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14 December 2021

UNIVERSITÀ DEGLI STUDI DI TORINO

Rubbing behavior of European brown bears: factors affecting rub tree selectivity and density

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12   Scent-mediated communication is considered the principal communication channel in

13   many mammal species. Compared with visual and vocal communication, odors persist

14   for a longer time, enabling individuals to interact without being in the same place at the

15   same time. The brown bear (*Ursus arctos*), like other mammals, carries out chemical

16   communication, for example, by means of scents deposited on marking (or rub) trees. In

17   this study, we assessed rub tree selectivity of the brown bear in the predominantly

18   deciduous forests of the Cantabrian Mountains (NW Spain). We first compared the

19   characteristics of 101 brown bear rub trees with 263 control trees. We then analysed the

20   potential factors affecting the density of rub trees along 35 survey routes along

21   footpaths. We hypothesized that: (1) bears would select particular trees, or tree species,

22   with characteristics that make them more conspicuous; and (2) that bears would select

23   trees located in areas with the highest presence of conspecifics, depending on the

24   population density or the position of the trees within the species' range. We used linear

25   models and Generalized Additive Models to test these hypotheses. Our results showed

26   that brown bears generally selected more conspicuous trees with a preference for

27   birches (*Betula* spp.). This choice may facilitate the marking and/or detection of

28   chemical signals and, therefore, the effectiveness of intraspecific communication.

29   Conversely, the abundance of rub trees along footpaths did not seem to depend on the

30   density of bear observations or their relative position within the population centre or its

31   border. Our results suggest that Cantabrian brown bears select trees based on their

32   individual characteristics and their location, with no influence of characteristics of the

33   bear population itself. Our findings can be used to locate target trees that could help in

34   population monitoring.

35   **Keywords:** *Ursus arctos*, rub trees, rubbing behaviour, tree selectivity, chemical

36   communication

La comunicación olfativa se considera el principal canal de comunicación en muchas especies de mamíferos. En comparación con la comunicación visual y la vocal, los olores persisten durante más tiempo, lo que permite a los individuos interactuar sin estar en el mismo lugar al mismo tiempo. El oso pardo (*Ursus arctos*), al igual que otros mamíferos, emplea la comunicación química, por ejemplo, por medio de olores depositados en árboles a través del marcaje o rascado. En este estudio, evaluamos la selección de árboles de marcaje por el oso pardo en los bosques predominantemente caducifolios de la Cordillera Cantábrica (noroeste de España). En primer lugar, comparamos las características individuales de 101 árboles de marcaje de oso pardo con 263 árboles control. Después, analizamos los factores potenciales que afectan la densidad de árboles de marcaje en 35 trayectos de prospección a lo largo de caminos y pistas forestales. Planteamos las hipótesis que: (1) los osos seleccionan árboles particulares, o especies de árboles, con características que los hacen más conspicuos; y (2) que los osos seleccionan árboles ubicados en áreas con mayor presencia de conespecíficos, dependiendo de la densidad de población osera o de la posición de los árboles dentro del rango de distribución de la especie. Usamos modelos lineales y modelos aditivos generalizados para probar estas hipótesis. Nuestros resultados mostraron que los osos pardos generalmente seleccionaron árboles más conspicuos, con preferencia por los abedules (*Betula* spp*.).* Esta elección puede facilitar el marcaje y/o detección de señales químicas y, por tanto, la eficacia de la comunicación intraespecífica. Por el contrario, la abundancia de marcaje a lo largo de los trayectos no parece depender de la densidad de las observaciones de osos o de su posición relativa con respecto al centro o los límites del rango de la población. Nuestros resultados sugieren que los osos pardos cantábricos seleccionan árboles en función de sus características individuales y de su ubicación, sin que influyan en ello las características

62 de la población osera. Nuestros hallazgos pueden servir para localizar árboles

63 específicos que podrían ayudar al monitoreo de la población.

64 **Palabras clave:** *Ursus arctos*, árboles de marcaje, comportamiento de marcaje,

65 comunicación química, selección de árboles

66

67 Chemical signals that are spread by distinct means, such as urine, feces, or glandular

68 secretions (Müller-Schwarze 2006; Johnston and Del Barco-Trillo 2010), are considered

69 the principal channel of communication in many mammal species (Ralls 1971), more so

70 than visual or acoustic signals (Müller-Schwarze 2006; Penteriani and Delgado 2017).

71 Mammalian scent-marking strategies mostly depend on individual and social factors, as

72 well as on the physical characteristics of the environment (Barja and De Miguel 2010).

73 Scent-mediated communication has several advantages, including persistence for long

74 periods, and facilitation of interactions among individuals without any need for direct

75 interaction at a given site (Mills et al. 1980).

76 Chemical communication can have different functions that include: self-

77 advertising, i.e., communication of the state or characteristics of the individual, such as

78 age, sex, reproductive status, and health condition; conspecific localisation;

79 communication of dominance; and the defence of a resource (Brown 1979; Doty 1986,

80 Gosling 1990; Johnston 2008; Morales-González et al. 2019). Sometimes, this form of

81 indirect interaction also can prevent agonistic encounters (Gosling and McKay 1990;

82 Roberts and Gosling 2001). While scent-marking plays an important role when

83 defending or signalling territory occupancy in territorial species (Roberts and Gosling

84 2001; Müller and Manser 2008; Barja and De Miguel 2010), scent marking in non-

85 territorial species is more difficult to interpret (Clapham et al. 2012). Solitary species

86   must maintain effective communication to sustain a social structure that facilitates

87   reproduction (Clapperton 1989; Gosling and Roberts 2001), for example by

88   communicating male fitness (White et al. 2002) or the reproductive status of females

89   (Gorman and Trowbridge 1989; Rich and Hurst 1998; Barja and De Miguel 2010). In

90   particular, large-bodied solitary carnivorous species with large home ranges base much

91   of their communication on olfactory chemical signals (Macdonald 1980; Gorman and

92   Trowbridge 1989; Lamb et al. 2017), which usually are left on conspicuous and

93   permanent substrates, such as rocks and tree trunks (Kleiman 1966; Barja 2009; Allen et

94   al. 2017). Thus, intensive marking behaviour on those substrates increases detectability

95   and information transmission, reducing the investment of resources in communication

96   (Alberts 1992; Gosling and Roberts 2001).

97   As in other solitary and non-territorial carnivores (Smith et al. 1989; Barja

98   2009), bears perform scent-marking on different substrates (Filipczyková et al. 2016).

99   Indeed, rubbing behaviour has been documented in most ursid species, i.e., American

100   black bear *Ursus americanus* (Burst and Pelton 1983; Sawaya et al. 2012) and Asiatic

101   black bear *Ursus thibetanus* (Bromley 1965), giant panda *Ailuropoda melanoleuca*

102   (White et al. 2002; Swaisgood et al. 2004; Nie et al. 2012), sloth bear *Melursus ursinus*

103   (Laurie and Seidensticker 1977), Andean bear *Tremarctos ornatus* (Filipczyková et al.

104   2016; Kleiner et al. 2018) and brown bear *Ursus arctos* (Krott 1962; Shaffer 1971).

105   Brown bears exhibit a set of marking behaviours, including: urination; biting,

106   scratching, and stripping bark; rubbing the back, shoulders, and head (Green and

107   Mattson 2003; Puchkovskiy 2009; Clapham et al. 2012), and pedal and scent-marking at

108   the base of trees and the surrounding area (Clapham et al. 2012; Sergiel et al. 2017).

109   Marking, or rub trees (hereafter, RTs) have a key function in intraspecific

110   communication in brown bears (Green and Mattson 2003; Clapham et al. 2012, 2013;

Sato et al. 2014; Tattoni et al. 2015; Lamb et al. 2017). Indeed, some studies have

reported larger odoriferous glands and higher amounts of glandular secretion produced

in individuals that show more pronounced rubbing behaviour (Tomiyasu et al. 2017).

Other studies even have reported a different composition of glandular secretions

between males and females (Rosell et al. 2011; Sergiel et al. 2017; Tomiyasu et al.

2017), which may facilitate identification of sex among bears (Jojola et al. 2012). In

addition, the function of tree rubbing has been described as density-dependent,

prioritizing the communication of dominance in situations of a high density of

individuals (Lamb et al. 2017). There are two main functions and advantages of

chemical scents on RTs: (a) communication of dominance or fitness in adult males

(Clapham et al. 2012; Tattoni et al. 2015; Lamb et al. 2017) and related adult male

avoidance by subadults (Jojola et al. 2012; Tomiyasu et al. 2017); and, (b) increasing

the probability of finding a potential mate (Green and Mattson 2003; Clapham et al.

2012, 2014; Lamb et al. 2017).

The pool of RTs in a given area provides a communication network through

which individuals exchange information; this pool can be used over time for generations

(Green and Mattson 2003; Clapham et al. 2013; Morgan Henderson et al. 2015). RTs

commonly are located in the proximity of foot trails or unpaved roads that facilitate the

transit of bears (Lloyd 1979; Green and Mattson 2003; Sato et al. 2014), with trail-

oriented rubbing marks (Green and Mattson 2003), or at forest edges (Green and

Mattson 2003; Puchkovskiy 2009). Brown bears seem to select trees that allow for

greater conspicuousness of their markings. Preference also is given to certain species of

conifers (Puchkovskiy 2009; Sato et al. 2014), probably due to the resins that may

enhance the detectability or range of scent-markings (Green and Mattson 2003,

135   Clapham et al. 2013; Tattoni et al. 2015). This effect has been suggested to be enhanced

136   by producing wounds to the tree that increase resin flow (Sato et al. 2014).

137   Studies on RTs have mainly been focused on North American grizzlies *Ursus*

138   *arctos horribilis* (Green and Mattson 2003; Clapham et al. 2013; Morgan Henderson et

139   al. 2015), with a few also in Russia (Puchkovskiy 2009; Puchkovskiy et al. 2012) and

140   Japan (Sato et al. 2014); however, these studies considered large continuous

141   populations. To our knowledge, such a study has not previously been carried out in

142   smaller, vulnerable populations, nor in populations living in areas dominated by

143   deciduous forest. Here, by using (a) 101 RTs found in the Cantabrian Mountains (north-

144   western Spain) and (b) the density of RTs along 35 survey routes along footpaths, we

145   carried out a multilevel analysis to elucidate whether brown bears' RT selection is

146   determined by tree species, physical traits, landscape position, and whether RT

147   occurrence was related to their spatial location and observed bear density. Two main

148   hypotheses underlie this study. First, as previously reported in populations inhabiting

149   coniferous forests, RTs have characteristics that distinguish them from surrounding

150   trees (e.g., dendrometric characteristics, tree location), which probably enhance the

151   conspicuousness of chemical signalling and/or represent a better substrate for marking.

152   We thus hypothesized that bears would select specific trees, or tree species with

153   characteristics that make them more conspicuous. Second, we hypothesized that RTs

154   would be more abundant in areas with the highest presence of conspecifics, towards the

155   core of the bear distribution area and in areas where the density of bears is higher.

156   This study was carried out in a small and isolated, but still autochthonous, brown

157   bear population, at the southwestern limit of the current species distribution. An

158   overarching goal of the study therefore was to obtain information on scent-marking in

159   small populations, whose behaviour may differ from larger and less isolated

160 populations, because the smaller population size is likely to mean a higher number of

161 interactions between the same individuals. The results provide insights into the ecology

162 of a threatened population and therefore contribute to conservation and monitoring

163 actions.

164

165   **METHODS**

166   *Study area*.—The study area covers most of the geographic range of the western

167 sub-population of brown bears in the Cantabrian Mountains (northwestern Spain, Figure

168 1), which run for ~300 km in parallel to the coast (E–W) with an average and maximum

169 altitude of 1100 and 2648 m a.s.l, respectively (Martínez Cano et al. 2016; Penteriani et

170 al. 2019). The region has an oceanic climate, more humid and temperate in northern

171 slopes and continental and dryer on southern slopes (Ortega and Morales 2015). The

172 landscape is covered predominantly by forests, shrubs, and croplands (Mateo-Sánchez

173 et al. 2016). Forests of semi-deciduous and evergreen oaks (*Quercus* sp.) dominate

174 sunny slopes, whereas the north-facing slopes are covered by deciduous trees such as

175 beech (*Fagus sylvatica*) and common (*Q. robur*) and sessile oak (*Q. petraea*). Birches

176 (*Betula* sp.) occupy areas of acid soils, dominant towards the west of the study area, in

177 well illuminated areas with sufficient humidity and frequently colonizing degraded or

178 bare areas, with few monospecific stands (García de Celis et al. 2004). Non-forested

179 areas are mainly occupied by shrub species, such as heather (*Erica* sp*., Calluna* sp.) and

180 brooms (*Cytisus* sp.; Fernández-Gil et al. 2006; Mateo-Sánchez et al. 2016). Above the

181 treeline, berry-producing shrubs occur, including bilberries (*Vaccinium myrtillus*; Pato

182 and Obeso 2012; Martínez Cano et al. 2016). Most of the areas inhabited by bears are

183 surrounded by urbanized and cultivated areas, with a high density of transport

184 infrastructure; the main economic activities include livestock breeding, mining, timber

185 harvesting, and recreational activities (Zarzo-Arias et al. 2018, 2019).

186   *Description of the population.*—In northern Spain, there are two brown bear

187 populations that are isolated from other European populations, one in the Pyrenees and

188 another in the Cantabrian Mountains, separated from each other by almost 300 km. The

189 latter population is divided into two subpopulations, with little gene flow (Pérez et al.

190 2010; Gonzalez et al. 2016) and a genetic variability that is among the lowest of any

191 brown bear population in the world (García-Garitagoitia et al. 2007). In the 1990s, the

192 Cantabrian population consisted of a minimum of 70 – 85 bears (50 – 65 individuals in

193 the western nucleus and 14 – 20 in the eastern; Clevenger and Purroy 1991; Naves and

194 Palomero 1993; Pérez et al. 2014). Recent population trends seem positive, especially in

195 the western subpopulation (Pérez et al. [2014] reported 168 – 260 bears in the western

196 subpopulation and 12 – 40 in the eastern subpopulation), but this species is still

197 considered as "Endangered" in Spain (BOE 2011).

198   *Multilevel analysis*

199   *Location and characterisation of rub and control trees.*—We surveyed principal

200 trails and forest roads (hereafter footpaths) within the study area for RTs from October

201 2018 to March 2019 (Fig. 1). We looked for trees with rubbing signs such as smoothed

202 bark, discoloured surface, scratches, bites, or lack of vegetation at the base; however,

203 the tree was only considered an RT when the presence of bear fur snagged on the bark

204 was confirmed (a characteristic sign of bear tree rubbing behaviour). All the trees

205 located within a radius of 5 m around each marked tree (following Clapham et al. 2013)

206 were considered control trees (hereafter, CT). None of the CTs were found to have any

207 evidence of marking. This radius ensured that we sampled trees that showed the same

208 local habitat characteristics as the RT, and that were clearly available to the bear in that

10

location. We followed previous studies on brown bear tree rubbing behaviour (Green

and Mattson 2003; Clapham et al. 2013; Sato et al. 2014), to characterise each rub and

control tree, recording the following variables: (1) tree species (categorical with five

levels: birch [*Betula spp.*], oak [*Quercus* spp.], chestnut [*Castanea sativa*], conifer

[*Pinus* spp., *Pseudotsuga menziesii*], and other); (2) tree status (categorical with two

levels: dead and alive); (3) other brown bear tree marks (categorical with three levels:

bites, scratches, no other marks); (4) slope exposure, i.e., exposure where the tree was

located (categorical with eight levels: north, northeast, east, southeast, south, southwest,

west, northwest); (5) tree height, measured with NASA GLOBE Observer v 3.0 (NASA

2019); (6) trunk height, i.e., from the ground to the first branch, measured with a tape

measure; (7) diameter at breast height (DBH), measured with a diameter tape; (8)

distance to the nearest footpath (hereafter dist. to footpath), measured with a tape

measure; (9) tree spacing, i.e., average distance to the nearest tree located in each of the

four main cardinal directions, measured with a tape; and (10) terrain elevation (m.a.s.l.).

  Characterization of the landscape around rub trees.—To explore the landscape

characteristics of the areas in which the rub trees were found, both in terms of natural

and human features of rub trees, we calculated the following variables for each rub tree:

distance to the nearest (1) paved road (hereafter dist. to paved road); (2) unpaved road

(hereafter dist. to unpaved road); (3) river (hereafter dist. to river); and (4) human

settlement (hereafter dist. to human settlement). We attempted to identify the following

potential landscape predictors of RTs by measuring each within a 1 km radius of CTs

and RTs (based on Lamamy et al. 2019; Penteriani et al. 2020): (1) total paved road

length; (2) total unpaved road length; (3) total river length; (4) ruggedness (i.e., total

length of the linear development of level curves within the buffer); and (5) land use,

expressed as the percentage occupied by each land cover class within the 1 km radius.

234 We then extracted the information of the layers for each plot and calculated the area

235 occupied by each patch of habitat, which was successively converted to a percentage.

236   All spatial analyses were carried out using QGIS software. All the layers used

237 were extracted from transportation network information from CNIG

238 (http://centrodedescargas.cnig.es/). We reclassified the existing land cover classes in the

239 land use layer (IGN; Cartografía Temática Ambiental of the Principado de Asturias,

240 Hojas del Mapa de Vegetación, Litología, Roquedos y Hábitat del Oso. Escala 1:25000.

241 © Principado de Asturias, Spain) into six habitat types: (1) deciduous forests; (2)

242 conifer forests; (3) shrublands; (4) pastures; (5) rocky areas; and (6) crops.

243   *Characterization of the study footpaths.*—To analyse variability in the

244 abundance of RTs along footpaths, we estimated the following variables for each

245 footpath: 1) rub tree abundance, i.e., the kilometric abundance index of rub trees for

246 each footpath (the ratio of the total number of RTs observed along a footpath with

247 respect to the total footpath length covered at each site; hereafter, RT abundance on

248 footpaths); (2) predominant RT species (categorical variable with 6 levels: birch,

249 conifer, chestnut, oak, mixed, and other). Footpaths (length range 0.5 - 10.0 km) with at

250 least 60% of RTs belonging to the same species were classified as paths characterized

251 by that species, while footpaths without a predominant species were classified as

252 'mixed'; (3) density of bear observations (see below) in a ring buffer of 1 km around

253 each footpath where the RTs were found (hereafter, surrounding bear obs. density) as a

254 proxy for the bear density around the RTs; and (4) the ratio of the distance to the nearest

255 core cell with respect to the distance to the nearest border cell (ratio core/border). This

256 last variable was a proxy for the relative position of the footpath in the area occupied by

257 each population nucleus.

258   *Explanatory variables for RT abundance*.— We divided the area known to be

259   inhabited by the western subpopulation of brown bears in the Cantabrian Mountains

260   into cells of 3×3 km that were classified into: 1) border cells, i.e., cells with at least 3

261   years of confirmed bear presence; 2) core area cells, i.e., cells with at least 7 years of

262   confirmed bear presence; 3) core cells, i.e., cells within each core area that showed the

263   highest number of years of confirmed bear presence. Cells not included in any of these

264   categories were not considered to be inside the brown bear range and therefore were

265   discarded (Zarzo-Arias et al. 2019; Fig.1). By undergoing this process, we obtained four

266   different 'core areas' of bear distribution, i.e., cells with > 7 years of bear observations

267   (Fig. 1), whereas the border of this distribution represented our border of the bear

268   population. For each of these core areas, we selected one 'core cell', i.e., the cell with

269   the most years of bear observations for each core area (Fig. 1). We calculated the

270   distance from the central point of each footpath to: 1) the centroid of the nearest core

271   cell (i.e., distance to core cell); and 2) the centroid of the nearest border cell (i.e.,

272   distance to border cell). We undertook this procedure in QGIS.

273   Brown bear observations used to obtain the values of the variables (i.e.,

274   surrounding density of bear observations, distance to core cell, and distance to border

275   cell variables) were obtained for the period 2000 – 2017 by: (1) direct and indirect

276   observations (scats, hairs and footprints) that were georeferenced by rangers of

277   Principado de Asturias and Junta de Castilla y León, mainly by the 'Patrulla Oso' (Bear

278   Patrol), as well as by all the other rangers of both regional governments, by the Asturian

279   Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los

280   Animales Salvajes), by the Asturian Bear Foundation (FOA, Fundación Oso de

281   Asturias) and the Brown Bear Foundation (FOP, Fundación Oso Pardo); (2) remotely

282   triggered cameras that were randomly placed by the FAPAS and the Bear Patrol; and (3)

283   our own georeferenced observations (Sergiel et al. 2017; Lamamy et al. 2019;

284   Penteriani et al. 2020).

285   *Statistical analyses*

286   In analysing the effect of individual tree characteristics on the probability of brown bear

287   marking, it was necessary to account for the non-independence of rub and control trees

288   sampled at the same location. We addressed this by adopting an approach that explicitly

289   accounted for spatial autocorrelation using generalized additive models (GAMs; Hastie

290   and Tibshirani 1986). This approach fits smoothing functions to easting and northing

291   coordinates that account for non-linear spatial phenomena (i.e. spatial autocorrelation)

292   and thus for the likelihood that coordinates close together will be more similar than

293   those further apart. Given that rub and control trees have the same coordinates at a given

294   sampling location, this approach controls for non-independence of these observations,

295   as well as accounting for spatial autocorrelation at larger scales. GAMs were fitted with

296   tree type as the binomial response variable (0 = control tree; 1 = rub tree) and the

297   interaction between X and Y coordinates of trees as a smooth function (Wood 2004).

298   We used the thin plate regression spline method with $k = 20$. This level of k was chosen

299   through visual assessment of the residuals, to ensure sufficient smoothing while at the

300   same time avoiding overfitting. To maintain relatively simple models for running the

301   scenarios, and to minimise overfitting, smoothed terms were not used for the other

302   continuous explanatory environmental variables (e.g. Gili et al. 2020). The following

303   predictor variables were included in the models to be tested: tree species, tree height,

304   trunk diameter, trunk height, tree spacing, and distance to footpath. All the variables

305   were scaled, and there was no collinearity among explanatory variables (maximum

306   value of Variance Inflation Factor, VIF = 2.7).

307   Next, we investigated whether RT abundance on footpaths (the kilometric

308   abundance index) varied depending on local density of bear observations, location of

309   the footpaths with respect to bear population distribution, and the predominant tree

310   species around each footpath. Because RT abundance on footpaths was likely to vary

311   between the two main portions of the bear population (i.e. Asturias and León), we first

312   extracted the residuals of the linear model (LM) including the RT abundance on

313   footpaths as the response variable and the geographic location (two-level variable:

314   Asturias and León) as a predictor. These residuals thus included the variation derived

315   from the location of each footpath (geographic location) in the final model. Because the

316   residuals of the model did not follow a normal distribution, we carried out a logarithmic

317   transformation of RT abundance on footpaths (Gelman and Hill 2006) to achieve

318   normality. We then built LMs with these values as the response variable and the three

319   above-mentioned parameters as explanatory variables.

320   We carried out all statistical analyses with the package "lme4" (Bates et al.

321   2015) and "mgcv" (Wood 2004) for GAMs in R v.3.5.2 statistical software (R

322   Foundation for Statistical Computing 2018). To build both model classes (i.e., GAMSs

323   and LMs), we carried out the following procedure: to identify possible collinearity

324   among predictor variables, we calculated variance inflation factors (VIF; Fox et al.

325   2007) for coefficients in the full model. Influence diagnostics were used to assess the

326   presence of potential outliers and highly influential observations in our models, though

327   none were found. We used model selection to test all combinations of the predictor

328   variables (including the null model). Model selection was based on Akaike's

329   information criterion (AIC; Akaike 1973) using the library "MuMIn" (Bartoń 2013) and

330   models with a $\Delta AICc < 2$ were considered as equally competitive. We then employed

331   multi-model averaging on the models with ΔAICc < 2 to extract coefficients of each

332   explanatory variable.

333   *Ethical note*

334   This article does not contain any studies with human participants or animals carried out

335   by any of the authors. In this study, we used only observational data. For access to those

336   areas restricted to the general public, we had the authorization from the pertinent

337   environmental agencies of the regional governments of Castilla y León and the

338   Principado de Asturias.

339

340   **RESULTS**

341   *Location and characterisation of rub and control trees.*—During this study, we

342   found 101 RT and used 263 CT (Figure 1), with a range of 0 to 9 CT per RT. Only 3 of

343   the RTs (<3%) and 8 of the CTs (3%) were dead. Rubbing marks such as scratches and

344   bites were present in 81.2% and 80.2% of the RTs respectively. RTs were located at an

345   average altitude of 895 m a.s.l. and were predominantly on north-facing slopes: 31.7%

346   N ($n = 32$), 17.8% E ($n = 18$), 12.9% S ($n = 13$), 9.9% NE ($n = 10$), 9.9% NW ($n =10$),

347   7.9% W ($n = 8$), 5.0% SE ($n = 5$) and SW ($n = 5$). Birches were the most frequently

348   marked single tree type (28.7%), followed by oaks (16.3%), conifers (11.6%), and

349   chestnuts (10.1%). Birches and conifers were marked at a higher percentage than that in

350   which they appeared in the total pool of trees studied (18.6% and 7.5% respectively),

351   while the rest of tree classes were marked in a similar proportion to their abundance.

352   The results of the models testing for the effect of individual tree characteristics on the

353   probability of being marked suggested that, among the variables considered, trunk

354   DBH, mean distance to neighbouring trees, and tree species, were the most important

16

355   characters in explaining tree marking probability (Fig. 2; see also Supplementary Data

356   SD1). Indeed, the best ranked model showed this combination of explanatory variables

357   (Table 1). Specifically, RTs had larger DBHs and were in less dense parts of the forest

358   stand (i.e., they showed higher distances from the nearest trees) compared to CTs. In

359   addition, birches were the most frequently marked trees by bears among all tree classes

360   (Tables 1 and 2). The smoothed spatial term was not significant in the full model ($\chi^2_2 =$

361   2.36, $P = 0.31$), and no model including this term was in the best model set (ΔAIC

362   between the best model containing the smoothed term and the top model = 2.35),

363   suggesting limited influence of spatial effects between RTs and CTs.

364   *Characterization of the landscape around rub trees*.—The landscape

365   surrounding the RTs was covered predominantly by deciduous forest, followed by

366   scrubland and pastures, without any human settlements within a 1 km radius

367   (Supplementary Data SD2).

368   *Characterization of the study footpaths*.—To assess the kilometric abundance of

369   RTs, we included 35 footpaths. These footpaths had 0 to 11 RTs, with an average of 3.7

370   RTs per footpath ($SD = 2.6$, $n = 35$). The mean RT abundance on footpaths was 2.5

371   RTs/km ($SD = 2.1$, $n = 35$). The footpaths located in areas with a predominance of birch

372   showed on average a higher density of RTs (3.3 ± 3.5 RTs/km, $n = 9$) compared to

373   footpaths dominated by conifers (2.4 ± 1.5 RTs/km, $n = 5$), chestnut trees (1.9 ± 0.4

374   RTs/km, $n = 3$), oaks 1.9 ± 0.9 RTs/km, $n = 4$), other species (3.0 ± 3.4 RTs/km, $n = 3$),

375   and those without dominant species (mixed; 2.0 ± 0.7 RTs/km, $n = 11$). Along the

376   footpaths, we detected some notably dense clusters of RTs, particularly in some

377   footpaths located in birch forests (7 and 11 RTs in sections of 460 m and 930 m,

378   respectively). In one case, we found a cluster of RTs in a homogeneous beech forest,

379   with 7 RTs within 210 m of each other.

380   The set of models built to analyse potential factors affecting the intensity of bear

381   rubbing, measured as the number of RTs along a footpath, showed that none of the

382   variables under study played an important role. Indeed, the model with the lowest AICc

383   value was the null model (Table 3). The second ranked model showed a weak positive

384   relationship between RT abundance on footpaths and bear observation density (Table 3

385   and Fig. 3); however, the importance of this variable was very low (Tables 4).

386

387   **DISCUSSION**

388   In this study, we assessed brown bear selectivity of rub trees and the potential factors

389   associated with marking behaviour along forest paths. It seems that Cantabrian brown

390   bears select larger and more accessible trees, and that RT abundance is not determined

391   by the density of bear observations or their geographical position within the bears'

392   population range.

393   Specifically, brown bears preferentially used trees with greater trunk diameter. A

394   preference for larger diameter trees also has been reported in studies spread throughout

395   the brown bear range in North America (Green and Mattson 2003; Clapham et al.

396   2013), Russia (Puchkovskiy et al. 2012; Seryodkin 2014) and Japan (Sato et al. 2014).

397   Trees with larger diameters may stand out over the surroundings and thus be more

398   conspicuous (Green and Mattson 2003), which may also help if chemical signalling is

399   associated with visual marks such as bites and scratches (Sato et al. 2014). This

400   enhancement related to conspicuousness could be expected if the act of marking trees

401   produces scent, as occurs when the bark is altered or when the marks are produced by

402   pedal marking (Sergiel et al. 2017). Trunk height was almost significant, despite

403   appearing in the best models, which probably suggests a trend towards greater height

between the ground and the first branches in the selected trees. Greater trunk heights

(i.e., the available vertical space in which the bears can rub) have also been observed for

rub trees in North America (Green and Mattson 2003; Clapham et al. 2013) and Russia

(Seryodkin 2014), and might result in greater accessibility for signallers and facilitate

the action of rubbing (Seryodkin 2014), particularly for the largest bears. Rub trees were

predominantly located on north-facing slopes, as also reported by Seryodkin (2014).

Tattoni et al. (2015), in a study with camera traps, detected a higher cumulative camera

trapping rate in NE and S aspects, orientations that in this study represented the 3rd and

4th position. Because most of the tree species included in this study develop better in

the wetter conditions of northern slopes, e.g., beeches (Sánchez et al. 2003), chestnuts

(Blanco Andray et al. 2000), sessile oaks (Díaz-Maroto et al. 2006), and birches (García

et al. 2005), it seems plausible that the greater abundance of brown bear RTs is related

not to the exposure itself, but to the fact that on these northern slopes forest stands are

better developed and the trees grow larger than on the southern slopes.

Although our RT surveys were carried out exclusively along footpaths, we

highlight here that in most studies on bear marking, trees were predominantly located

along routes, game trails, and forest edges. Indeed, increasing distance to the footpath

represented an explanatory, negatively-related variable with the probability of rubbing

in other studies (86% in Green and Mattson 2003 and 100% in Clapham et al. 2013).

Similarly, higher intensity of usage of RTs on large trails and forestry roads have been

described in the Italian Alps, probably because they are preferred movement routes by

bears (Tattoni et al. 2015). Some authors argue that observations of rubbing hairs, bites

and scratches oriented towards roads and footpaths represent strong evidence that bears

prefer to perform chemical signalling specifically on those trees located on the sides of

footpaths and trails (Lloyd 1979; Burst and Pelton 1983; Green and Mattson 2003; Nie

429 et al. 2012), which also are routes of brown bear displacement (Burst and Pelton 1983;

430 Seryodkin 2014).

431 Even though we did not carry out an extensive census of all the tree species

432 within the marking tree stand, we established whether the RT species were similar to

433 those in their surroundings by comparing the RTs with their surrounding CTs. Thus, we

434 discovered that birch was the tree species most frequently marked by brown bears,

435 because it was found in greater proportion among marked trees than among all trees.

436 Conifers also were marked in a greater proportion to their availability. However, the

437 conifer species marked by bears in our study (Monterey pine [*Pinus radiata*] and

438 Douglas fir]*Pseudotsuga menziesii*]) do not occur naturally in the study area, and the

439 individuals included corresponded to plantations or groups of feral trees. Conifers are

440 frequently identified as preferred rub trees because of the aromas they produce when

441 they are lacerated (Puchkovskiy 2009; Nie et al. 2012; Clapham et al. 2013; Sato et al.

442 2014), which can enhance or help maintain the bear's scent and/or attract recipient

443 bears. However, our study area did not have enough locations where coniferous and

444 deciduous species co-occur to test for a potential preference for conifer rubbing by

445 Cantabrian brown bears.

446 In our study area, birch is distributed irregularly, generally in acidic and wet

447 soils or near water at forest boundaries or in cleared areas, forming continuous forests

448 only in a few areas at high elevation (García de Celis et al. 2004). Nevertheless, it was

449 proportionally the most marked tree species. For instance, in those places where several

450 birches occurred along a path, most of them were marked, sometimes every few meters.

451 Similar findings have been reported by studies conducted in boreal conifer-dominated

452 forests, where birches were found to be marked more frequently than other deciduous

453 species. For example, Puchkovskiy (2009) reported that in several forests of the Russian

454 taiga, birch was the most frequently marked deciduous tree and that when birches were

455 present, brown bears always chose it preferentially over other deciduous species. In

456 addition, Seryodkin (2014) described the appearance of brown bear marking trees in

457 Kamchatka forests dominated by the stone birch *Betula ermanii*. Preference for birch

458 species also was reported in the Middle Sikhote-Alin, SE Russia (Seryodkin et al.

459 2014), suggesting that brown bears selected birch not only for their availability, but also

460 for physiognomic characteristics that favour marking. In fact, birches tend to have a

461 large diameter with no branches on the first few metres of the trunk, and the stratified

462 bark is lacerated easily by scratches and bites. Also, the birch has a whitish outer layer

463 contrasting with a dark inner layer, so when it is removed or lacerated the marks are

464 very evident, even after healing, which may increase the conspicuousness of brown bear

465 visual markings. In addition, in the common case of a birch RT surrounded by other tree

466 species, generally characterised by darker barks (*Quercus* spp., beech, chestnut, etc.),

467 the RT itself would stand out in the surroundings, thus making its visual traceability

468 easier for bears and therefore becoming an advantageous and long-lasting substrate for

469 marking. Marking has been suggested to include visual and olfactory signalling in

470 different bear species, including brown bears (e.g., Sergiel et al. 2017), and different

471 types of marking behavior have been documented in social and solitary carnivores (e.g.,

472 Paquet 2011; Vogt et al. 2014).

473 It is worth noting that the sections dominated by birches had the highest rubbing

474 densities. RT densities in the Cantabrian Mountains are higher than those recorded by

475 Henderson et al. (2015) in conifer forests of the northwest US, where they compared RT

476 abundances between developed trails and roads (1.0 ± 1.1 RTs/km; $n = 30$) and game

477 trails (0.8 ± 1.1 RTs/km; $n = 30$). In several Kamchatka valleys dominated by stone

478 birch, Seryodkin (2014) reported very variable abundances (from 40 RTs / km to 0.4

479 RTs / km) and RTs groupings in short sections of the footpath (7 RTs in 20 m or 5 RTs

480 in 8 m). We detected similar but lower density aggregations, especially in birch-

481 dominated forests. This indicates a trend towards more intense or greater marking on

482 them, supporting the positive selectivity towards birches described above.

483 Understanding wildlife behaviour can prove useful for conservation and management

484 (e.g., Greggor et al. 2019). In the context of our study, the noticeable selection of birch

485 by marking bears might provide a tool to monitor bear presence, e.g., in areas

486 immediately surrounding the present range of the species, where targeting birches in

487 monitoring programs that search for bear signs might help detect dispersing individuals.

488   To our knowledge, this is the first time that the density of brown bear rub trees

489 has been compared with some features of the bear population or its proxies. In our

490 study, neither the density of bear observations (as a proxy for bear density), nor the

491 position of the track within the bear distribution area, affected the kilometric abundance

492 of RTs. Because the null model had the lowest AIC, we deduce that the determinants of

493 the intensity of rubbing in our population are different from those analysed in this study,

494 hence the assessment of other possible variables may be necessary. The lack of an effect

495 of the density of observations on the density of rub trees may be due to the fact that

496 differences in bear density, or more specifically of bear observations around each foot

497 path, are not large enough to affect abundance from rub trees. More research in this

498 field is needed to elucidate whether variations in bear density can affect rubbing

499 behaviour in other ways, such as modifications in the frequency of rubbing or the

500 proportion of rubbing between sex and age classes, as Lamb et al. suggested (2017). In

501 one study considering the distribution of rubbing sites in a territorial carnivore, the tiger

502 (*Panthera tigris*), rubbing increased towards the limits of the territory (Smith et al.

503 1989). This might not be applicable to brown bears that are non-territorial species in

504 which individuals of the same population can have overlapping home ranges (Seryodkin

505 et al. 2017, Frank et al. 2018).

506   There are three potential biases in this study. First, searches for RTs were

507 undertaken mostly (but not exclusively) from footpaths. The findings that RTs were

508 closer to, and orientated towards, footpaths may thus have been the result of greater

509 detectability from those paths. However, we do not believe this to have affected our

510 results given the large amount of evidence that footpaths are common routes of brown

511 bear displacement and that RTs occur more frequently along such routes (e.g., Nie et al.

512 2012; Seryodkin 2014; see above). Second, the lighter coloured bark of birch trees may

513 have made them more conspicuous to observers. We believe this potential bias was

514 minimised by very careful observations of all potential RTs. Furthermore, preference

515 for birch has been found in several other studies (see above). Third, we used proxy

516 measures to estimate bear density and distribution. We cannot know whether our

517 measures are fully accurate representations of the population but nevertheless, our

518 measures were the best available, being based largely on observations made by trained

519 forest rangers and researchers. While we believe the above potential biases were

520 minimised in our study, their effects only can be properly elucidated through further

521 research based on intensive telemetry studies.

522   To conclude, our results suggest that Cantabrian brown bears select rub trees

523 based on characteristics related to the tree, rather than their position relative to areas

524 with a high density of conspecifics and/or with the distribution of individuals within the

525 population range. Thus, even in small and isolated bear populations, such as the one

526 under study here, some aspects of rubbing behaviour such as tree selection and marking

527 effort may not be affected by population size and/or structure.

545

SUPPLEMENTARY DATA

547 **Supplementary Data SD1**. — Mean value, standard deviation (SD) and minimum (Min)

548 and maximum (Max) values of each of the parameters used to characterise both rub and

549 control trees.

550 **Supplementary Data SD2**. — Mean value, standard deviation (SD) and range of

551 landscape features surrounding rub trees, including the- percent of the different land cover

552 within a 1km buffer around each rub tree.

553

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FIGURE LEGENDS

781 **Fig. 1**.—Locations of the RTs included in the study and the range of the western

782 subpopulation of Cantabrian brown bear, divided into cells of different observation

783 frequency. Inset shows location of mapped area within the geographic confines of

784 Spain. Locations of the 101 brown bear rub trees located in the Cantabrian Mountains

785 (NW Spain; provinces of Asturias and León) are represented with purple dots. Due to

786 the short distance that separates rub trees in some cases, several trees can be under the

787 same spot. The range of the western subpopulation of Cantabrian brown bear was

788 calculated as 3x3 km cells with at least three continuous years of bear observations

789 (since 2000; Lamamy et al. 2019). The cells with only three continuous years of bear

790 observations are in blue and were considered as the 'border cells'. The core areas, i.e.,

791 areas with at least seven years of bear presence, are in orange. Within the core areas, we

792 calculated the 'core cells' (in red), i.e., cells within each of the core areas that showed

793 the highest number of continuous years of bear presence.

794

795 **Fig. 2**.—Characteristics of parameters used to describe rub trees (RT) used by brown

796 bears ($n = 101$ RT; dark grey) and control trees (CT; $n = 363$; light grey) in the

797 Cantabrian Mountains of NW Spain.

798

799 **Fig. 3**.— Changes of the logarithm of the RT abundance on footpaths of brown bear rub

800 trees (LogIKA) along footpaths in the Cantabrian Mountains with respect to a proxy of

801 brown bear density (left panel) and the position of the trail (right panel) within the bear

802 population's range (see also Fig. 2). Details on the proxy of bear density and the ratio

803 core/border distance are provided in the main text.

804 **TABLES**

805 **Table 1.**—Competing models from GAMs built to investigate individual tree

806 characteristics ($n = 364$ trees) determining marking probability in the Cantabrian brown

807 bear population. Competitive models are ranked from the lowest (best model) to the

808 highest AICc value. Only models with ΔAICc < 2 are shown. Binomial response

809 variable: tree type (0 = control tree (CT) and 1 = marked tree (RT)). R-squared of the

810 most parsimonious model is 0.26. Note that a smoothed spatial coordinate term was

811 included in the full model, but it was not selected in any of the top models.

812

Dependent variable	Competing models	df	AICc	ΔAICc	Weight
Tree type (CT/RT)	**Trunk diameter + tree spacing + trunk height + tree species**	8	368.58	0.00	0.23
	Trunk diameter + tree spacing + tree height + trunk height + tree species	9	368.91	0.32	0.20
	Trunk diameter + tree spacing + tree species	7	369.30	0.72	0.16
	dist. to footpath + trunk diameter + tree spacing + tree height + trunk height + tree species	10	369.36	0.78	0.16
	dist. to footpath + trunk diameter + tree spacing + trunk height + tree species	9	369.46	0.88	0.15
	Distance to nearest footpath + trunk diameter + tree spacing + tree species	8	370.18	1.60	0.10

813

814 **Table 2.**—Effects of individual tree characteristics ($n = 364$ trees) on the probability

815 that a given tree was a bear rubbing tree in the Cantabrian Mountains. For each

816 explanatory variable, we report the estimate (β), standard error (SE), significance (p),

817 confidence intervals (CI) and relative importance values (RIV) obtained from model

818 averaging on the models with ΔAICc < 2. Binomial response variable: tree type (0 =

819 control tree (CT) and 1 = marked tree (RT)). Baseline level for the categorical variable

820 tree species is "other". The most important parameters are highlighted in bold.

821

Dependent variable	Explanatory variable	Model-averaged coefficients and relative importance values				
		β	SE	p	CI	RIV
Tree type (CT/RT)	Intercept	-1.088	0.230	2.40e-06	(-1.539; -0.637)	-
	Trunk diameter	**0.917**	**0.226**	**5.14e-05**	**(0.474; 1.360)**	**1.00**
	Tree spacing	**0.698**	**0.143**	**1.10e-06**	**(0.419; 0.979)**	**1.00**
	Trunk height	**0.275**	**0.152**	**0.072**	**(-0.023; 0.573)**	**0.73**
	Birch	**0.834**	**0.385**	**0.031**	**(0.079; 1.589)**	**1.00**
	Chestnut	-0.363	0.447	0.418	(-1.239; 0.513)	1.00
	Conifer	0.055	0.602	0.928	(-1.125; 1.235)	1.00
	Oak	-0.558	0.383	0.146	(-1.309; 0.193)	1.00
	Tree height	-0.301	0.217	0.168	(-0.726; 0.124)	0.35
	Dist. to footpath	-0.181	0.167	0.279	(-0.508; 0.093)	0.41

822

823   **Table 3.**—Competing models built to investigate the effect of ecological characteristics

824   of the surroundings of the study footpaths ($n = 35$) on the abundance of brown bear rub

825   trees. Competitive linear models are ranked from the lowest (best model) to the highest

826   AICc value. Only models with ΔAICc < 2 are shown. R-squared of the model including

827   bear obs. density = 0.062.

828

Dependent variable	Competing models	df	AICc	ΔAICc	Weight
RT abundance on footpath residuals	Null model	2	66.50	0.00	0.52
	Surrounding bear obs. density	3	66.66	0.16	0.48

829

830   **Table 4.**—Effects of ecological characteristics of the surroundings of the footpaths ($n =$

831   35) located in the Cantabrian Mountains on the abundance of brown bear rub trees. For

832   each explanatory variable, we report the estimate (β), standard error (SE), significance

833   (p), confidence intervals (CI), and relative importance values (RIV) obtained from model

834   averaging on the models with ΔAICc < 2.

835

Dependent variable	Explanatory variable	Model-averaged coefficients and relative importance values				
		β	SE	p	CI	RIV
RT abundance on footpath residuals	Intercept	3.354e-18	9.998e-02	1.000	(-0.196; 0.196)	-
	Bear obs. density	1.485e-01	1.005e-01	0.155	(-0.048; 0.345)	0.48

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838