for the *tree rubbing* model, the estimates of the *age_sex*
5 parameters correspond with the comparison of those classes with females, which is the reference
6 class (as defined by the intercept of the model). See Table 1 for a description of the variables.

Model	Estimate	SE	p
bear visit (all classes of individuals)			
(intercept)	0.859	0.267	0.001
days_male	-1.823	0.196	<0.0001
season	-0.379	0.177	0.032
R^2 (marginal) = 0.30			
R^2 (conditional) = 0.30			
sniff pedal marks (all classes of individuals except cubs)			
(intercept)	-2.069	0.797	0.009
days_pedal	-0.725	0.389	0.062
Prec_pedal	-0.013	0.006	0.036
Temp_pedal	-0.011	0.005	0.013
season	2.046	0.546	<0.001
R^2 (marginal) = 0.21			
R^2 (conditional) = 0.26			
pedal marking (males)			
(intercept)	1.946	0.494	<0.0001
days_pedal	-1.255	0.477	0.009
tree_rubbing	1.315	0.527	0.013
R^2 (marginal) = 0.20			
R^2 (conditional) = 0.20			
sniff tree (all classes of individuals except cubs)			
(intercept)	-0.090	0.249	0.717
days	0.885	0.379	0.019
Prec_tree	-0.011	0.005	0.047
R^2 (marginal) = 0.06			
R^2 (conditional) = 0.06			
tree rubbing (all classes of individuals except cubs)			
(intercept)	-3.611	0.651	<0.0001
days_tree	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

R^2 (marginal) = 0.36
R^2 (conditional) = 0.37

Figure 1

Monthly distribution of brown bear visits to the marking site

The average number of individual visits per day of sampling (left axis, indicating the total number and those identified as males) and the sampling effort (right axis), measured as the proportion of days that the camera trap was active every month (x-axis) between April 2012 and December 2015. See Table S1 in Supplementary material for numerical data.
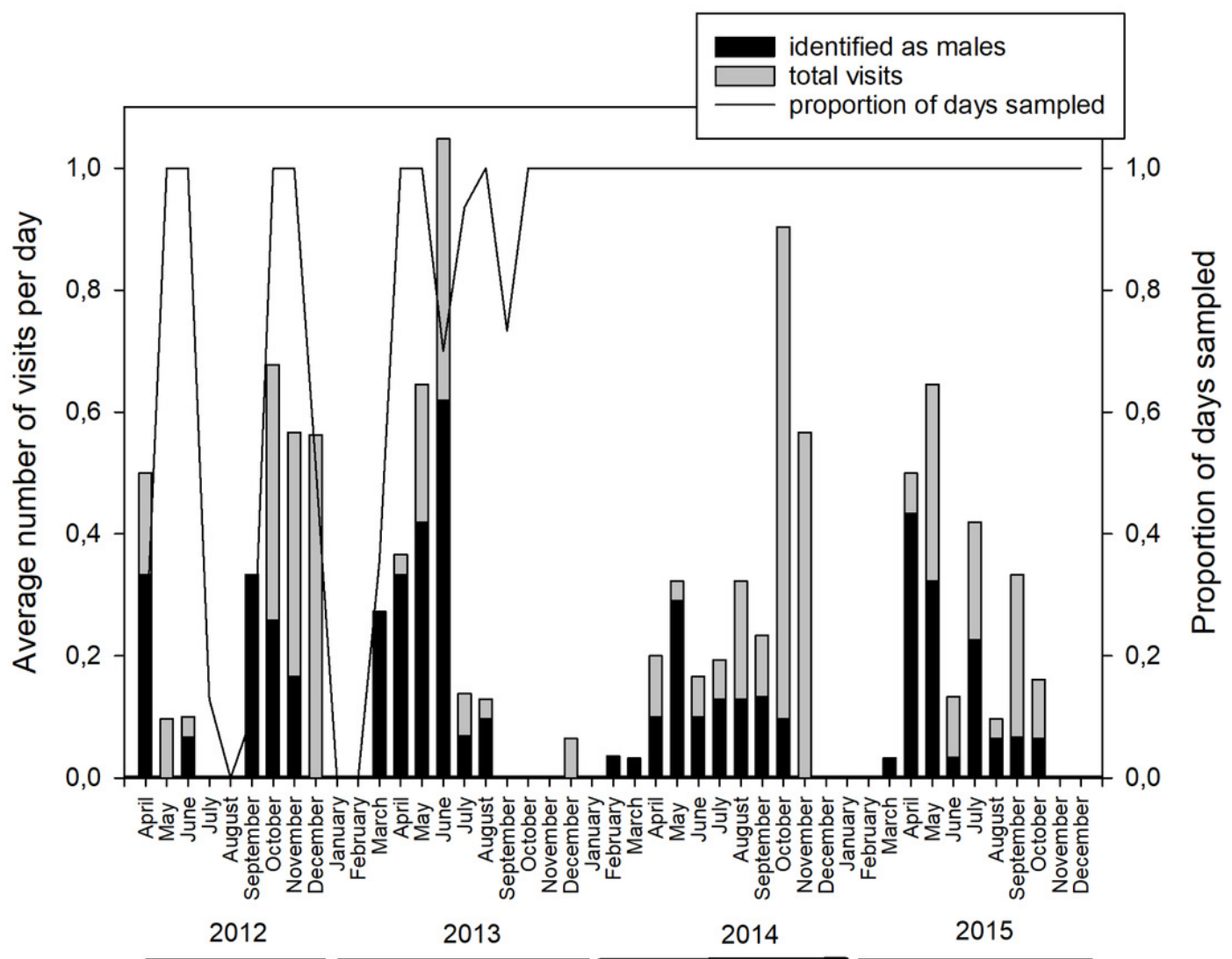
Figure 2

Proportion of the different behaviors

Proportion of all observed behaviors performed by age and sex classes (panels A and B) and per month (panels C and D). Proportions were calculated as the number of observations within each class divided by the total number of observations of all behaviors in all size classes. Data in Tables S4 and S5.