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

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Scent-mediated communication is considered the principal communication channel in many mammal species. Compared with visual and vocal communication, odors persist for a longer time, enabling individuals to interact without being in the same place at the same time. The brown bear (*Ursus arctos*), like other mammals, carries out chemical communication, for example, by means of scents deposited on marking (or rub) trees. In this study, we assessed rub tree selectivity of the brown bear in the predominantly deciduous forests of the Cantabrian Mountains (NW Spain). We first compared the characteristics of 101 brown bear rub trees with 263 control trees. We then analyzed the potential factors affecting the density of rub trees along 35 survey routes along footpaths. We hypothesized that: (1) bears would select particular trees, or tree species, with characteristics that make them more conspicuous; and (2) that bears would select trees located in areas with the highest presence of conspecifics, depending on the population density or the position of the trees within the species' range. We used linear models and generalized additive models to test these hypotheses. Our results showed that brown bears generally selected more conspicuous trees with a preference for birches (*Betula* spp.). This choice may facilitate the marking and/or detection of chemical signals and, therefore, the effectiveness of intraspecific communication. Conversely, the abundance of rub trees along footpaths did not seem to depend on the density of bear observations or their relative position within the population center or its border. Our results suggest that Cantabrian brown bears select trees based on their individual characteristics and their location, with no influence of characteristics of the bear population itself. Our findings can be used to locate target trees that could help in population monitoring.

Key words: chemical communication, rub trees, rubbing behavior, tree selectivity, *Ursus arctos*

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 de la población osera. Nuestros hallazgos pueden servir para localizar árboles específicos que podrían ayudar al monitoreo de la población.

Palabras clave: árboles de marcaje, comportamiento de marcaje, comunicación química, selección de árboles, *Ursus arctos*

Chemical signals that are spread by distinct means, such as urine, feces, or glandular secretions (Müller-Schwarze 2006; Johnston and del Barco-Trillo 2009), are considered the principal channel of communication in many mammal species (Ralls 1971), more so than visual or acoustic signals (Müller-Schwarze 2006; Penteriani and Delgado 2017). Mammalian scent-marking strategies mostly depend on individual and social factors, as well as on the physical characteristics of the environment (Barja and De Miguel 2010). Scent-mediated communication has several advantages, including persistence for long periods, and facilitation of interactions among individuals without any need for direct interaction at a given site (Mills et al. 1980).

Chemical communication can have different functions that include: self-advertising, i.e., communication of the state or characteristics of the individual, such as age, sex, reproductive status, and health condition; conspecific localization; communication of dominance; and the defense of a resource (Brown 1979; Doty 1986; Gosling 1990; Johnston 2008; Morales-González et al. 2019). Sometimes, this form of indirect interaction also can prevent agonistic encounters (Gosling and McKay 1990; Roberts and Gosling 2001). While scent-marking plays an important role when defending or signaling territory occupancy in territorial species (Roberts and Gosling 2001; Müller and Manser 2008; Barja and De Miguel 2010), scent-marking in nonterritorial species is more difficult to interpret (Clapham et al. 2012). Solitary species must maintain effective communication to sustain a social structure that facilitates reproduction (Clapperton 1989; Gosling and Roberts 2001), for example, by communicating male fitness (White et al. 2002) or the reproductive status of females (Gorman and Trowbridge 1989; Rich and Hurst 1998; Barja and De Miguel 2010). In particular, large-bodied solitary carnivorous species with large home ranges base much of their communication on olfactory chemical signals (Macdonald 1980; Gorman and Trowbridge 1989; Lamb et al. 2017), which usually are left on conspicuous and permanent substrates such as rocks and tree trunks (Kleiman 1966; Barja 2009; Allen et al. 2017). Thus, intensive marking behavior on those substrates increases detectability and information transmission, reducing the investment of resources in communication (Alberts 1992; Gosling and Roberts 2001).

As in other solitary and nonterritorial carnivores (Smith et al. 1989; Barja 2009), bears perform scent-marking on different substrates (Filipczyková et al. 2016). Indeed, rubbing behavior has been documented in most ursid species, i.e., American black bear *Ursus americanus* (Burst and Pelton 1983; Sawaya et al. 2012) and Asiatic black bear *Ursus thibetanus* (Bromley 1965), giant panda *Ailuropoda melanoleuca* (White et al. 2002; Swaisgood et al. 2004; Nie et al. 2012), sloth bear *Melursus ursinus* (Laurie and Seidensticker 1977), Andean bear *Tremarctos ornatus* (Filipczyková et al. 2016; Kleiner et al. 2018), and brown bear *Ursus arctos* (Krott 1962; Shaffer 1971).

Brown bears exhibit a set of marking behaviors, including: urination; biting, scratching, and stripping bark; rubbing the back, shoulders, and head (Green and Mattson 2003; Puchkovskiy 2009; Clapham et al. 2012); and pedal and scent-marking at the base of trees and the surrounding area (Clapham et al. 2012; Sergiel et al. 2017). Marking, or rub trees (hereafter, RTs) have a key function in intraspecific 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 behavior (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, Clapham et al. 2013; Tattoni et al. 2015). This effect has been suggested to be enhanced by producing wounds to the tree that increase resin flow (Sato et al. 2014).

Studies on RTs have focused mainly on North American grizzlies *Ursus arctos horribilis* (Green and Mattson 2003; Clapham et al. 2013; Morgan Henderson et al. 2015), with a few also in Russia (Puchkovskiy 2009; Puchkovskiy et al. 2012) and Japan (Sato et al. 2014); however, these studies considered large continuous populations. To our knowledge, such a study has not previously been carried out in smaller, vulnerable populations, nor in populations living in areas dominated by deciduous forest. Here, by using (a) 101 RTs found in the Cantabrian Mountains (northwestern Spain) and (b) the density of RTs along 35 survey routes along footpaths, we carried out a multilevel analysis to elucidate whether brown bears' RT selection is determined by tree species, physical traits, landscape position, and whether RT occurrence was related to their spatial location and observed bear density. Two main hypotheses underlie this study. First, as previously reported in populations inhabiting coniferous forests, RTs have characteristics that distinguish them from surrounding trees (e.g., dendrometric characteristics, tree location), which probably enhance the conspicuousness of chemical signaling and/or represent a better substrate for marking. We thus hypothesized that bears would select specific trees, or tree species with characteristics that make them more conspicuous. Second, we hypothesized that RTs would be more abundant in areas with the highest presence of conspecifics, toward the core of the bear distribution area and in areas where the density of bears is higher.

This study was carried out in a small and isolated, but still autochthonous, brown bear population, at the southwestern limit of the current species distribution. An overarching goal of the study therefore was to obtain information on scent-marking in small populations, whose behavior may differ from larger and less isolated populations, because the smaller population size is likely to mean a higher number of interactions between the same individuals. The results provide insights into the ecology of a threatened population and therefore contribute to conservation and monitoring actions.

Methods

Study area.—The study area covers most of the geographic range of the western subpopulation of brown bears in the Cantabrian Mountains (northwestern Spain; Fig. 1), which run parallel to the coast (E–W) for 300 km, with an average and maximum altitude of 1,100 and 2,648 m a.s.l., respectively (Martínez Cano et al. 2016; Penteriani et al. 2019). The region has an oceanic climate, more humid and temperate on northern slopes and continental and dryer on southern slopes (Ortega and Morales 2015). The landscape is covered predominantly by forests, shrubs, and croplands (Mateo-Sánchez et al. 2016). Forests of semi-deciduous and evergreen oaks (*Quercus* sp.) dominate sunny slopes, whereas the north-facing slopes are covered by deciduous trees such as beech (*Fagus sylvatica*) and common (*Q. robur*) and sessile oak (*Q. petraea*). Birches (*Betula* sp.) occupy areas of acid soils, dominant toward the west of the study area, in well-illuminated areas with sufficient humidity and frequently colonizing degraded or bare areas, with few monospecific stands (García de Celis et al. 2004). Nonforested areas are mainly occupied by shrub species, such as heather (*Erica* sp., *Calluna* sp.) and brooms (*Cytisus* sp.— Fernández-Gil et al. 2006; Mateo-Sánchez et al. 2016). Above the treeline, berry-producing shrubs occur, including bilberries (*Vaccinium myrtillus*—Pato and Obeso 2012; Martínez Cano et al. 2016). Most of the areas inhabited by bears are surrounded by urbanized and cultivated areas, with a high density of transport infrastructure; the main economic activities include livestock breeding, mining, timber harvesting, and recreational activities (Zarzo-Arias et al. 2018, 2019).

Description of the population.—In northern Spain, there are two brown bear populations that are isolated from other European populations, one in the Pyrenees and another in the Cantabrian Mountains, separated from each other by almost 300 km. The latter population is divided into two subpopulations, with little gene flow (Pérez et al. 2010; Gonzalez et al. 2016) and a genetic variability that is among the lowest of any brown bear population in the world (García-Garitagoitia et al. 2007). In the 1990s, the Cantabrian population consisted of a minimum of 70–85 bears (50–65 individuals in the western nucleus and 14–20 in the eastern—Clevenger and Purroy 1991; Naves and Palomero 1993; Pérez et al. 2014). Recent population trends seem positive, especially in the western subpopulation (Pérez et al. [2014] reported 168–260 bears in the western subpopulation and 12–40 in the eastern subpopulation), but this species is still considered as "Endangered" in Spain (BOE 2011).

Multilevel Analysis

Location and characterization of rub and control trees.—We surveyed principal trails and forest roads (hereafter footpaths) within the study area for RTs from October 2018 to March 2019 (Fig. 1). We looked for trees with rubbing signs such as
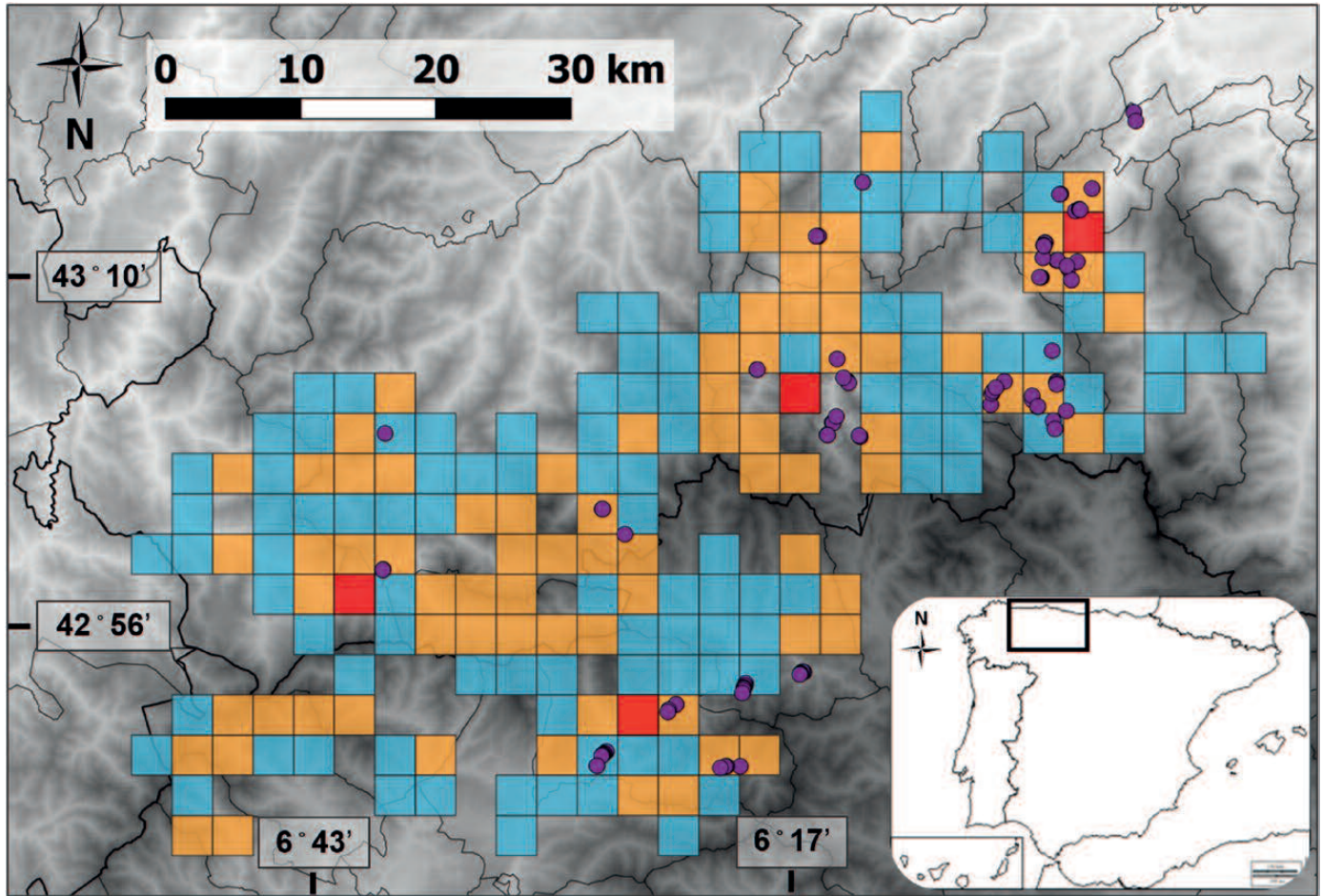
Fig. 1.—Locations of the rub trees (RTs) included in the study and the range of the western subpopulation of Cantabrian brown bear, divided into cells of different observation frequency. Inset shows location of mapped area within the geographic confines of Spain. Locations of the 101 brown bear RTs located in the Cantabrian Mountains (NW Spain; provinces of Asturias and León) are represented with purple dots. Due to the short distance that separates RTs in some cases, several trees can comprise a single spot. The range of the western subpopulation of Cantabrian brown bear was calculated as 3 × 3 km cells with at least three continuous years of bear observations (since 2000—Lamamy et al. 2019). The cells with only three continuous years of bear observations are in blue and were considered as the "border cells." The core areas, i.e., areas with at least 7 years of bear presence, are in orange. Within the core areas, we calculated the "core cells" (in red), i.e., cells within each of the core areas that showed the highest number of continuous years of bear presence.

smoothed bark, discolored surface, scratches, bites, or lack of vegetation at the base; however, the tree was only considered an RT when the presence of bear fur snagged on the bark was confirmed (a characteristic sign of bear tree rubbing behavior). All the trees located within a radius of 5 m around each marked tree (following Clapham et al. 2013) were considered control trees (hereafter, CTs). None of the CTs were found to have any evidence of marking. This radius ensured that we sampled trees that showed the same local habitat characteristics as the RT, and that were clearly available to the bear in that location. We followed previous studies on brown bear tree rubbing behavior (Green and Mattson 2003; Clapham et al. 2013; Sato et al. 2014), to characterize 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 RTs.—To explore the landscape characteristics of the areas in which the RTs were found, both in terms of natural and human features of RTs, we calculated the following variables for each RT: 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. We then extracted the information of the layers for each plot and calculated the area occupied by each patch of habitat, which was successively converted to a percentage.

All spatial analyses were carried out using QGIS software. All the layers used were extracted from transportation network information from CNIG (http://centrodedescargas.cnig.es/). We reclassified the existing land cover classes in the land use layer (IGN; Cartografía Temática Ambiental of the Principado de Asturias, Hojas del Mapa de Vegetación, Litología, Roquedos y Hábitat del Oso. Escala 1:25000. © Principado de Asturias, Spain) into six habitat types: (1) deciduous forests; (2) coniferous forests; (3) shrublands; (4) pastures; (5) rocky areas; and (6) crops.

Characterization of the study footpaths.—To analyze variability in the abundance of RTs along footpaths, we estimated the following variables for each footpath: (1) RT abundance, i.e., the kilometric abundance index of RTs for each footpath (the ratio of the total number of RTs observed along a footpath with respect to the total footpath length covered at each site; hereafter, RT abundance on footpaths); (2) predominant RT species (categorical variable with six levels: birch, conifer, chestnut, oak, mixed, and other). Footpaths (length range 0.5–10.0 km) with at least 60% of RTs belonging to the same species were classified as paths characterized by that species, while footpaths without a predominant species were classified as "mixed"; (3) density of bear observations (see below) in a ring buffer of 1 km around each footpath where the RTs were found (hereafter, surrounding bear obs. density) as a proxy for the bear density around the RTs; and (4) the ratio of the distance to the nearest core cell with respect to the distance to the nearest border cell (ratio core/border). This last variable was a proxy for the relative position of the footpath in the area occupied by each population nucleus.

Explanatory variables for RT abundance.—We divided the area known to be inhabited by the western subpopulation of brown bears in the Cantabrian Mountains into cells of 3 × 3 km that were classified into: (1) border cells, i.e., cells with at least 3 years of confirmed bear presence; (2) core area cells, i.e., cells with at least 7 years of confirmed bear presence; (3) core cells, i.e., cells within each core area that showed the highest number of years of confirmed bear presence. Cells not included in any of these categories were not considered to be inside the brown bear range and therefore were discarded (Zarzo-Arias et al. 2019; Fig. 1). By undergoing this process, we obtained four different "core areas" of bear distribution, i.e., cells with > 7 years of bear observations (Fig. 1), whereas the border of this distribution represented our border of the bear population. For each of these core areas, we selected one "core cell," i.e., the cell with the most years of bear observations for each core area (Fig. 1). We calculated the distance from the central point of each footpath to: (1) the centroid of the nearest core cell (i.e., distance to core cell); and (2) the centroid of the nearest border cell (i.e., distance to border cell). We undertook this procedure in QGIS.

Brown bear observations used to obtain the values of the variables (i.e., surrounding density of bear observations, distance to core cell, and distance to border cell variables) were obtained for the period 2000–2017 by: (1) direct and indirect observations (scats, hairs, and footprints) that were georeferenced by rangers of the Principado de Asturias and the Junta de Castilla y León, mainly by the "Patrulla Oso" (Bear Patrol), as well as by all the other rangers of both regional governments, by the Asturian Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los Animales Salvajes), by the Asturian Bear Foundation (FOA, Fundación Oso de Asturias) and the Brown Bear Foundation (FOP, Fundación Oso Pardo); (2) remotely triggered cameras that were randomly placed by the FAPAS and the Bear Patrol; and (3) our own georeferenced observations (Sergiel et al. 2017; Lamamy et al. 2019; Penteriani et al. 2020).

Statistical Analyses

In analyzing the effect of individual tree characteristics on the probability of brown bear marking, it was necessary to account for the nonindependence of rub and control trees sampled at the same location. We addressed this by adopting an approach that explicitly accounted for spatial autocorrelation using generalized additive models (GAMs—Hastie and Tibshirani 1986). This approach fits smoothing functions to easting and northing coordinates that account for nonlinear spatial phenomena (i.e., spatial autocorrelation) and thus for the likelihood that coordinates close together will be more similar than those further apart. Given that rub and control trees have the same coordinates at a given sampling location, this approach controls for nonindependence of these observations, as well as accounting for spatial autocorrelation at larger scales. GAMs were fitted with tree type as the binomial response variable (0 = CT; 1 = RT) and the interaction between X and Y coordinates of trees as a smooth function (Wood 2004). We used the thin plate regression spline method with $k = 20$. This level of k was chosen through visual assessment of the residuals, to ensure sufficient smoothing while at the same time avoiding overfitting. To maintain relatively simple models for running the scenarios, and to minimize overfitting, smoothed terms were not used for the other continuous explanatory environmental variables (e.g., Gili et al. 2020). The following predictor variables were included in the models to be tested: tree species, tree height, trunk diameter, trunk height, tree spacing, and distance to footpath. All the variables were scaled, and there was no collinearity among explanatory variables (maximum value of variance inflation factor, VIF = 2.7).

Next, we investigated whether RT abundance on footpaths (the kilometric abundance index) varied depending on local density of bear observations, location of the footpaths with respect to bear population distribution, and the predominant tree species around each footpath. Because RT abundance on footpaths was likely to vary between the two main portions of the bear population (i.e., Asturias and León), we first extracted the residuals of the linear model (LM) including the RT abundance on footpaths as the response variable and the geographic location (two-level variable: Asturias and León) as a predictor. These residuals thus included the variation derived from the location of each footpath (geographic location) in the final model. Because the residuals of the model did not follow a normal distribution, we carried out a logarithmic transformation of RT abundance on footpaths (Gelman and Hill 2006) to achieve normality. We then built LMs with these values as the response variable and the three abovementioned parameters as explanatory variables.

We carried out all statistical analyses with the package "lme4" (Bates et al. 2015) and "mgcv" (Wood 2004) for GAMs in R v.3.5.2 statistical software (R Foundation for Statistical Computing 2018). To build both model classes (i.e., GAMs and LMs), we carried out the following procedure: to identify possible collinearity among predictor variables, we calculated VIFs (Fox 2007) for coefficients in the full model. Influence diagnostics were used to assess the presence of potential outliers and highly influential observations in our models, though none were found. We used model selection to test all combinations of the predictor variables (including the null model). Model selection was based on Akaike's information criterion (AIC—Akaike 1973) using R library "MuMIn" (Bartoń 2013) and models with a ΔAICc < 2 were considered as equally competitive. We then employed multimodel averaging on the models with ΔAICc < 2 to extract coefficients of each explanatory variable.

Ethical Note

This article does not contain any studies with human participants or animals carried out by any of the authors. In this study, we used only observational data. For access to those areas restricted to the general public, we had the authorization from the pertinent environmental agencies of the regional governments of Castilla y León and the Principado de Asturias.

RESULTS

Location and characterization of rub and control trees.—During this study, we found 101 RTs and used 263 CTs (Fig. 1), with a range of 0–9 CTs per RT. Only three of the RTs (< 3%) and eight of the CTs (3%) were dead. Rubbing marks such as scratches and bites were present in 81.2% and 80.2% of the RTs, respectively. RTs were located at an average altitude of 895 m a.s.l. and were predominantly on north-facing slopes: 31.7% N ($n = 32$), 17.8% E ($n = 18$), 12.9% S ($n = 13$), 9.9% NE ($n = 10$), 9.9% NW ($n = 10$), 7.9% W ($n = 8$), 5.0% SE ($n = 5$), and SW ($n = 5$). Birches were the most frequently marked single tree type (28.7%), followed by oaks (16.3%), conifers (11.6%),

and chestnuts (10.1%). Birches and conifers were marked at a higher percentage than that in which they appeared in the total pool of trees studied (18.6% and 7.5%, respectively), while the rest of tree classes were marked in a similar proportion to their abundance. The results of the models testing for the effect of individual tree characteristics on the probability of being marked suggested that, among the variables considered, trunk DBH, mean distance to neighboring trees, and tree species were the most important characters in explaining tree marking probability (Fig. 2; see also Supplementary Data SD1). Indeed, the best-ranked model showed this combination of explanatory variables (Table 1). Specifically, RTs had larger DBHs and were in less dense parts of the forest stand (i.e., they showed higher distances from the nearest trees) compared to CTs. In addition, birches were the most frequently marked trees by bears among all tree classes (Tables 1 and 2). The smoothed spatial term was not significant in the full model ($\chi^2_2 = 2.36$, $P = 0.31$), and no model including this term was in the best model set (ΔAIC between the best model containing the smoothed term and the top model = 2.35), suggesting limited influence of spatial effects between RTs and CTs.

Characterization of the landscape around RTs.—The landscape surrounding the RTs was covered predominantly by deciduous forest, followed by scrubland and pastures, without any human settlements within a 1-km radius (Supplementary Data SD2).

Characterization of the study footpaths.—To assess the kilometric abundance of RTs, we included 35 footpaths. These footpaths had 0 to 11 RTs, with an average of 3.7 RTs per footpath ($SD = 2.6$, $n = 35$). The mean RT abundance on footpaths was 2.5 RTs/km ($SD = 2.1$, $n = 35$). The footpaths located in areas with a predominance of birch showed on average a higher density of RTs (3.3 ± 3.5 RTs/km, $n = 9$) compared to footpaths dominated by conifers (2.4 ± 1.5 RTs/km, $n = 5$), chestnut trees (1.9 ± 0.4 RTs/km, $n = 3$), oaks 1.9 ± 0.9 RTs/km, $n = 4$), other species (3.0 ± 3.4 RTs/km, $n = 3$), and those without dominant species (mixed; 2.0 ± 0.7 RTs/km, $n = 11$). Along the footpaths, we detected some notably dense clusters of RTs, particularly in some footpaths located in birch forests (7 and 11 RTs in sections of 460 m and 930 m, respectively). In one case, we found a cluster of RTs in a homogeneous beech forest, with 7 RTs within 210 m of each other.

The set of models built to analyze potential factors affecting the intensity of bear rubbing, measured as the number of RTs along a footpath, showed that none of the variables under study played an important role. Indeed, the model with the lowest AICc value was the null model (Table 3). The second-ranked model showed a weak positive relationship between RT abundance on footpaths and bear observation density (Table 3; Fig. 3); however, the importance of this variable was very low (Table 4).

DISCUSSION

In this study, we assessed brown bear selectivity of RTs and the potential factors associated with marking behavior along forest paths. It would appear that Cantabrian brown bears
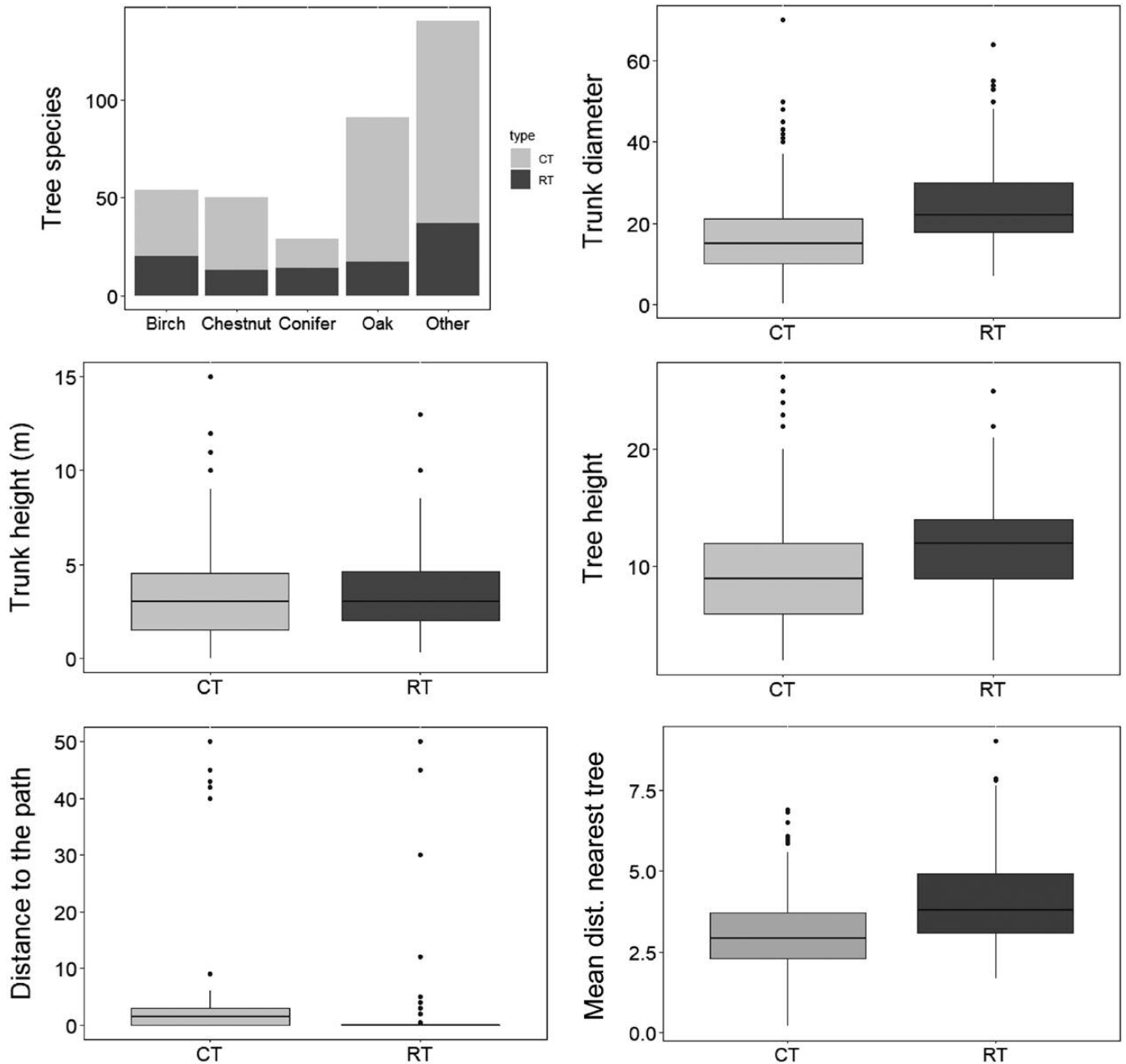
Fig. 2.—Characteristics of parameters used to describe rub trees (RTs) used by brown bears (n = 101 RTs; dark gray) and control trees (CTs; n = 363; light gray) in the Cantabrian Mountains of NW Spain.

Table 1.—Competing models from generalized additive models (GAMs) built to investigate individual tree characteristics (n = 364 trees) determining marking probability in the Cantabrian brown bear population. Competitive models are ranked from the lowest (best model) to the highest AICc value. Only models with ΔAICc < 2 are shown. Binomial response variable: tree type (0 = control tree [CT] and 1 = marked tree [RT]). R-squared of the most parsimonious model is 0.26. Note that a smoothed spatial coordinate term was included in the full model, but it was not selected in any of the top models.

Dependent variable	Competing models	d.f.	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
	Distance to footpath + trunk diameter + tree spacing + tree height + trunk height + tree species	10	369.36	0.78	0.16
	Distance 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

Table 2.—Effects of individual tree characteristics (*n* = 364 trees) on the probability that a given tree was a bear rubbing tree in the Cantabrian Mountains. For each explanatory variable, we report the estimate (β), standard error (*SE*), significance (*P*), confidence intervals (*CI*s), and relative importance values (RIV) obtained from model averaging on the models with ΔAICc < 2. Binomial response variable: tree type (0 = control tree [CT] and 1 = marked tree [RT]). Baseline level for the categorical variable tree species is "other." The most important parameters are highlighted in bold.

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
	Distance to footpath	−0.181	0.167	0.279	(−0.508; 0.093)	0.41

Table 3.—Competing models built to investigate the effect of ecological characteristics of the surroundings of the study footpaths (*n* = 35) on the abundance of brown bear rub trees (RTs). Competitive linear models are ranked from the lowest (best model) to the highest AICc value. Only models with ΔAICc < 2 are shown. *R*-squared of the model including bear obs. density = 0.062.

Dependent variable	Competing models	*d.f.*	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

select larger and more accessible trees, and that RT abundance is not determined by the density of bear observations or their geographical position within the bears' population range.

In particular, brown bears preferentially used trees with greater trunk diameter. A preference for larger diameter trees also has been reported in studies spread throughout the brown bear range in North America (Green and Mattson 2003; Clapham et al. 2013), Russia (Puchkovskiy et al. 2012; Seryodkin 2014), and Japan (Sato et al. 2014). Trees with larger diameters may stand out over the surroundings and thus be more conspicuous (Green and Mattson 2003), which also may help if chemical signaling is associated with visual marks such as bites and scratches (Sato et al. 2014). This enhancement related to conspicuousness could be expected if the act of marking trees produces scent, as occurs when the bark is altered or when the marks are produced by pedal marking (Sergiel et al. 2017). Trunk height was almost significant, despite appearing in the best models, which probably suggests a trend toward 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) also have been observed for RTs in North America (Green and Mattson 2003; Clapham et al. 2013) and Russia (Seryodkin 2014), and might result in greater accessibility for signalers and facilitate the action of rubbing (Seryodkin 2014), particularly for the largest bears. RTs 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 third and fourth 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 toward roads and footpaths represent strong evidence that bears prefer to perform chemical signaling specifically on those trees located on the sides of footpaths and trails (Lloyd 1979; Burst and Pelton 1983; Green and Mattson 2003; Nie et al. 2012), which also are routes of brown bear displacement (Burst and Pelton 1983; Seryodkin 2014).

Even though we did not carry out an extensive census of all the tree species within the marking tree stand, we established whether the RT species were similar to those in their surroundings by comparing the RTs with their surrounding CTs. Thus, we discovered that birch was the tree species most frequently marked by brown bears, because it was found in
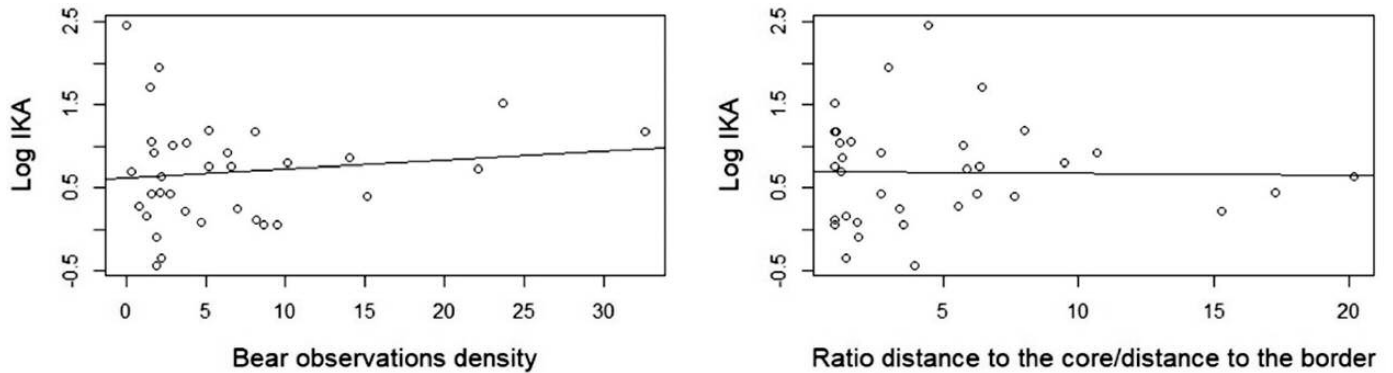
Fig. 3.—Changes of the logarithm of the rub tree (RT) abundance on footpaths of brown bear RTs (Log IKA) along footpaths in the Cantabrian Mountains with respect to a proxy of brown bear density (left panel) and the position of the trail (right panel) within the bear population's range (see also Fig. 2). Details on the proxy of bear density and the ratio core/border distance are provided in the main text.

Table 4.—Effects of ecological characteristics of the surroundings of the footpaths ($n = 35$) located in the Cantabrian Mountains on the abundance of brown bear rub trees (RTs). For each explanatory variable, we report the estimate (β), standard error (*SE*), significance (*P*), confidence intervals (*CI*), and relative importance values (RIV) obtained from model averaging on the models with ΔAICc < 2.

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

greater proportion among marked trees than among all trees. Conifers also were marked in a greater proportion to their availability. However, the conifer species marked by bears in our study (Monterey pine [*Pinus radiata*] and Douglas-fir [*P. menziesii*]) do not occur naturally in the study area, and the individuals included corresponded to plantations or groups of feral trees. Conifers are frequently identified as preferred RTs because of the aromas they produce when they are lacerated (Puchkovskiy 2009; Nie et al. 2012; Clapham et al. 2013; Sato et al. 2014), which can enhance or help maintain the bear's scent and/or attract recipient bears. However, our study area did not have enough locations where coniferous and deciduous species co-occur to test for a potential preference for conifer rubbing by Cantabrian brown bears.

In our study area, birch is distributed irregularly, generally in acidic and wet soils or near water at forest boundaries or in cleared areas, forming continuous forests only in a few areas at high elevation (García de Celis et al. 2004). Nevertheless, it was proportionally the most marked tree species. For instance, in those places where several birches occurred along a path, most of them were marked, sometimes every few meters. Similar findings have been reported by studies carried out in boreal conifer-dominated forests, where birches were found to be marked more frequently than other deciduous species. For example, Puchkovskiy (2009) reported that in several forests of the Russian taiga, birch was the most frequently marked deciduous tree and that when birches were present, brown bears always chose it preferentially over other deciduous species. In addition, Seryodkin (2014) described the appearance of brown bear marking trees in Kamchatka forests dominated by the stone birch *Betula ermanii*. Preference for birch species also was reported in the Middle Sikhote-Alin, SE Russia (Seryodkin et al. 2014), suggesting that brown bears selected birch not only for their availability, but also for physiognomic characteristics that favor marking. In fact, birches tend to have a large diameter with no branches on the first few meters of the trunk, and the stratified bark is lacerated easily by scratches and bites. Also, the birch has a whitish outer layer contrasting with a dark inner layer, so when it is removed or lacerated the marks are very evident, even after healing, which may increase the conspicuousness of brown bear visual markings. In addition, in the common case of a birch RT surrounded by other tree species, generally characterized by darker barks (*Quercus* spp., beech, chestnut, etc.), the RT itself would stand out in the surroundings, thus making its visual traceability easier for bears and therefore becoming an advantageous and long-lasting substrate for marking. Marking has been suggested to include visual and olfactory signaling in different bear species, including brown bears (e.g., Sergiel et al. 2017), and different types of marking behavior have been documented in social and solitary carnivores (e.g., Paquet 1991; Vogt et al. 2014).

It is worth noting that the sections dominated by birches had the highest rubbing densities. RT densities in the Cantabrian Mountains are higher than those recorded by Henderson et al. (2015) in conifer forests of the northwest United States, where they compared RT abundances between developed trails and roads (1.0 ± 1.1 RTs/km; $n = 30$) and game trails (0.8 ± 1.1 RTs/km; $n = 30$). In several Kamchatka valleys dominated by stone birch, Seryodkin (2014) reported very variable abundances (from 40 RTs/km to 0.4 RTs/km) and RTs groupings

in short sections of the footpath (7 RTs in 20 m or 5 RTs in 8 m). We detected similar but lower density aggregations, particularly in birch-dominated forests. This indicates a trend toward more intense or greater marking on them, supporting the positive selectivity toward birches described above. Understanding wildlife behavior can prove useful for conservation and management (e.g., Greggor et al. 2019). In the context of our study, the noticeable selection of birch by marking bears might provide a tool to monitor bear presence, e.g., in areas immediately surrounding the present range of the species, where targeting birches in monitoring programs that search for bear signs might help detect dispersing individuals.

To our knowledge, this is the first time that the density of brown bear RTs has been compared with some features of the bear population or its proxies. In our study, neither the density of bear observations (as a proxy for bear density), nor the position of the track within the bear distribution area, affected the kilometric abundance of RTs. Because the null model had the lowest AIC, we deduce that the determinants of the intensity of rubbing in our population are different from those analyzed in this study, hence the assessment of other possible variables may be necessary. The lack of an effect of the density of observations on the density of RTs may be due to the fact that differences in bear density, or more specifically of bear observations around each foot path, are not large enough to affect abundance from RTs. More research in this field is needed to elucidate whether variations in bear density can affect rubbing behavior in other ways, such as modifications in the frequency of rubbing or the proportion of rubbing between sex and age classes, as Lamb et al. suggested (2017). In one study considering the distribution of rubbing sites in a territorial carnivore, the tiger (*Panthera tigris*), rubbing increased toward the limits of the territory (Smith et al. 1989). This might not be applicable to brown bears that are nonterritorial species in which individuals of the same population can have overlapping home ranges (Seryodkin et al. 2017; Frank et al. 2018).

There are three potential biases in this study. First, searches for RTs were undertaken mostly (but not exclusively) from footpaths. The findings that RTs were closer to, and orientated toward, footpaths may thus have been the result of greater detectability from those paths. However, we do not believe this to have affected our results given the large amount of evidence that footpaths are common routes of brown bear displacement and that RTs occur more frequently along such routes (e.g., Nie et al. 2012; Seryodkin 2014; see above). Second, the lighter colored bark of birch trees may have made them more conspicuous to observers. We believe this potential bias was minimized by very careful observations of all potential RTs. Furthermore, preference for birch has been found in several other studies (see above). Third, we used proxy measures to estimate bear density and distribution. We cannot know whether our measures are fully accurate representations of the population but nevertheless, our measures were the best available, being based largely on observations made by trained forest rangers and researchers. While we believe the above potential biases were minimized in our study, their effects only can be properly elucidated through further research based on intensive telemetry studies.

To conclude, our results suggest that Cantabrian brown bears select RTs based on characteristics related to the tree, rather than their position relative to areas with a high density of conspecifics and/or with the distribution of individuals within the population range. Thus, even in small and isolated bear populations, such as the one under study here, some aspects of rubbing behavior such as tree selection and marking effort may not be affected by population size and/or structure.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Mean value, standard deviation (*SD*), and minimum (Min) and maximum (Max) values of each of the parameters used to characterize both rub and control trees.

Supplementary Data SD2.—Mean value, standard deviation (*SD*), and range of landscape features surrounding rub trees, including the percent of the different land cover within a 1-km buffer around each rub tree.

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SUPPLEMENTARY DATA S1

	Rub trees				Control trees			
	Mean	*SD*	*Min*	*Max*	*Mean*	*SD*	*Min*	*Max*
Trunk diameter (cm)	26.5	19.0	7	180	17.3	10.1	0.3	70
Tree height (m)	11.9	4. 5	2	25	9.9	4.6	2	26.2
Trunk height (m)	3.6	2.2	0.3	13	3.2	2.4	0	15
Tree spacing (m)	4.1	1.6	1.7	9.0	3. 1	1.2	0.2	6.9
Distance to footpath (m)	1.6	7.4	0	50	2.4	6.4	0	50

Supplementary Data S1.- Mean value, standard deviation (SD) and minimum (Min) and maximum (Max) values of each of the parameters used to characterise both rub and control trees.

SUPPLEMENTARY DATA S2

Parameters	Mean ± SD	Max - Min
% Deciduous forest	62.1 ± 21.6	97.3 - 22.1
% Conifer forest	0.93± 4.1	23.6 – 0.0
% Shrubland	16.7 ± 15.6	56.2 – 0.0
% Pasture	7.7 ± 8.8	37.9 – 0.0
% Crops	2.4 ± 5.4	31.0 – 0.0
% Rocky areas	5.9 ± 12.1	46.8 – 0.0
Ruggedness	18435.9 ± 2965.6	25841.3 - 13436.5
Distance to the nearest paved road (m)	927.1 ± 1008.4	5617.7 - 12.4
Distance to the nearest unpaved road (m)	1267.2 ± 672.1	2948.1 - 156.0
Distance to the nearest river (m)	298.1 ± 282.1	1310.1 - 1.1
Distance to the nearest human settlement(m)	10522.0 ± 4929.6	18768.7 - 2781.9
Total length of paved roads (m) (1km buffer)	1489.47 ± 1409.87	6118.82 - 0.00
Total length of unpaved roads (m) (1km buffer)	447.87 ± 855.04	3407.23 - 0.00
Total length of rivers (m) (1km buffer)	2442.65 ± 1098.83	4849.03 - 0.00

Supplementary Data S2. Mean value, standard deviation (SD) and range of landscape features surrounding rub trees, including the- percent of the different land cover within a 1km buffer around each rub tree.