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Andean bear tree selectivity for scent-marking in Ecuadorian cloud forests

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Research Article

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Abstract

Olfactory signaling is the most efficient mode of animal communication when the interval between signaller and receiver is delayed. Scent-marking requires selective strategies to increase the likelihood that these signals persist in the environment and are successfully received. Bears are solitary, non-territorial carnivores, which scent-mark trees, substrate, and other objects to communicate with conspecifics. Signallers place scent-marks on trees to increase the detectability of their signals, possibly also to communicate their size and status. We assessed scent-marking tree selectivity of Andean bears, *Tremarctos ornatus*, in Ecuadorian cloud forests at two spatial scales: the individual-tree level and at a local scale. We recorded characteristics of marked and unmarked trees along bear trails (5.49 km in total) in the Eastern Cordillera of the Ecuadorian Andes, near the Sumaco Biosphere Reserve. To decrease dimensionality and multicollinearity before explanatory analyses, we performed Principal Component Analysis on data from 467 trees of 48 tree species. We then used Generalized Linear Models, model selection, and model averaging to discover that Andean bears preferred rubbing leaning trees, aromatic tree species, and hardwood trees with smaller and thicker leaves containing less nitrogen. Ten of 59 marking sites contained multiple marked trees, but site-level data do not indicate why bears marked multiple trees at some sites but not others. We thus encourage further analyses of marked-tree cluster sites and their relationship to productive food resources and reproduction, which might present important communication hubs for ursids.

Introduction

Animal communication can only succeed if signals are both fully transmitted and received. Although carnivores may use different types of signals to communicate, olfactory signals have certain advantages over visual, acoustic, or tactile signals (Gorman and Trowbridge, n.d.)can be detected during the day or night, and in the absence of the signaller (Gorman and Trowbridge, n.d.). Placing scent marks on trees functions as chemical, and perhaps also as visual, signaling (Gorman and Mills, 1984). Elevating height from the ground likely improves the detectability of scent marks within the odorsphere (Muller-Schwarze, 2006). Moreover, it is possible that the height of the scent mark indicates the size, and therein status, of the signaler (Alberts, 1992; White et al., 2002). Tree selectivity for scent-marking has been studied especially in Artiodactyla and Carnivora to better understand the functional significance of marking behavior and related reproductive success. Selection can be based on a range of tree characteristics (Table 1), conspicuousness of the tree (Piñeiro and Barja, 2012), or its form, e.g. to protect scent-marks from weather conditions (Smith et al., 1989). Collectively, these studies indicate that large mammals select trees with specific properties to scent-mark.

Table 1
Example literature on tree selectivity for scent-marking in members of the Artiodactyla and Carnivora. The tree property, which affected tree selectivity, is displayed for each reviewed animal species.

Tree Property	Species Common Name	Scientific Name	Example Literature
Bark texture	Moose	Alces alces	(Bowyer et al., 1994)
	White-tailed deer	Odocoileus virginianus	(Benner and Bowyer, 1988)
DBH	Fallow deer	Dama dama	(Massei and Bowyer, 1999)
	Red deer	Cervus elaphus	(Ramos et al., 2006)
	Roe deer	Capreolus capreolus	(Ramos et al., 2006)
	White-tailed deer	Odocoileus virginianus	(Benner and Bowyer, 1988)
	European wildcat	Felis silvestris	(Piñeiro and Barja, 2012)
	Grey wolf	Canis lupus	(Barja, 2009)
Tree lean	Tiger	Panthera tigris	(Smith et al., 1989)
Tree height	Fallow deer	Dama dama	(Massei and Bowyer, 1999)
	Grey wolf	Canis lupus	(Barja, 2009)
Tree species	Fallow deer	Dama dama	(Massei and Bowyer, 1999)
	Wild boar	Sus scrofa	(Ichen et al., 2023)
	European wildcat	Felis silvestris	(Piñeiro and Barja, 2012)
	Grey wolf	Canis lupus	(Barja, 2009)
	Kalahari leopard	Panthera pardus	(Bothma and le Riche, 1995)
	Tiger	Panthera tigris	(Smith et al., 1989)
DBH = diameter at breast height			

Bears (*Ursidae*) are solitary non-territorial carnivores which scent-mark trees, objects and substrate for communication (Burst and Pelton, 1983; Filipczyková et al., 2017; Swaisgood et al., 2004). Marking behavior is thought to be an important method of intraspecific communication for giant pandas (*Ailuropoda melanoleuca*) (Liu et al., 2008; Nie et al., 2012; Swaisgood et al., 2004; White et al., 2004), brown bears (*Ursus arctos*) (Bowersock et al., 2022; Clapham et al., 2023, 2014, 2012; González-Bernardo et al., 2021; Morehouse et al., 2021; Sato et al., 2014; Sergiel et al., 2017), and other ursid species (Bowersock et al., 2022; Filipczyková et al., 2017; Khadpekar et al., 2021; Owen et al., 2015; Taylor et al., 2015). Chemical signaling in bears, as solitary large carnivores, serves as means for communication of dominance (Clapham et al., 2012; Lamb et al., 2017), mate attraction (Lamb et al., 2017), familial identification (Swaisgood et al., 2004, 1999), or competition over mates and resources (Swaisgood et al., 2004). While we are starting to better understand chemical signaling and its functional significance in bears of the northern hemisphere, there is a very limited knowledge on chemical signaling of bears from tropical regions (Steyaert et al., 2021). This knowledge gap is impacted by the elusive and wide-ranging nature of Andean bears (Castellanos, 2011), inhabiting challenging environments (Castellanos, 2011; Kattan et al., 2004), and a scarcity of resources and support for wildlife research in the tropics.

The Andean bear is classified globally as 'Vulnerable' to extinction (Velez-Liendo and García-Rangel, 2017) and in Ecuador as 'Endangered' (Tirira, 2021). Populations are steadily declining (Velez-Liendo and García-Rangel, 2017) due to habitat loss and fragmentation (Cardillo et al., 2004; Kattan et al., 2004; Velez-Liendo and García-Rangel, 2017), illegal killing and human-bear conflict (Goldstein et al., 2006; Jorgenson and Sandoval-A, 2005; Zukowski and Ormsby, 2016), and climate change (Tovar et al., 2013; Velez-Liendo and García-Rangel, 2017). Despite the Andean bear's recognized conservation status and its importance as a flagship species (Crespo-Gascón and Guerrero-Casado, 2019), their ecology, behavior, and the status of local populations remain understudied. (Filipczyková et al., 2017) previously described wild Andean bear marking behavior in Ecuadorian cloud forests using remote cameras: Andean bears sniffed marked-trees, rubbed their heads, necks, and/or shoulders against the trees, rubbed their flanks while remaining on all four legs, and rubbed their napes and backs against trees and objects. However, we so far lack an evaluation of Andean bear marked-tree selectivity in cloud forests and habitat selection related to scent-marking. Although there is evidence of reproductive seasonality of wild Andean bears in Peruvian tropical dry forest (Appleton et al., 2018), there has been no such study performed in cloud forests and very little is known about Andean bear reproductive behavior across their range. Ecosystem seasonality is not as profound in cloud forests as in the tropical dry forests, which could impact the trees selected for marking, the location of those marked trees, and associated habitat selection in ways that have not yet been described. Examining variation between Andean bear marked tree selection in different forest types may help to determine the functional significance of scent marking in the species.

As non-territorial mammals, bears create a network of marked-trees which are overmarked repeatedly by different individuals (Burst and Pelton, 1983; Clapham et al., 2013; Filipczyková et al., 2017). There is a general consensus in the literature that bears choose conspicuous trees to mark (Bowersock et al., 2022; Clapham et al., 2013; González-Bernardo et al., 2021; Green and Mattson, 2003; Kleiner et al., 2018; Sato et al., 2014). Tree conspicuousness in these studies is expressed by selection for trees that vary compared to the surrounding environment, be that marginal sizes of diameter or tree height, or rarer tree species. Brown bears select larger trees, i.e. trees of larger diameter (Clapham et al., 2013; González-Bernardo et al., 2021; Green and Mattson, 2003; Sato et al., 2014) and rarer tree species to scent-mark (Clapham et al., 2013) such as birches *Betula* spp. (González-Bernardo et al., 2021), which have conspicuous and unique white bark. When both coniferous and deciduous species are present, bears often prefer coniferous trees (Clapham et al., 2013; Puchkovskiy, 2009; Sato et al., 2014), as also do black bears (Bowersock et al., 2022). Authors have suggested that bears select coniferous over deciduous tree species due to aromatic properties (Clapham et al., 2013; Green and Mattson, 2003; Sato et al., 2014), which might enhance the longevity of the chemical signal (Alberts, 1992). However, no studies have explicitly tested selection for aromatic tree species, or against other traits that render trees conspicuous.

Some bears appear to spatially concentrate their chemical signals by creating clusters of marked trees at sites adjacent to important resources (e.g., food, water). While this has been rarely addressed in the literature, (Clapham et al., 2013) observed clustering of marked trees by brown bears close to food resources during respective productive seasons (i.e., estuary sedge in the spring, salmon spawning river in the fall). Additionally, (Kleiner et al., 2018), who worked in the Peruvian tropical dry forest where water is a scarce resource, reported an increasing frequency of marking sites with decreasing distance to waterholes. (Lee et al., 2019) and (Hwang et al., 2021) assessed sun bear (*Helarctos malayanus*) habitat use based on density of their claw marks on trees. The density of sun bear claw marks was higher in the least disturbed forested areas with higher tree biomass, taller trees, more closed tree canopy and less herbaceous cover. Older, least disturbed, stands of Ecuadorian cloud forests typically possess lower tree density but more large and fruit-bearing trees, and less bamboo (*Chusquea* sp.; (Fadrique et al., 2021; Mariscal et al., 2022). However, no research has addressed questions related to clusters of bear marked-trees, or provided data to examine their occurrence.

We examined marked-tree selectivity by Andean bears to address crucial gaps in the knowledge of Andean bear social ecology, targeting chemical communication, as well as habitat factors affecting selectivity. In addition, we aimed to examine intra- and interspecies (ursids) variation in marking tree selection to determine behavioral plasticity across habitats, geographic ranges, and species. Based on previous research and our prior field observations, we hypothesized that (1) Andean bears in Ecuadorian cloud forests mark trees that are deemed conspicuous according to specific characteristics (e.g., diameter, aromaticity, tree lean, tree species). Further, we hypothesized that Andean bears create clusters of marked trees in habitats of high quality, namely in (2) older forest stands, and (3) at sites with more seasonal food resources (i.e, stands with greater fruit tree basal area).

Material and Methods

Study site

The study area is located in the Eastern Cordillera of the Ecuadorian Andes, on the border of the Sumaco Biosphere reserve (0.55 °S and 77.87 °W) in the province of Napo, and encompasses approximately 20 km2 (Fig. 1). Elevations of the study area range from ~ 1900 to 2700 m above sea level. The study area encompasses these habitats in successional order: cattle pastures, recently cleared areas to be used as pastures, bamboo forest, secondary cloud forest, and primary cloud forest. Primary cloud forest refers to a forest that has not been cleared within the last 80 years (Wilson and Rhemtulla, 2016). Cloud forests persist in the Andes at altitudes between 1000 and 3000 m above sea level (Beck et al., 2008), and are very humid ecosystems, obtaining most of their humidity from clouds (i.e., fog) and precipitation (Nadkarni and Wheelwright, 2000). Specific to cloud forests and this study area are epiphytes, forming a large part of forest biomass (Myers et al., 2000; Veneklaas and Van Ek, 1990). Primary cloud forests moreover, both in general and in this study area, possess exceptionally high levels of plant species richness and endemism (Myers et al., 2000). Contrary to secondary cloud or bamboo forests, primary cloud forests contain older and larger trees, including large fruit-bearing trees (an important part of

Andean bear diet), higher heterogeneity in tree age and sizes, and less bamboo (Mariscal et al., 2022; Pinto et al., 2018). The climate of the study area is warm and humid with an average annual temperature of 14.3°C, an average precipitation of 2,613 mm/year (Instituto Nacional de Meteorología e Hidrología del Ecuador (INAMHI), 2019), and a dry season lasting from September to February (Filipczyková et al., 2017). The human population of the study area is estimated at 700 (F. Torres, personal communication). Most humans live along the paved road (see Fig. 1), however their agricultural activities such as cattle farming, and cultivation of naranjilla *Solanum quitoense*, tamarillo *Solanum betaceum*, and caigua *Cyclanthera pedata*, expand up to 2.5 km from the paved road (F. Torres, personal communication). Extensive cattle farming is the primary occupation of local inhabitants and is the main cause of deforestation in the study area.

Data collection

To find Andean bear marked trees we searched the entire study area for bear trails (approx. 20 km2; Fig. 1). Our searches included all existing habitat types (clearcut forests, cattle pasture, secondary cloud forest, and primary cloud forest), which we grouped into the following classes: pastures (approximately 30% of the searched area), primary forest (approximately 50% of the area), and secondary forest (approx. 20% of the area). Once candidate trails were found, we focused on four trails that showed signs of frequent use: on the trails were fresh bear footprints, scats, marked-trees, evidence of foraging, and beds. These trails were very noticeable, except when they crossed a bamboo patch, and they were approximately 1-5m wide, depending on the forest stage. From November to December 2018 we followed these bear trails (i.e., four separate transects) that collectively measured 5.49 km (0.85 km + 2.44 km + 1.32 km + 0.88 km), recording the GPS positions of the bear trails and both live and dead marked trees. Then, from October to December 2019, we collected detailed species and tree characteristics on 60 marked trees and 60 trees that showed no evidence of marking by bears (i.e., ‘control’ trees), in both primary and secondary cloud forests.

We defined a marked-tree as a tree repeatedly marked by Andean bears at the approximate height of a bipedal Andean bear (1.6m – 1.9m), with apparent signs of bear body rubbing, clawing, bite marks, and presence of bear hair (as in (Burst and Pelton, 1983; Clapham et al., 2013). Bear rubbing changes the bark structure of tropical trees in a way that bark is smoothed or missing; bark, or exposed wood, changes color. Some tree species in the study area discharge latex or resin (Foisy et al., 2019) when freshly clawed/bitten by a bear. Fresh claw and rub marks are lighter in color than old ones, which become darker over time, so color indicates the time since the tree was marked.

To assess selection of trees for marking, we also collected data on trees not marked by bears, but situated near marked trees, and classed these as control trees. Control trees were situated on bear trails, but ≥ 10 m from any marked tree and ≥ 7 m from any other control tree. Once there were no marked trees on the trail we started registering control trees, to a maximum of 8 sequential control trees. As GPS precision declined to 32 m due to tree canopy cover, we used a measuring tape to verify distances. We sampled both control and marked trees with a diameter at breast height (DBH) ≥ 2 cm. For each sampled tree we recorded a local species name (if available), DBH (using a DBH tape), and lean relative to the trail

(3 categories: 1 = 0° – 30°, 2 = 30° – 60°, 3 = 60° – 90°). For each sampled species we collected a sample of its branch and, when available, of its flower and/or fruit, for later identification.

All sampled tree species were then identified in the herbarium of Universidad Técnica Particular de Loja (HUTPL, sensu (Thiers, 2019)), validating scientific names using the International Plant Name Index (IPNI 2021). We identified each sampled species, considering the high levels of plant species diversity in the region. Given the frequent absence of flower/fruit, we could sometimes identify sampled trees only to genus (Supplementary Table S1). For each species we used the literature to determine presence of bark aromaticity (hereafter 'aromatic', (Gentry, 1993; Renner, 1997; Rohwer, 1993; Tebbs, 1993; Todzia, 1993). The variable 'Tree species' consisted of 49 different categories (i.e. each category presents one species) with many species appearing only once or twice in the data. Such a multi-level factor could not point out any preferential species, among our available data. We therefore generated as many continuous plant traits as possible from the global TRY plant trait database (https://www.try-db.org; (Kattge et al., 2020)) for each sampled species; morphological, anatomical, physiological, and biochemical plant traits were generated from the database. For the majority of sampled species that were rare, often endemic, the TRY plant trait database contained only a limited number of traits. To generate ≥ 6 plant traits for each sampled species, we therefore had to extrapolate missing data. To do so, we assigned traits from 2–10 other species based on genetic or morphological affinity and similar geographic distributions as the focal species.

To determine if tree selection occurs on a local spatial scale, we followed (Clapham et al., 2013) and (Kleiner et al., 2018) by collecting data from all trees in a small radius around marked-trees. However, high tree density and diversity in our study area, compared to those prior studies, forced us to restrict sampling to all trees in a 3-m radius (not a 5-m radius) around each marked-tree (hereafter 'radius trees'). A typical radius site usually included one marked-tree and several non-marked trees, but occasionally a radius site had multiple marked trees. We differentiated these two types of sites as 'cluster' and 'no-cluster' sites. As leaning trees were situated mainly on bear trails, we did not collect data on tree lean for radius trees, because many trees in radius plots were not on bear trails. For each sampled radius tree we recorded a local species name and DBH, then later identified the tree species (as above).

Data analysis

Principal component analysis (PCA)

We carried out all analyses in Program R version 4.2.2 (R Core Team, 2022). Our tree species information was contained in 10 plant traits, which were multicollinear. To minimize such multicollinearity, the number of dimensions and loss of information, yet increase interpretability of tree species information, we used principal component analysis (PCA) (Jolliffe and Cadima, 2016). As we were not able to identify species of dead trees, we could not generate plant traits for these trees from the TRY plant trait database; we thus excluded them from the PCA. We excluded additional tree species from the PCA if the database lacked trait data that could not be inferred from database information on close relatives, or from species with similar traits. We used the package *missMDA* (Josse and Husson, 2016) to estimate the number of dimensions and to impute missing data into a dataset containing plant trait data of all the collected trees (marked trees, control trees, and radius trees) excluding dead trees and species with no data in the TRY plant trait database. We then performed a PCA with data standardization using the package *FactoMineR* (Husson et al., 2016)). Trait data that were available for more than 50% of analyzed trees were included in the PCA (Clavel et al., 2014; Josse et al., 2011; Madley-Dowd et al., 2019). We chose the number of dimensions for interpretation using the *missMDA*::estim_ncpPCA() function and a bar plot of eigenvalues. We calculated the correlation coefficients between variables and chosen dimensions (*FactoMineR*::dimdesc()), and then extracted PCA scores.

To obtain missing PCA scores of marked and control trees (n = 16), we imputed missing values into the dataset using the *missForest* package and function (Stekhoven and Bühlmann, 2011)). This package calculates missing values based on a random forest algorithm and builds an algorithm for each variable separately. To assess its performance we calculated a Normalized Root Mean Squared Error (NRMSE) for the missing values of the extracted PCA scores (Stekhoven and Bühlmann, 2011)). NRMSE is an out-of-bag error for the continuous part of the dataset; a lower NRMSE indicates a better variable estimation (Oba et al., 2003).

Modeling tree selection at the individual-tree level

We examined the relationship between sampled tree parameters and marked-tree selection using generalized linear models (GLM) with a binomial error distribution and logit link function (*stats*::glm function). We considered using linear mixed effect models with 'trail' as a random factor, however with only 4 trails (i.e., potential levels of the random factor), the variance estimate collapsed to zero (Gelman and Hill, n.d.). Our binary response variable was whether a tree was marked/not marked (1/0). We constructed a set of candidate models based on existing hypotheses and our field observations, in combination with an intercept-only null model (M0) and a global model (MG) containing all used parameters ('DBH', 'tree lean', and species as represented by 'aromatic' and the PCA scores of species traits (hereafter 'D1, D2, and D3'); see Supplementary Table S2, based on (Harrison et al., 2018). Treating the parameter 'tree lean' as an ordinal variable pooled the variable into two dummy variables, causing loss of variance. Following (Robitzsch, 2020) and (Gertheiss and Tutz, 2009) we treated 'tree lean' as a continuous variable and used the R package *ordPens* (Hoshiyar, 2021) to penalize it. The function *ordPens*::ordSmooth 'smoothes' the independent variable by fitting its dummy coefficients with the sum of squared differences of adjacent dummy coefficients (i.e., penalization). Penalty parameter lambda was selected in accordance with the lambda of the central smoothing curve.

For multimodel inference, we applied an information-theoretic (I-T) approach (Burnham and Anderson, 2002). Only models with a variance inflation factor (VIF) < 10 were included (Quinn and Keough, 2002); the VIF of all our models did not exceed the value of 3. We applied the 'model.sel' function from the *MuMIn* package (Barton, 2009)) to select the best model based on the corrected AIC (AICc; (Burnham and Anderson, 2004)). We followed (Burnham and Anderson, 2002) and (Grueber et al., 2011) by using the ΔAICc = 2 for the selection of best candidate models, calculation of AICc weights for each model and each parameter of the best candidate model set, and standardization of the best candidate models.

Because we did not focus on investigating the effect size(s) of (a) particular parameter(s), but rather questioned which parameter(s) affected Andean bear scent marking, we chose the zero method of model averaging (Burnham and Anderson, 2002) using *MuMIn*::model.avg. From model averaging we generated parameter-averaged estimates with their corresponding 95% confidence intervals (CIs) for all predictors. We used a revised formula for the variance estimator (Burnham and Anderson, 2004) and adjusted standard errors (Burnham and Anderson, 2002) to calculate the CIs. Using the estimates and the CIs, we determined whether the predictors were significantly different from 0 and of what size and direction their effect was (du Prel et al., 2009). We also calculated explained variance of the global model and each candidate model using theoretical marginal R^2 (Nakagawa and Schielzeth, 2013).

Modeling tree selection on a local spatial scale

To assess the relationship between sampled tree parameters and marked tree selection on a local spatial scale (i.e., radius of 3m around marked trees), we used GLMs with a binomial error distribution and logit link function (*stats*::glm function). The binary response variable was again whether a tree was marked/not marked (1/0). The candidate models contained all the previously used parameters (i.e., DBH, aromatic, PCA scores) except for the parameter tree lean (Supplementary Table S2). We applied model selection and averaging (as required) as described previously to the remaining candidate models: M0, M1, M4 and M5 (see Supplementary Table S2).

Modeling formation of marked-tree clusters

We investigated the relationship between habitat properties and Andean bears forming marked-tree cluster sites through GLMs with a binomial error distribution and logit link function. The binomial dependent variable was whether a marking site contained a cluster of marked trees or not (1/0). We calculated stand basal area (m^2 per ha) for each radius site for all tree species combined except bamboo (‘stand basal area’), for bamboo (*Chusquea* sp. (Fadrique et al., 2021); ‘bamboo basal area’), and for fruit tree species which are an Andean bear food source (F. Torres, personal communication; ‘fruit tree basal area’). We also calculated the number of trees per each radius site (‘nr_trees’). Using these site-level parameters of radius sites we constructed a set of candidate models based on existing literature and our field observations, only for models with VIF < 10 (see Supplementary Table S3). We applied the MuMIn::model.sel function, the corrected AIC (AICc), and ΔAICc ≤ 2 to select the best model.

Results

PCA

We collected data from 505 trees: 76 marked trees, 60 control trees, and 369 radius trees. In the PCA we included 467 trees (65 marked trees, 54 control trees, and 348 radius trees), after excluding 29 dead trees and 9 trees for which no plant trait data were found (two *Barnadesia parviflora*, two *Hippotis* sp., two *Saurauia prainiana*, one *Delostoma integrifolium*, and two individuals of unknown species of *Solanum*).

We entered into the PCA 10 plant traits (Table 2). We estimated and extracted PCA scores of the first three dimensions (i.e., D1, D2, and D3 with cumulative variance 91.8%, Table 2, Supplementary Table S4).

Table 2
Physiological plant trait numbers, names, and units from the TRY plant trait database (Kattge et al., 2020) entered into the principal component analysis (PCA), and their associations with the first three dimensions of the PCA quantified by correlation coefficients (r, > 0.6, (Lomberk et al., 2018)) and significance tests.

Trait number	**Trait name (units)**	**Dimension 1**		**Dimension 2**		**Dimension 3**	
		r	**P-value**	**r**	**P-value**	**r**	**P-value**
4	Wood density; stem specific density; wood specific gravity (g/cm^3)	0.619	< 0.001	-	-	-	-
14	Leaf nitrogen (N) content per leaf dry mass (%)	-0.950	< 0.001	-	-	-	-
26	Seed dry mass (g/1000 seeds)	-	-	0.857	< 0.001	-	-
46	Leaf thickness (mm)	0.911	< 0.001	-	-	-	-
48	Leaf density (leaf tissue density, leaf dry mass per leaf volume) (mg/cm^3)	0.948	< 0.001	-	-	-	-
55	Leaf dry mass (single leaf) (g)	0.602	< 0.001	0.777	< 0.001	-	-
3106	Maximum plant species height (m)	-	-	-	-	0.961	< 0.001
3109	Leaf area (in case of compound leaves: leaflet, petiole excluded) (cm^2)	0.816	< 0.001	-	-	-	-
3112	Leaf area (in case of compound leaves: leaf, undefined if petiole in- or excluded) (cm^2)	-0.707	< 0.001	-	-	-	-
3115	Leaf area per leaf dry mass (specific leaf area, SLA or 1/LMA): petiole excluded (cm^2/g)	-0.903	< 0.001	-	-	-	-

- = insignificant results at alpha 0.05

Modeling tree selection at the individual-tree level

To assess characteristics of marked trees in relation to control trees for GLMs we used 120 trees: 60 marked trees and 60 control trees (for further information see Supplementary Table S1). Sixteen of the 120 trees (13%) missed values for D1, D2 and D3, because no physiological plant trait data were found for these 10 marked trees (8 dead trees, one *D. integrifolium*, and one *S. prainiana*) and 6 control trees (4 dead trees, one *B. parviflora*, and one *S. prainiana*). We imputed the missing data with an acceptable value for NRMSE of the missing data (0.026), therefore we used all 120 trees for further analysis.

When comparing Andean bear selection of marked trees against control trees, model selection and averaging (Table 3; Table 4) suggested that bears selected leaning trees and were selective for tree species when rubbing (species is represented here by variables D1, D2, D3 and aromatic). Within species traits, bears preferred rubbing trees of species with greater values of D1, and with aromatic bark (Table 4). DBH was the only difference between the two competitive models, but it was a less important predictor overall (Table 3; Table 4). The theoretical marginal R^2 of the global model was 0.62.

Table 3
Results of model selection ranked by AIC_c showing order of the candidate models explaining which variables affect Andean bear preferences for selecting marked trees over control trees. Based on the ΔAICc = 2 selection criterion, M6 and MG were further ranked and averaged.

Model #	Response Variable ~ Independent Variables	logLik	AICC	ΔAICC	weight
M6	Marked/not marked ~ D1 + D2 + D3 + aromatic + tree lean	-59.31	131.40	0.00	0.58
MG	Marked/not marked ~ D1 + D2 + D3 + aromatic + tree lean + DBH	-58.52	132.00	0.66	0.42
M4	Marked/not marked ~ D1 + D2 + D3 + aromatic	-68.03	146.60	15.22	0.00
M5	Marked/not marked ~ D1 + D2 + D3 + aromatic + DBH	-67.79	148.30	16.95	0.00
M3	Marked/not marked ~ tree lean + DBH	-72.78	151.80	20.40	0.00
M2	Marked/not marked ~ tree lean	-74.05	152.20	20.83	0.00
M0	Marked/not marked ~ 1	-83.18	168.40	37.02	0.00
M1	Marked/not marked ~ DBH	-82.69	169.50	38.12	0.00

Table 4
Parameter-averaged estimates, adjusted standard errors, and 95% CIs for each parameter resulting from the zero method of model averaging of best candidate models (i.e., M6, MG) explaining Andean bear preferences for marked trees over control trees.

Parameter	Estimate	Adjusted SE	CI 2.5%	CI 97.5%
Intercept	-0.235	0.300	-0.823	0.354
D1	2.786	1.073	0.684	4.889
D2	-0.666	0.500	-1.647	0.315
D3	-1.002	0.647	-2.271	0.267
aromatic	2.897	1.252	0.444	5.351
tree lean	2.099	0.645	0.835	3.363
DBH	0.225	0.403	-0.565	1.014

Modeling tree selection on a local spatial scale

From data collected on 505 trees, all of which were found in primary cloud forest, we included 444 trees after excluding 60 control trees and one marked tree for which we collected no radius plot data. These 444 trees encompassed 75 marked trees and 369 non-marked trees, from 59 radius sites. The mean DBH of marked and unmarked trees was 15.85 cm (± SD 23.3 cm, range 1.2–235.0 cm, median 8 cm). Forty-one (9.2%) out of the 444 trees had aromatic bark. The mean number of trees per radius site was 7.67 (range 1–18, median = 7). Thirty-two of the 444 trees (7%) missed values for D1, D2 and D3, because no physiological plant trait data were found for these 11 marked trees (9 dead trees, one *D. integrifolium*, and one *S. prainiana*), and 21 non-marked trees (16 dead trees, two individuals of unknown species of *Solanum*, two *Hippotis sp.*, and one *B. parviflora*). We imputed the missing data of these 32 trees with a favorable result for NRMSE of the missing data (0.001), and used all 444 trees for further analysis.

When comparing Andean bear selection of marked trees against non-marked trees at the local spatial scale (radius plot data), model selection and averaging failed to show clear inference. M1 and M0 were selected as the top models (ΔAICc = 0.46 (difference between M1 and M0)) and averaged (for the model list, see models M0, M1, M4, and M5 from Table 2). However, DBH, the only variable of one (M1) of the two selected and averaged models, did not show to be an important predictor (95% CI -0.006, 0.014; variable weight 0.56). M5 (ΔAICc = 2.75) and M4 (ΔAICc = 3.79) were not competitive. The theoretical marginal R^2 of the global model (M5) was 0.04.

Modeling formation of marked-tree clusters

To investigate factors affecting Andean bear formation of marked-tree clusters we used the 59 radius sites. Of 59 radius sites, 46 had one marked tree (‘no cluster’), 10 radius sites had two marked trees (‘cluster’), and three radius sites had three marked trees (‘cluster’). The mean stand basal area was 165.75

m^2/ha (± SD 324.29 m2/ha, range 1.62–1848.92 m^2/ha, median 81.82 m^2/ha). The mean basal area of fruit trees was 84.75 m^2/ha (± SD 259.72 m^2/ha, range 0.00–1841.79 m^2/ha, median 21.74 m^2/ha), approximately half of the mean stand basal area. The mean basal area of bamboo was 0.32 m^2/ha (± SD 0.55 m^2/ha, range 0.00–2.25 m^2/ha, median 0.00 m^2/ha), apparently occupying the minimum area of the radius sites.

The global model (MG: Cluster/no cluster ~ fruit_BA + bamboo_BA + nr_trees) was selected by AICc as the top model, but no variables included appeared to be important predictors of cluster formation (Table 5). The theoretical marginal R^2 of MG was 0.13.

Table 5
Parameters, their estimates, standard errors and 95% CI's for the global model (MG) of the cluster analysis using GLM.

Parameter	Estimate	SE	CI 2.5%	CI 97.5%
Intercept	-0.710	0.930	-2.580	1.128
fruit_BA	0.002	0.001	-0.001	0.005
bamboo_BA	-1.360	1.029	-4.005	0.263
nr_trees	-0.052	0.115	-0.293	0.167

Discussion

To address crucial gaps in our knowledge of Andean bear social ecology and communication, we investigated tree selectivity for scent-marking in Ecuadorian cloud forests at the individual-tree level and on a local spatial scale. Additionally, we assessed how local forest structure affected creation of marked-tree clusters by Andean bears. Our study generated three key findings. First, Andean bears preferred to rub leaning trees (1). Second, bears selected trees for marking based on their species (1). And thirdly, bears selected aromatic tree species for marking (1). Contrary to our predictions, DBH did not affect selection of marked trees. Also, we found no parameters assessed that predicted Andean bear selection of marked trees at the local spatial scale (radius plot data). Finally, we confirm that Andean bears form clusters of marked trees at specific sites. However, at a local spatial scale, we did not identify any tested parameter of the local forest structure linked with the formation of such clusters.

Ecuadorian cloud forests are one of the most biodiverse ecosystems on Earth (Báez et al., 2010; Brooks et al., 2006; Bruijnzeel, 2004; Myers et al., 2000). To understand whether Andean bears select trees for scent-marking based on their species, we analyzed physiological and morphological traits of 48 tree species, which makes this the most methodologically complex study focused on scent-marking tree selection by bears to date. Rather than being able to assess selection for independent species, this complex data required the use of PCA to reduce variability, which allowed us to assess selection for tree species traits grouped by dimensions rather than specific species. Several studies examining marking at sites with fewer tree species variability (Clapham et al., 2013; González-Bernardo et al., 2021; Kleiner et al., 2018) found that bears select rarer, and therefore more conspicuous tree species to mark (Clapham et al., 2013; González-Bernardo et al., 2021; Kleiner et al., 2018). Andean bears in our study selected hardwood species for marking, with traits that include smaller, thicker leaves that contain less nitrogen. Such properties correspond with those of climax tree species (Dalling, 2008). In general, climax trees are rarer to find, and occur in older, least disturbed, forest stands (Dislich and Huth, 2012).

It is likely that by placing scent marks on conspicuous trees bears increase their detectability. Trees may be deemed conspicuous by their physical traits or location (Burst and Pelton, 1983). Leaning trees may be conspicuous due to their form or appearance. Moreover, leaning trees may protect scent marks from weather elements (Clapham et al., 2013; Smith et al., 1989), and we postulate that positioning of the scent mark (leaned and closer to the trail) may facilitate its detectability. Contrary to findings on brown bears (Clapham et al., 2013), Andean bears living in Ecuadorian cloud forests selected leaning trees for marking, which could be a reflection of the high levels of humidity and precipitation in cloud forests rendering leaning trees effective in contributing to scent longevity

Aromatic tree species may be deemed conspicuous because of the pungent odors produced by volatile chemicals in their resin, latex and/or bark. Moreover, based on our sampling, trees with aromatic bark in Ecuadorian cloud forests are rare, which may contribute to their conspicuousness and enhance detection (Bowyer et al., 1994), or enhance the chemical signal (Sato et al., 2014), ultimately aiding detection. Various studies (Clapham et al., 2013; Green and Mattson, 2003; Sato et al., 2014) have theorized that some bear species may prefer rubbing certain tree species because of their aromatic properties. Our quantitative approach indicates that Andean bears select aromatic tree species for rubbing, which might be explained by the above-mentioned, and not mutually exclusive, theories (Bowyer et al., 1994; Sato et al., 2014).

Contrary to the findings of previous studies in which brown bears selected trees with larger DBH for marking (Clapham et al., 2013; González-Bernardo et al., 2021; Green and Mattson, 2003; Sato et al., 2014), we did not find DBH to be an important parameter affecting selection of marking trees, both at the individual-tree level and on a local spatial scale (radius plot data). However, on a local spatial scale, DBH was the only parameter selected in the final averaged model. Its result may suggest that there is a tendency towards rubbing larger trees in cloud forests, nevertheless two factors may explain why DBH was not a significant parameter in our study. First, cloud forests are very diverse ecosystems with a forest structure which is much more complex than forest structures of the ecosystems of these other studies (Homeier et al., 2010). Second, a limitation of our study is that we sampled radius trees adjacent to marked trees, but not around the non-marking (control) trees, which may possibly be growing in more disturbed forest stands with trees of a smaller DBH. (Kleiner et al., 2018) is the only study to assess the effect of DBH on selection of marked trees in Andean bears. In their study, Andean bears in Peruvian dry forests did not selectively mark trees of larger DBH, but did select trees of smaller height. However, their analyses pooled data from woody vegetation on which bears rubbed vertically with data from shrubs that the bears straddled, making it difficult to interpret the effect of height or DBH on Andean bear marking behavior in comparison with our study (van Horn pers. comm.). Taking our study collectively with existing literature, ursids, similar to other mammalian groups, appear to possess extraordinary phenotypic plasticity in their behavior (Stirling and Derocher, 1990). Marking behavior appears to be adapted to varied ecosystems, from arctic tundra and sea ice (Owen et al., 2015) to tropical cloud forests. Each of these diverse ecosystems that bears inhabit differs in landscape and forest composition, yet the *Ursidae* seem to consistently select a strategy of choosing conspicuous trees, objects and sites to scent-mark, with ‘conspicuousness’ being determined by habitat. Given this similarity in marking strategy, we might expect the reproductive success of Andean bears to be affected by their marking behavior choices, similar to brown bears (Morehouse et al., 2021).

Although the phenomenon of creating marked-tree clusters by bears has been reported by several studies (Clapham et al., 2013; Kleiner et al., 2018), we are the first to assess it quantitatively. We observed that during the fruiting season in our study area, the valuable high-fat fruit of pinchimuyo *Nectandra reticulata* trees attracts many bears to groves of pinchimuyo-bearing trees, a behavior similar to the high-fat diet presented by the salmon spawning rivers in North America (e.g., (Clapham et al., 2013), or aguacatillo fruit of *Nectandra acutifolia* trees in Maquipucuna Reserve, Ecuador (Molina Proaño, 2012). Therefore, during the fruiting season these most-valuable feeding sites might also become important intraspecific communication hubs, where bears are able to communicate, directly and indirectly. Such a fruiting season in cloud forests might moreover coincide with the timing of the reproduction season, which is reported to be affected by the seasonal variation in food abundance (Appleton et al., 2018). We recommend further research on the relationship between valuable food resources, presence of clusters of marking sites, and Andean bear reproduction. Although we did not find a relationship between presence of the clusters and local forest structure, we encourage future studies to investigate this phenomenon more broadly. Despite the fact that our study area is covered by forests of different levels of degradation, from clearcut to primary cloud forest, we found all marking and cluster sites in primary cloud forests. Therefore it is possible that the differences in the age and quality of the primary forest between cluster and no-cluster sites were too subtle to show up in our analysis. We recommend a further macrohabitat analysis assessing larger-scale forest properties between cluster, marking, and control sites, along with analyses to address other landscape-level factors.

In conclusion, we found that conspicuousness appears to be the main driver affecting Andean bear selection of marked trees at the individual-tree level, which is consistent with research on other bears living in different ecosystems. Andean bears in our study selected conspicuous trees to scent-mark based on their aromaticity, lean, and species characteristics. Such conspicuousness of the selected trees likely enhances the probability of the scent mark to be detected by a receiver. Leaning trees, moreover, may protect the scent mark from challenging weather conditions, especially relevant to cloud forests. Contrary to previous research, we did not find DBH to be an important parameter affecting bear selection of marked trees. This might be due to a very high heterogeneity of Ecuadorian cloud forests. Similar to brown bears in North America and Andean bears in Peru, we report that Andean bears in Ecuadorian cloud forests also form clusters of marking sites. We did not find an important microhabitat parameter affecting creation of these clusters. Future research should focus on investigation of macrohabitat features which might affect site selection and formation of marking tree clusters. Finally, we also recommend that future studies examine a relationship between the valuable food sources, clusters of marking sites, and reproductive seasonality in Andean bears.

Declarations

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Eva Filipczyková and Jorge Luis Armijos Barros. The first draft of the manuscript was written by Eva Filipczyková and Eva Filipczyková, Melanie Clapham, Russell C. Van Horn, Owen T Nevin, Jorge Luis Armijos Barros, and Aleš Vorel contributed critically to versions of the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

Our field work was performed in compliance with the Framework Agreement for access to genetic resources called "Biodiversity Study of Ecuador " made between the Ecuadorian Ministry of Environment and the UTPL. The code for the Agreement is MAE-DNB-CM-2015-0016-M-0002.

Competing interests

We declare no competing interests.

Availability of data and material

Data and code used for analysis will be made publicly available prior to publication.

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Figures

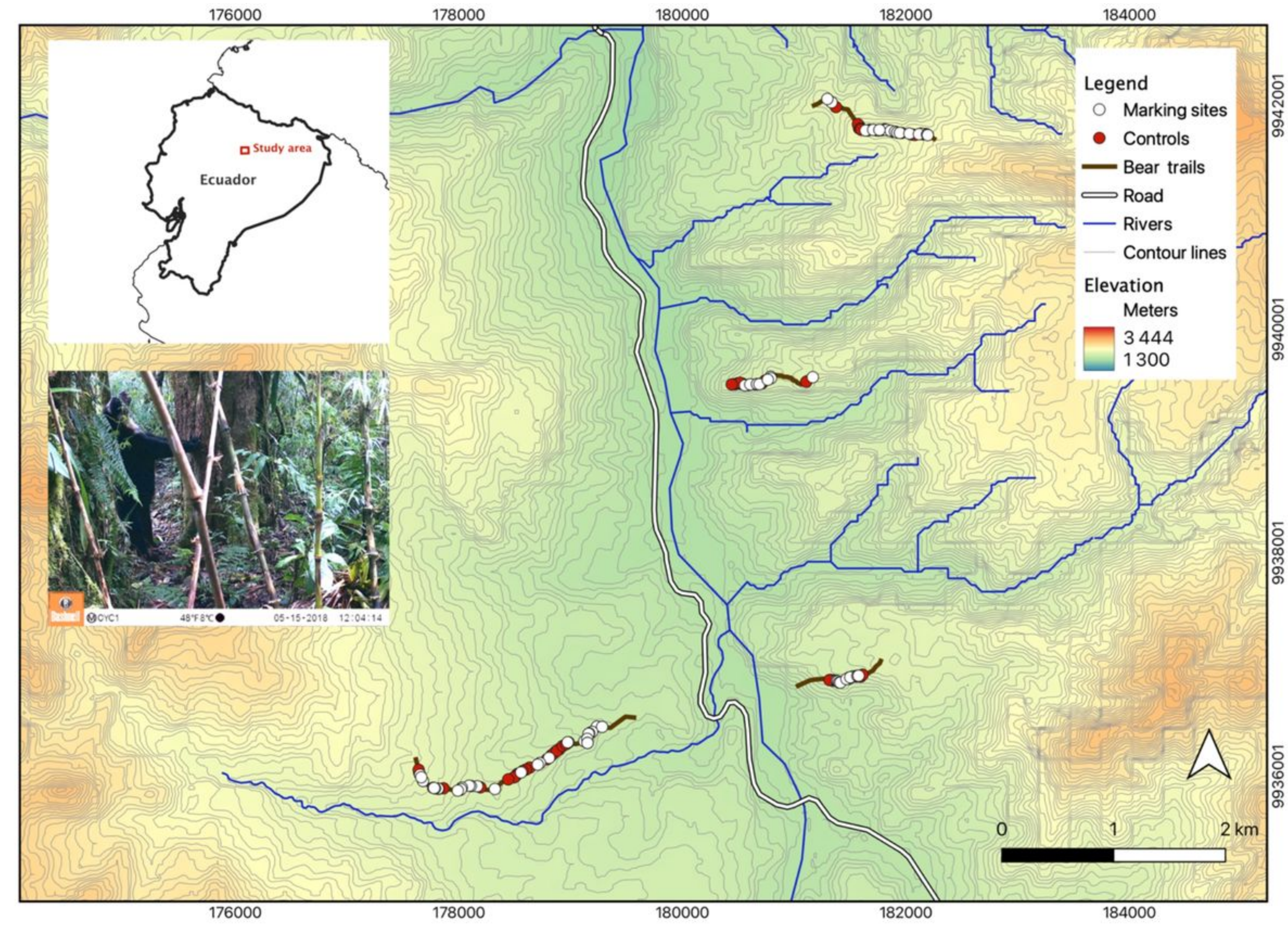

Figure 1

Map of the study area in northeastern Ecuador, showing positions of Andean bear *Tremarctos ornatus* marking sites and controls used to analyze characteristics of marked trees. Marking sites were surveyed along 4 sampled bear trails, November to December 2018. Contour lines represent 50-m elevation intervals.

Supplementary Files

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