# ORIGINAL PAPER

# The plant physical features selected by wildcats as signal posts: an economic approach to fecal marking

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Abstract The chemical signals of solitary and territorial felid species are essential for their intraspecific communication. We studied the selection of plant substrates during the fecal marking behavior of the European wildcat Felis silvestris from September 2008 to June 2009 in a protected area in Northwest Spain. The aim of the study was to examine the selection of plants as signal posts with respect to their physical characteristics. We hypothesized that wildcats deposit their fecal marks on plants with physical characteristics (e.g., size, species, and visual conspicuousness) that enhance the olfactory and visual effectiveness of the signal. Our results indicate that diameter, plant group, visual conspicuousness, and interaction between the diameter and plant group influence the decision of wildcats to deposit their fecal marks on plants. The wildcats chose plants with greater diameters and greater visual conspicuousness as scent-marking posts. Moreover, the wildcats chose woody and herbaceous plants, and certain plant species were marked more frequently than expected at random. Indeed, our results indicate that the fecal marks were not randomly distributed on the plants: the wildcats chose to place their marks on plants with certain physical characteristics that maximized the detectability of the signal by intruders and potential mates, thus facilitating the spatial distribution of the species.

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### Introduction

Carnivores use different types of signals to communicate, including acoustic, tactile, visual, and chemical signals (Eisenberg and Kleiman 1972). However, scent marks are advantageous because they can be used where other signals may be difficult to detect, such as in dense vegetation, at night, or underground (Gorman and Trowbridge 1989). In addition, such signals can remain active for a long time, thus other animals can smell individual signals even when the signaler is absent (Gosling and Roberts 2001).

Carnivores use urine, glandular secretions, and feces as chemical signals (Brown and Macdonald 1985; Robinson and Delibes 1988). The roles that these scent marks may play are well known and include territory defense (Eaton 1970; Smith et al. 1989; Zub et al. 2003); indicators of reproductive status (Wemmer and Scow 1977; Molteno et al. 1998; Broomhall et al. 2003); identifying individuals, groups, and species (Wemmer and Scow 1977; Müller and Manser 2007); preventing agonistic encounters (Smith et al. 1989; Müller and Manser 2007); indicators of social status (Ralls 1971; Gorman and Trowbridge 1989); and immune and physiological conditions (Zala et al. 2004). Nevertheless, despite the relevance of chemical signals in the lives of carnivores, few studies on fecal marking behavior in felids have been conducted. Most of the existing studies reference urine marking (Smith et al. 1989; Bothma and le Riche 1995; Molteno et al. 1998; Andersen and Vulpius 1999), whereas only two articles have been published on fecal marking (lynx-Robinson and Delibes 1988; Geoffroy's cat-Soler et al. 2009).

Although wildcats are solitary animals with some home range overlap, these carnivores interact with other conspecifics throughout its territorial borders and during the reproductive period (Sunquist and Sunquist 2002); therefore, chemical signals are essential in the intraspecific communication. For many species of felids as wildcat, rates of scent marking are higher during periods of reproductive activity (Mellen 1993), being the males dependent on the presence of chemical signaling systems for attracting mates. The European wildcat (*Felis silvestris*) is a solitary and crepuscular animal whose contact with other conspecifics is restricted mostly to the breeding season (Kitchener 1995; Sunquist and Sunquist 2002). In addition, this felid is a territorial carnivore for which the home range of one male overlaps the home ranges of several females (Corbett 1979; Stahl et al. 1988), and the wildcats use scent marks to proclaim their territory (Stahl and Leger 1992).

However, the production and maintenance of scent marks incur costs (Gosling and Roberts 2001). Accordingly, carnivores frequently deposit scent marks in locations that increase their effectiveness as visual and olfactory signals (Peters and Mech 1975; Vilá et al. 1994; Barja et al. 2004, 2005; Barja 2009). Similarly, Gosling (1981) proposes an economic approach of scent marking in ungulates, which predicts that scent marks should be placed in zones that maximize the chances of being detected by conspecifics. Therefore, the chemical signals should not be distributed randomly but should be placed at strategic sites (e.g., visually conspicuous substrates, above the ground level, or at crossroads) to maximize their detectability and increase the active space of the chemical components (Alberts 1992; Gosling and Roberts 2001). Many animals use local landmarks as points of reference to create internal maps of the environment during their spatial navigation (Etienne et al. 1999). Local landmarks are often visually prominent objects (e.g., shrubs or logs) that allow precise the location of scent marks (Cheng and Spetch 1998). However, when environmental cues are unavailable or in the absence of light, scent marks can be used for orientation through the formation of trails marks (Lavenex and Schenk 1996; De León et al. 2003; Kulvicius et al. 2008).

Plants are often used as scent-marking posts by different carnivore species (cheetah—Eaton 1970; wildcat—Corbett 1979; tiger—Smith et al. 1989; leopard—Bothma and le Riche 1995; wolf—Barja 2009; civet—Tsegaye et al. 2008; Wondmagegne et al. 2011). The use of plants as the substrates on which to deposit scent marks confers certain advantages over deposition on the ground or other types of substrates. In this sense, Smith et al. (1989) showed that urine marks are detectable for a longer period when deposited on vegetal substrates than on the ground. However, despite the advantages of plant substrates as marking posts, few studies have been performed on mammalian species to determine the physical characteristics of plants that are selected for depositing scent marks (shape and size of the urinated trees in tigers—Smith et al. 1989; height, diameter, inclination, and leafiness of marked branches in klipspringer, *Oreotragus oreotragus*—Roberts 1997; plant species in African civet—Tsegaye et al. 2008; diameter, height, and species of defecated plants in Iberian wolf—Barja 2009). Furthermore, to date, few published studies are available on the ability of carnivores to discriminate plants by species and size during scent marking behavior.

Wildcats frequently deposit scent marks on certain plants, such as grass tussocks (Corbett 1979), which could be because of the abundance of these specific plants in the wildcats' habitat or the benefits of these substrates for the deposition of scent marks, as suggested for other mammals (Roberts 1997; Barja 2009). However, not all plants appear to be equally suitable for depositing scent marks. Therefore, wildcats should deposit their feces on plants with certain physical characteristics that increase the effectiveness of the signal. If this is true, it is possible to predict that wildcats will select larger, more obvious plants.

### Materials and methods

#### Study area

The study area is located in Northwest Spain, covers 5,722 ha, and includes the Montes do Invernadeiro Natural Park. This area is located in a transition zone between the Eurosiberian and Mediterranean biogeographical regions (Castroviejo 1977). The elevation ranges between 830 and 1,707 m. The plant community includes large areas of bush, with heather (*Erica australis*), prickled broom (*Pterospartum tridentatum*), broom (*Genista* sp.), Spanish white broom (*Cytisus multiflorus*), and yellow rock rose (*Halimium lasian-thum*) being the predominant species. The original deciduous forest exists in the valleys and along watercourses and mainly includes oak (*Quercus robur*), birch (*Betula celtiberica*), and holly (*Ilex aquifolium*). In some areas, there are planted forests of Scots pine (*Pinus sylvestris*) (Pulgar 2004).

### Wildcat feces survey

The data were collected between September 2008 and June 2009. Wildcats (Corbett 1979) and other felids (Iberian lynx—Robinson and Delibes 1988; ocelot— Emmons 1988; cheetahs—Broomhall et al. 2003) often use roads for traveling and frequently defecate on them as a means of scent marking. Therefore, we established a total of nine routes along roads (Electronic supplementary materials), ranging in length from 1 to 12 km; the routes were separated from each other by an average distance of 3.4 km (range, 0.5–6.8 km). Routes were chosen based on previous studies on wildcat distribution and habitat selection in this area (Barja and Bárcena 2005). For each route, 300-m-long transects were surveyed; the transects were separated from each other by 700 m, and a total of 32 transects were surveyed monthly. The number of transects on each route varied between one and eight, depending on the length of the route. All of transects included along the routes were conducted on foot to locate fresh wildcat scats deposited on plants, while scats deposited on other substrates were ignored.

# Specific, individual, and sexual identification of fecal samples

In general, wildcat scats are long, cylindrical, and thick (with a length of 10–20 cm and a diameter of 1.4–3.0 cm), with several fragments that fit perfectly (Corbett 1979). Because of their shape and size, wildcat feces are difficult to distinguish from those of other medium-sized carnivores, mainly feral cats and hybrids. Therefore, it is necessary to use a multifaceted approach involving DNA methods to distinguish between the feces of different felid species (Davison et al. 2002). To perform the specific, individual, and sexual identification among the fresh wildcat scats found on the vegetation, we genotyped 41 subsamples that were spread evenly throughout the study area. We considered a scat to be fresh when it had a moist layer of mucus, a strong smell, and no signs of dehydration.

DNA was extracted from fecal samples by salting-out and phenol-chloroform extraction based on the protocol described in Sambrook et al. (1989). For species identification, we used a molecular test based on the polymorphisms detected on a small nuclear gene fragment (221 bp of the IRBP— *Interphoto-receptor Retinoid-Binding Protein*—exon 1). This fragment reveal 51 variable sites (including 12 nonsynonymous and 19 species-specific sites), which enable the successful distinction of different carnivore species native to South-western Europe (for more details to see Oliveira et al. 2009). The specific identification was conducted to determine the specific origin (i.e., wildcats rather than feral cats, hybrids, or other carnivores) of the scats and the reliability of the obtained data.

The individual genotyping was performed as described by Oliveira et al. (2008) to determine the minimum number of individual wildcats from which the scats originated. This information was necessary to determine whether the number of detected scats was representative of the wildcat population and to minimize pseudoreplication. The individual multilocus genotypes were assessed using 12 neutral unlinked microsatellites that were previously isolated and characterized in the domestic cat (Mennoti-Raymond and O'Brien 1995; Menotti-Raymond et al. 1999): Fca008, Fca023, Fca026, Fca043, Fca045, Fca058, Fca077, Fca088, Fca096, Fca126, Fca132, and Fca149. Polymerase chain reaction (PCR) amplification of individual microsatellites was performed according to the procedure given by Randi et al. (2001). PCR products were separated by electrophoresis on a 6 % denaturing polyacrylamide gel and visualized by silver staining. Allele frequencies, standard diversity indices, and observed (H<sub>O</sub>) and expected (H<sub>E</sub>) heterozygosities for each locus and population were calculated using GENETIX 4.05 (Belkhir et al. 1996-2004). In addition, genotypes were analyzed with STRUCTURE 2.1 (Falush et al. 2003), a Bayesian procedure designed to model admixture linkage disequilibrium, which promises to assess efficiently older admixture events using tightly linked markers. In order to assess the statistical power of the admixture analysis to detect hybrids, we used HYBRIDLAB v. 1.0 (Nielsen et al. 2006) to simulate hybrid genotypes. We evaluated differences in allelic diversity and richness using FSTAT 2.9.3.2 (Goudet 2001). Finally, the fecal samples were sexed and individually identified by visualizing two samples under low amplification to identify the sex of the animal. The gender-specific marker ZFXY, which produces a 163-bp Y allele and a 166-bp X allele, was used for the identification of female/male fecal samples according to the protocol described in Lipinski et al. (2007). All samples were amplified twice.

### Plant physical characteristics

To determine the characteristics of the plants that are crucial in the decision-making process of wildcats to deposit fecal marks, each time a fresh scat was located on a plant substrate, the plant species was identified, and its maximum height and diameter were measured with a measuring tape (Table 1). When the same plant was marked with feces again, this plant with its immediate neighbors was not included in the sample to avoid replication. In addition, to estimate the availability of different sizes and species of plants in the environment and to determine whether there was indeed a selection process, 196 plots  $(1 \times 3 \text{ m})$  were established on the roads where the transects were performed. The plots were distributed evenly throughout the study area. In each plot, the plant species and maximum height and diameter were recorded for the four largest plants (Table 1). In addition, we determined the visual conspicuousness of plants both marked and unmarked by feces putting us at the height of a wildcat to know whether each plant was that most stood out within the established circumference (Table 1).

### Data analysis

A generalized linear mixed model (GLMM) was used to examine the relationships between the presence/absence of fecal marks on the plants and the different predictor

Variables	Definition	Hypothesis
Plant group (herbaceous/pulse/ woody)	We classified the plants into three categories: (1) herbaceous—false brome, <i>Brachypodium</i> <i>sylvaticum</i> ; (2) pulse—tall oatgrass, <i>Arrhenatherum</i> <i>elatius</i> , Yorkshire fog, <i>Holcus lanatus</i> , and quacking grass, <i>Briza media</i> ; (3) woody—broom, prickled broom, bell heather, <i>Erica cinerea</i> , blackberry, <i>Rubus</i> sp., and yellow rock rose	Some carnivores selected plants on which to deposit their scent marks in relation to their specific characteristics, which seem to increase the detection probability of the mark and the persistence over time (Schaller et al. 1985; Clevenger and Purroy 1991; Barja 2009). Therefore, the wildcats will choose those plant species that best enhance the effectiveness of the fecal marks
Visual conspicuousness (conspicuous/inconspicuous)	We considered that a scat was on a visually conspicuous plant when that plant was the most obvious to a human observer within a circle with a 2-m radius, with the plant at the center (Barja 2009)	The scent marks are expected to be placed on visually conspicuous substrates to maximize their detectability by other animals (Gosling and Roberts 2001), as observed for other carnivores (Macdonald 1980; Barja et al. 2005; Barja 2009)
Height and diameter (cm)	We measured the maximum diameter and height of the plants	Plants with a greater height and diameter are expected to be selected more often for the deposition of scent marks. These substrates enhance the scent component of the signal, thus facilitating the release of volatile compounds (Alberts 1992), and also enhance the visual component, thereby increasing their effectiveness

Table 1 Variables related to the plant physical characteristics considered as potential factors influencing the plant fecal-marking behavior of wildcats

variables, as follows: (1) factors, plant group, and visual conspicuousness; and (2) covariates, height, and diameter (Table 1). The number of each scat was included as a random factor. The dependent variable "fecal marking/ non-fecal marking on plants" was modeled with a binomial error distribution and a logit link function. The Akaike Information Criterion (Burnham and Anderson 2003) was used to select the most parsimonious models. To select the best GLMM models, the Akaike weights of each model were estimated by following the procedures described by Burnham and Anderson (2003). The variables with the highest weight ( $\sum \omega_m = 0.95$ ) were considered more important than other variables. The candidate models were selected according to the rule in which the models with  $\Delta i \leq 2$  were considered to have substantial empirical support (Burnham and Anderson 2003). Spearman's correlation was used to test the relationship between the height and the diameter of the plants marked.

The different plant species were pooled into three categories for the statistical analysis: herbaceous, pulse, and woody plants (Table 1). Jacobs' selection index (*D*) was estimated for each plant group in the determination of the groups of plants selected by the wildcats on which to deposit their fecal marks and those that were avoided. Jacobs' selection index ranges from -1 (total avoidance) to 1 (strongest preference); a value of 0 indicates a random selection (i.e., the plant group was selected according to its availability) (Jacobs 1974).

The chi-squared test  $(\chi^2)$  was used to analyze the differences between the observed frequencies (use of plants) and expected frequencies (availability of plants) with respect to their conspicuousness, plant group, and species.

The height and diameter of the plants marked with feces and the availability of plants in the study area are expressed as the means $\pm$ standard error (SE). The level of significance was set at *p* <0.05. All of the analyses were performed using STATISTICA v.8.0 software for Windows (StatSoft Inc., Tulsa, OK, USA).

## Results

Of 41 analyzed fecal samples from throughout the study area, we successfully identified 26 as being from the wildcat and none from other carnivore species. Consequently, 63.4 % of the collected fecal samples could be assigned to a species; in the remaining 36.6 %, the DNA extracted was not amplified. The coefficient of genetic differentiation of 0.17 over all loci revealed a genetic differentiation between our samples and reference domestic cat samples. The individual genotyping and the sexual identification confirmed the presence of 16 distinct individuals including five males and 11 females.

During the study, a total of 104 fresh wildcat scats were found on plants evenly distributed among routes and months. Only 22.4 % wildcat scats were found on other substrates. The physical characteristics of 519 plants available in the environment (not used for depositing fecal marks) were also analyzed.

The model selection process for the fecal marking on plants indicated that 31 occurrence models and six models were regarded as plausible. The diameter and plant group variables were given the most importance in the process of selecting the occurrence models, with both having positive values (Table 2), with the plants more frequently marked with feces by the wildcats having greater diameters and belonging to the herbaceous and woody plant groups. The mean diameter of the feces-marked plants was greater than that of the unmarked plants, whereas the mean height of the feces-marked plants was similar to that of the unmarked plants (Fig. 1). The mean height of the feces to the ground was 10.33 cm. The diameter × vegetal group interaction was another robust finding (Table 2). A low positive correlation was found between the height and diameter of the plants (Spearman correlation—r=0.202, p=0.0001, n=623).

The wildcats deposited fecal marks on plants with diameters >26 cm even though plants with diameters of 6-20 cm were the most abundant in the environment (Fig. 2a). The average height of the plants marked with feces was 39.54 cm (see Fig. 1), and the average distance from the ground to the excrement height was 10.33 cm. However, the wildcats did not exhibit a pattern in the selection of the plant height because the heights of the marked plants were similar to those expected if chosen at random in the environment (Fig. 2b).

Moreover, the visual conspicuousness had a high importance in the model-averaging inference (Table 2). Our results suggest that wildcats deposited their fecal marks more frequently on visually conspicuous plants (77.9 %) than on inconspicuous plants (22.1 %) even though the proportion of visually conspicuous (49.1 %) and inconspicuous plants (50.9 %) was very similar in the environment ( $\chi^2$ =34.39, *df*=1, *p*=0.0001, *n*=104).

With respect to the feces deposition, 66.3 %, 22.2 %, and 11.5 % feces were deposited on herbaceous, woody, and pulse plants, respectively. Both herbaceous and woody

 Table 2 Results of generalized linear mixed model (GLMM)-averaging inference for the occurrence of the fecal marking of plants by wildcats

Variable	$\sum w_i$	β	SE
Intercept		99.72	29.61
Diameter	1.00	69.87	8.93
Plant group	1.00	8.04	8.93
Visual conspicuousness	0.57	0.52	0.85
Diameter×plant group	0.30	8.99	10.78

For each variable, the table shows the weight across the most parsimonious models  $(\sum w_i)$ ,  $\beta$  coefficient, and standard error (SE)

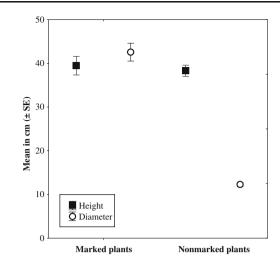


Fig. 1 Comparison of the mean height and diameter of feces-marked plants (n=104) and non-marked plants (n=519). The mean±SE is shown for both groups

plants were more often marked with feces than expected if chosen at random; in contrast, the plants included in the pulse group were used less frequently than would be expected by their availability in the environment. Given the environmental availability of these plant groups, these differences in the use of different plant groups for depositing fecal marks were statistically significant ( $\chi^2$ =154.15, *df*=2, *p*=0.0001, *n*=623). The values of Jacobs' selection index indicated that the woody and herbaceous plants were neither selected nor rejected according on their availability in the environment (*D*=-0.12 and -0.17, respectively), whereas

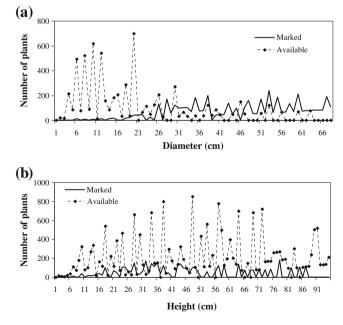


Fig. 2 Frequency distributions of the a diameter and the b height of feces-marked plants compared with those of non-marked plants

plants in the pulse group were rejected for the deposition of fecal marks (D=-0.74).

The differences in the use of different plant species for depositing fecal marks in relation to their environmental availability were also significant ( $\chi^2$ =162.13, df=8, p= 0.0001, n=104). False brome (*Brachypodium sylvaticum*), bell heather (*Erica cinerea*), prickled broom (*Pterospartum tridentatum*), broom (*Genista* sp.), blackberry (*Rubus* sp.), and yellow rock rose (*Halimium lasianthum*) were marked more frequently than expected based on their availability, whereas tall oatgrass (*Arrhenatherum elatius*), quacking grass (*Briza media*), and Yorkshire fog (*Holcus lanatus*) were marked at frequencies lower than their relative environmental availability (Fig. 3).

## Discussion

The results of this study showed that certain characteristics of plants, namely the size, plant group, and visual conspicuousness, determine their selection as fecal-marking posts by wildcats. The wildcats in the study area selected plants with greater diameters, possibly because this characteristic enhances the visual component of the mark, as suggested for other carnivore species (Barja 2009). In addition, plants with greater diameters can support the fecal weight better, and thus help to prevent feces falling to the ground as to prolong the detectability of the scent mark.

The fact that the studied wildcats deposited their fecal marks on the visually conspicuous plants in addition to choosing plants with a greater diameter seems to increase the probability of the detection of the fecal marks by other individuals, including both competitors (reflected in a more effective territorial defense) and potential mates. Furthermore, because wildcats defend large territories in which constant monitoring is impossible, scent marks must be able to function in their temporary absence and indirectly communicate to intruders of the potential of being discovered by the owner (Richardson 1993). The present results support the economic

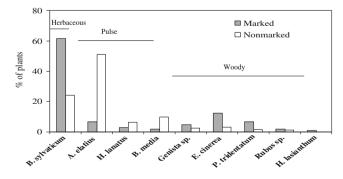


Fig. 3 The proportion of each plant species that was marked with feces by the wildcats relative to the proportion of the number of plants of each species at the study site

approach to scent marking proposed by Roberts and Gosling (2001) in which scent marks are placed to maximize their chance of being detected by competitors and potential mates. Territory owners deposit scent marks to intercept intruders and also to announce their presence for facilitating their own detection and maximizing the resulting benefits. Thus, many carnivores deposit their scent marks in potential contact zones between territories, including trails and crossroads (Smith et al. 1989; Zub et al. 2003; Barja et al. 2004).

Our results indicated that the wildcats did not select the plants on which to deposit their fecal marks according to the plant height. This behavior may be because the available plants in the environment exhibited heights that were similar to the marked plants, which seem to be the optimum height for wildcats to deposit their feces. However, by depositing their fecal signals on plants, wildcats increase the diffusion of the signal, thereby increasing their active field (Alberts 1992). This idea is supported by the diffusion model of Bossert and Wilson (1963), which states that the parameters of pheromone transmission have been adjusted in the course of evolution to obtain a high degree of efficiency. In this way, the frequent use of tall substrates as marking posts is observed for other carnivore species (Peters and Mech 1975; Barja et al. 2001; Tsegaye et al. 2008; Barja 2009).

Wildcats might use plants with larger diameter for selforientation. In this sense, mammals are generally well equipped to perceive and memorize visual landmarks (Etienne et al. 1999). Wildcats are generally more active at dawn and dusk and during the night also show peaks of activity (Corbett 1979; Urra 2003), but they show a good vision in dark conditions because the presence of tapetum lucidum improves their night vision. Therefore, nocturnal species and with large territories such as the wildcat may depend more on scent marks for orientation than diurnal species and with small territories. Thus, the deposition of fecal marks on visually conspicuous plants could enhance the presence of visual landmarks or use them as olfactory landmarks to form a cognitive map. Lyall-Watson (1964) suggested that the green acouchi (Myoprocta pratti) adds odor to specific visual landmarks to familiarize itself with its environment. Similarly, other animals combine visual and olfactory landmarks to navigate (toads, Bufo bufo, Sinsch 1987; various monkeys species, Bicca-Marques and Garber 2004) because bimodal sensory input accelerates the acquisition of landmark information (Steck et al. 2011).

Another characteristic that appears to influence the decision making of wildcats in the deposition of their fecal marks is the group to which a plant belongs. Our results indicate that herbaceous and woody plants were used more often than expected according to their availability; in contrast, pulse plants were generally rejected for fecal mark deposition. The selection of woody plants may be related to their characteristics (e.g., rough-textured evergreen leaves) that allow the signal to remain for a longer period of time, thus maximizing the probability of detection by intruders and potential mates. The substrate texture is an important factor during scent marking in brown bears (*Ursus arctos*) (Clevenger and Purroy 1991) and giant pandas (*Ailuropoda melanoleuca*) (Schaller et al. 1985). Thus, the strong odor of a freshly marked plant might add an olfactory signal to the scent marks (Bowyer et al. 1994). In contrast, wildcats may not deposit fecal marks on pulse plants because of their smaller size, which makes them less visually conspicuous, and because they represent sparse foliage, leaving the mark most exposed to the elements and causing both the scent and visual signal to deteriorate rapidly.

The choice of false brome as the most common plant species on which the wildcats deposited their fecal marks may be related to its size. In addition, the many broad leaves of this species ensure that the scent mark remains detectable for longer as they prevent the feces falling to the ground. However, further studies are necessary to determine which characteristics of plants increase the persistence time of the fecal marks of carnivores. Indeed, the selection of certain plant species by carnivores for the deposition of their scent marks has been sparsely documented [grizzly bear (Ursus arctos) and black bear (Ursus americanus)-Lloyd 1979; wolf (Canis lupus)-Barja 2009]. Another aspect that may explain the high frequency of fecal marking on false brome is the defense and marking of an important resource. Bromes have appeared frequently in the diet of wildcats in the study area (Piñeiro and Barja 2011). In fact, cats seem to eat rough grass to regurgitate hairballs or intestinal parasites (Engel 2003). Other mammalian species are reported to have a preference for placing scent marks on plants on which they feed as a method of proclaiming their ownership, including klipspringers (Oreotragus oreotragus) (Roberts 1997), common marmosets (Callithrix jacchus) (Lázaro-Perea et al. 1999), golden lion tamarins (Leontopithecus rosalia) (Miller et al. 2003), and Verreaux's sifaka (Propithecus verreauxi) (Lewis 2005).

The results of the present study suggest that the visual components of a vegetal substrate determine whether a wildcat selects the plant to deposit its fecal marks. Although wildcats may intentionally select certain plants as visual and olfactory landmarks merely for spatial orientation, further studies are required to clarify this issue. Because of the importance of certain plant substrates in the fecal marking behavior of wildcats and the need to select the most effective locations so that the marks are detected by other conspecifics, removing these marks while clearing the vegetation may alter the marking behavior and orientation of wildcats, eliminating the potential marking sites and navigation marks and thus affecting the spacing of the animals. Acknowledgments We thank the Nature Conservation Service of Ourense (Regional Government of Galicia) for providing the permits required to conduct this study in the Montes do Invernadeiro Natural Park, with particular thanks to Víctor Manuel Gil. Thanks are due to Centro de Investigação em Biodiversidade e Recursos genéticos (CIBIO/CTM, Portugal) for conducting the molecular work. We are grateful to gamekeepers Ricardo Prieto, Tomás Pérez, Paco Barja, and Antonino Núñez who kindly provided us logistical assistance during the fieldwork.

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