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Evaluating the function of wildcat faecal marks in relation to the defence of favourable hunting areas

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To date, there have been no studies of carnivores that have been specifically designed to examine the function of scent marks in trophic resource defence, although several chemical communication studies have discussed other functions of these marks. The aim of this study was to test the hypothesis that faecal marks deposited by wildcats (*Felis silvestris*) serve to defend their primary trophic resource, small mammals. Field data were collected over a 2-year period in a protected area in northwestern Spain. To determine the small mammal abundance in different habitat types, a seasonal live trapping campaign was undertaken in deciduous forests, mature pine forests, and scrublands. In each habitat, we trapped in three widely separated UTM (Universal Transverse Mercator) cells. At the same time that the trapping was being performed, transects were conducted on foot along forest roads in each trapping cell and in one adjacent cell to detect fresh wildcat scats that did or did not have a scent-marking function. A scat was considered to have a presumed marking function when it is located on a conspicuous substrate, above ground level, at a crossroad or in a latrine. The number of faecal marks and the small mammal abundance varied by habitat type but not by seasons. The results of the ANCOVA analysis indicated that small mammal abundance and the habitat type were the factors that explained the largest degrees of variation in the faecal marking index (number of faecal marks in each cell/number of kilometres surveyed in each cell). This result suggests that wildcats defended favourable hunting areas. They mark most often where their main prey lives and so where they spend most time hunting (in areas where their main prey is more abundant). This practice would allow wildcats to protect their main trophic resource and would reduce intraspecific trophic competition.

KEY WORDS: defence, faecal marking behaviour, small mammal abundance, trophic

resource, wildcat.

Short title: Faecal marks in the defence of food resources in wildcats

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INTRODUCTION

Animals compete for resources, such as food, mates, and shelter (MAHER & LOTT 1995; GESE 2001), and defend these resources by such means as intraspecific communication by depositing visual and olfactory signals. These chemical marks should not be distributed randomly but should be placed at strategic sites to indicate

local and/or global landmarks; to fix certain sites, such as the current position or their own nest or hive; and to signal the changing location of food sources (SHETTLEWORTH 1998; ETIENNE & JEFFERY 2004). Thus, GOSLING (1981) predicts in his economic approach to scent marking in ungulates that scent marks should be placed in those zones that maximise the chances of being detected by conspecifics, for instance, in elevated and conspicuous places (GOSLING & ROBERTS 2001a). Thus, many mammals, including wildcats, deposit their faecal marks on conspicuous substrates, above ground level, at crossroads, and in latrines (PETERS & MECH 1975; CORBETT 1979; GORMAN & MILLS 1984; ROBINSON & DELIBES 1988; ZUB et al. 2003; BARJA et al. 2004, 2005; BARJA & LIST 2006; BARJA 2009; PIÑEIRO & BARJA 2012). Felids use urine, faeces and secretions of different glands as visual and scent marks. These scent marks are often deposited along forest roads, on relevant sites to increase their efficiency (CORBETT 1979; PANAMAN 1981; GOSLING 1985; MACDONALD 1985; SCHMIDT & KOWALCZYK 2006; PIÑEIRO & BARJA 2012).

Studies conducted on carnivores have revealed that scent marks have important functions, including defending territory [brown hyaenas, *Hyaena brunnea*: GORMAN & MILLS 1984; snow leopard, *Uncia uncia*: AHLBOM & JACKSON 1988; ocelot, *Leopardus pardalis*: SHINN 2002; cheetahs, *Acinonyx jubatus*: BROOMHALL et al. 2003; black-footed cat, *Felis nigripes*: MOLTENO et al. 2006]; advertising reproductive condition [snow leopard: AHLBOM & JACKSON 1988; cheetahs: BROOMHALL et al. 2003; black-footed cat: MOLTENO et al. 2006]; advertising social status [snow leopard: AHLBOM & JACKSON 1988]; identifying individuals, groups, and species and preventing intrasexual competition [mongoose, *Mungos mungo*: MÜLLER & MANSER 2007]; indicating previously used food patches [wildcats, *Felis silvestris*, and domestic cats, *Felis silvestris catus*: CORBETT 1979; Otter, *Lutra lutra*: KRUUK et al. 1993; wolves, *Canis lupus*: ZUB et al. 2003]; and assisting in optimal foraging [Ethiopian wolves, *Canis simensis*: SILLERO-ZUBIRI & MACDONALD 1998]). Some studies have indicated that the deposition of scent marks serves to minimise the forage time in carnivores such as foxes, *Vulpes vulpes* (HENRY 1977); wolves, *Canis lupus* (HARRINGTON 1981); otters, *Lutra lutra* (KRUUK 1993); badgers, *Meles meles* (ROPER et al. 1993) and coyotes, *Canis latrans* (GESE & RUFF 1997).

Scent marking behaviour in the territorial boundaries may be an individually distinctive signature of territory occupancy (GORMAN & MILLS 1984; GORMAN 1990), thereby excluding competitors from an area containing one or more key resources (GOSLING & ROBERTS 2001b). For several mammal species, scent marking seems to be related to the availability of trophic resources (otter: KRUUK 1992; REMONTI et al. 2011; ALMEIDA et al. 2012; wolf: ZUB et al. 2003; jaguar: AZEVEDO & MURRAY 2007). The importance of the principal prey abundance on the habitat selection and the home range size has been documented for many species of felids (jaguar: RABINOWITZ & NOTTINGHAM 1986; snow leopard: AHLBOM & JACKSON 1988; Eurasian lynx: JEDRZEJEWSKI et al. 2002; cheetahs: BROOMHALL et al. 2003; Geoffroy's cat: MANFREDI et al. 2006; wildcat: LOZANO et al. 2006, 2007). In this way, visual and scent marks deposited by resource holders provide a means of reducing the cost of resource defence if the recipients of this scent mark decide to avoid the conflict (ERLINGE et al. 1982; RICHARDSON 1993; MAHER & LOTT 1995; RICH & HURST 1998; GOSLING & ROBERTS 2001a). Thus, in studies performed in mammals, the intruders can identify residents using these scent marks and assess the costs and benefits of competing for the defended resources (GOSLING & MACKAY 1990; GOSLING &

ROBERTS 2001a). Taking into account, competition for food should be lower in areas with a high availability of resources and when defence costs are lower than the benefits of having exclusive use of a resource (AZEVEDO & MURRAY 2007). Despite this prediction, visual and scent marks (e.g., faeces, urine, and glandular secretions) in the wildcat could be deposited to identify territory edges and to defend trophic resources from potential competitors, as occurs in other felids, such as snow leopards (AHLBOM & JACKSON 1988).

The wildcat is a solitary and territorial carnivore in which intraspecific contact is mainly limited to the breeding season (SUNQUIST & SUNQUIST 2002). Both sexes share a territory and associate only during the mating season, during which chemical communication is very important. In our study area, individual genotyping through molecular analysis using 41 samples of fresh faeces identified a total of 25 different wildcat genotypes (6 males and 19 females), with the home ranges averaging 953.7 ha for males and 301.2 ha for females. Males typically have home ranges that overlap those of several females (URRA 2003). Studies conducted on wildcats have shown that this species uses scent marking to defend its territories from potential competitors (CORBETT 1979; KITCHENER 1991).

This study was designed to test the hypothesis that the faecal marks deposited by wildcats serve to defend their principal trophic resource. Therefore, one could predict that (1) wildcats vary the deposition of faecal marks by season in parallel with the increase in the abundance of their main prey (small mammals); (2) wildcats place more faecal marks in habitats that contain a higher abundance of their main prey; and (3) the faecal marks deposited by wildcats serve to defend their main trophic resource and reduce intraspecific competition.

MATERIAL AND METHODS

Study area

The study area was located in the northwest region of the Iberian Peninsula and included Os Montes do Invernadeiro Natural Park, which covers an area of 5,722 ha. The altitude varies from 830 to 1,707 m. The study area occupies a transitional zone between the Eurosiberian and Mediterranean biogeographical regions, which is manifested by the alternation between Atlantic relict forest and Mediterranean plant species (PULGAR 2004). The predominant vegetation is made up of scrubland, original deciduous forests, and pine forests. The principal plant community in the park is scrubland and is primarily formed by associations of heather (*Erica australis*), prickled broom (*Pterospartum tridentatum*), and sandling (*Halimium lasianthum*). The valleys and water courses contain original deciduous forests formed principally by the associations of oak (*Quercus robur*), birch (*Betula celtiberica*), holly (*Ilex aquifolium*), and yew (*Taxus baccata*). Large extensions are occupied by repopulated Scot pine (*Pinus sylvestris*) forests (PULGAR 2004).

Abundance of small mammals

Previous studies conducted in the study area indicated that small mammals constitute the principal prey of wildcats and that their abundance varies with habitat type (PIÑEIRO & BARJA 2011). Therefore, to determine the abundance of small mammals, the main trophic resource of the wildcat in the study area (PIÑEIRO & BARJA 2011), from August 2005 to June 2007, live trapping were undertaken over 9 days per season in the most representative habitats of the study area (deciduous forest, mature pine, and scrubland). In each habitat, three trapping sites spaced at least 3 km apart were selected in a total of 9 different 1-km² UTM (Universal Transverse Mercator) cells to conduct the live trapping. In each cell, we placed 25 Sherman traps in a grid, where traps were located 10 m apart (total effort, 4,725 traps-nights). The distance between trapping sites was established based on the home range mean size of wildcats in the study area (PIÑEIRO & BARJA 2012). Thus, we increase the likelihood of obtaining data from different individuals and minimise pseudoreplication. The percentages of the three main habitats in each trapping cell and adjacent cells were quantified using a geographical information system (GIS) database (scale 1:25,000) on topographic maps (Sistema de Información y Ocupación del suelo in Spain and the Base Cartográfica Nacional 2005). In this way, we identify as similar cells those with habitat types that coincided by at least 95%. We extrapolated the number of small mammals captured in each trapped cell to the adjacent cell.

In each cell, we placed a grid containing 25 Sherman traps, separated by 10 m and covering 0.25 ha at each sampling point. The traps were left open for 24 hr for 3 consecutive nights, and bread soaked in oil was used as bait. To minimise the time that small mammals were in the traps and their potential vulnerability to predators, traps were monitored at least every 12 hr (sunrise and sunset) (GURNELL & FLOWERDEW 1994; POWELL & PROULX 2003). During study, bedding was included in the live-traps to reduce mortalities; we used raw wool with natural lanolin because it is an excellent insulator that repels water. Additionally, traps were set under the cover of shrubs or dense herbs to conceal them from harassment by predators and to provide some thermal insulation (GURNELL & FLOWERDEW 1994; POWELL & PROULX 2003). No evidence of predators approaching the traps was recorded during the study. To allow the identification of each individual for later recapture and to thus avoid pseudoreplication in the abundance data, a minimum amount of non-toxic, waterproof, permanent, coloured paint was applied to the chest, paws or tail root of all individuals during their first capture for identification. In each captured animal, the coloured paint was placed in a different place. Thus, this capture-recapture technique allowed us to determine the minimum number of small mammals alive in each cell trapped. After handling, the small mammals were released at the point of capture.

The number of pregnant or lactating females caught was very low (3.4%), and only 2.6% of the small mammals died as a result of the trapping conducted for this study. We followed ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching (SHERWIN 2006). Research was undertaken under the permission of the Xunta Galicia Wildlife Authority (letters of 18/04/05, 18/09/06, 13/07/07).

Detection of faecal marks

To detect the scats of wildcats, we established transects along forest roads (trails, tracks and paths) because wildcats, as well as other medium-size carnivores [e.g., red fox and pine marten (*Martes martes*)], use roads for travelling and frequently defecate on the roads as a means of visual and scent marking (CORBETT 1979; BARJA 2005). From August 2005 to June 2007, 300-m transects along forest roads were conducted seasonally on foot in the trapped cells and on adjacent cells to locate wildcat fresh scats and to record the number of scats deposited with a presumed marking function or without a marking function. We surveyed a total of 200 transects uniformly distributed throughout the study area with a total area surveyed of 60 km². In each

cell, the 300-m transects were separated by a distance of 700 m to increase the probability of locating scats from different individuals of wildcat and to minimise the pseudoreplication. All transects were conducted at the same time as the trapping campaign; therefore, we repeated the same transects each season during the study to detect faeces with a presumed marking function and without a marking function. The number of 300-m transects performed in each cell to locate fresh wildcat scats varied in relation to the length of road that crossed each cell. Thus, the length of roads surveyed in the cells was different, ranging between 1.6 km and 4.0 km. Therefore, we used an abundance kilometric index that was obtained by dividing the number of scats with or without a marking function that were detected per the number of kilometres surveyed in each cell.

A scat was considered to have a presumed marking function if its location exhibited at least two of the following characteristics: (1) on a conspicuous substrate; (2) above ground level; (3) at a crossroad; or (4) in a latrine (accumulation of two or more scats; BARJA et al. 2005). Substrates were classified as inconspicuous or conspicuous, where the latter describes scats that stood out from the surroundings, such as rocks, plants, and mounds. We considered a scat to be on a conspicuous substrate when the substrate was the most obvious to a human observer within a circle with a 1-m radius, with the scat at the centre. Inconspicuous substrates were all others (e.g., bare ground) (BARJA et al. 2004; BARJA 2009; PIÑEIRO & BARJA 2012). A scat that did not exhibit at least two of the above features was considered not to have a marking function.

Wildcat scats were differentiated from those of other medium carnivores present in the study area by their morphological characteristics (size and shape). The scats of wildcats, domestic cats, and their hybrids are very similar and are difficult to differentiate. However, the nearest human population was 7 km to the south of the study area; the presence of domestic cats would, therefore, at the very least be minimal. Additionally, during this study, 24 cats were observed and another 8 were photographed using camera traps; all cats showed typical wildcat external morphology (KITCHENER 1995; SUNQUIST & SUNQUIST 2002). None of the faeces detected along the transects were buried; indeed, they often had a marking function and were deposited in prominent locations. Wildcats are reported to show this behaviour (CORBETT 1979; BARJA & BÁRCENA 2005), while domestic cats tend to bury their faeces in areas where both domestic and wildcats occur (CORBETT 1979; SCHAUBENBERG 1981). For more details about wildcat scat-based studies see a wide discussion in LOZANO et al. (2013).

Data analyses

As the data were not normally distributed, we performed a logarithmic transformation of the quantitative variables prior to analysis to ensure normality (Kolmogorov-Smirnov test) and homoscedasticity (Levene's test). To determine whether the faecal marking index was influenced by the abundance of small mammals, a Pearson correlation was performed between the two variables.

We used a mixed general linear model (ANCOVA) to test whether the faecal marking index varied in relation to habitat type and season (fixed factors). We included small mammal abundance as a covariate. The months of the year were pooled into seasons: April-June (spring), July-September (summer), October-December (autumn), January-March (winter). One-way analyses of variance (ANOVAs) were used to determine the effects of habitat type and season on the faecal marking index and on the abundance of small mammals. The results are given as the means \pm standard error (SE). The significance was set at $P < 0.05$. All analyses were performed with SPSS v.15.0 software for Windows (SPSS Inc, Chicago, IL, USA).

RESULTS

During the study, 194 fresh wildcat scats were observed (51.5% with a presumed marking function and 48.5% without a presumed marking function), and 232 small mammals were captured. The abundance of small mammals varied by UTM cell, and the average (\pm SD) was 3.21 ± 0.74 animals captured. We found a significant positive correlation between the variables small mammal abundance and the index of faeces with a presumed marking function ($r = 0.303$, $P = 0.0001$). In contrast, the correlation between the variables small mammal abundance and the index of faeces without a presumed marking function was not significant ($r = 0.157$, $P = 0.130$). There was a significant difference between UTM cells in faecal marking index ($\chi^2 = 79.18$, $df = 9$, $P = 0.0001$, $N = 193$) and in small mammal abundance ($\chi^2 = 182.08$, $df = 2$, $P = 0.0001$, $N = 232$). In contrast, we did not find a significant difference in the effect of season in either the small mammal abundance (ANOVA: $F_{3,232} = 1.776$, $P = 0.157$; Games-Howell test, $P > 0.05$ for all seasons) or the frequency of faeces with a presumed marking function (ANOVA: $F_{3,99} = 1.521$, $P = 0.214$; Games-Howell test, $P > 0.05$ for all seasons). Regarding habitat type, we captured significantly more small mammals in scrubland (43.5%) than in deciduous forest (38.4%) or pine forest (18.1%) (Fig. 1; ANOVA: $F_{2,191} = 740.67$, $P = 0.0001$; Games-Howell test, $P < 0.05$ for all habitats). The faecal marking index was significantly higher in scrubland than in deciduous forest or mature pine forest (Fig. 1; ANOVA: $F_{2,97} = 11.15$, $P = 0.0001$; the Games-Howell test was used to compare mature pine with scrubland and deciduous forest with scrubland, $P < 0.05$). The index of faeces without a presumed marking function was significantly higher in deciduous forest than in scrubland and mature pine forest (Fig. 1; ANOVA: $F_{2,93} = 14.81$, $P = 0.0001$; Games-Howell test for all habitats, $P < 0.05$).

The results of the ANCOVA analysis (Table 1) indicated that the abundance of small mammals in the adjacent and trapped cells and, to a lesser extent, the habitat type determined the largest amount of variation in the faecal marking index. In contrast, the season and the interaction between habitat and season did not influence in the faecal marking index (Table 1).

DISCUSSION

The results of this study showed that the abundance of principal prey and habitat type were the factors that best explained faecal marking patterns in wildcats. Therefore, in those habitats with a higher abundance of small mammals (scrubland and deciduous forests), wildcats deposited a greater number of faecal marks. In contrast, wildcats did not respond differently in the deposition of their faeces with a presumed marking function among seasons. Therefore, our results suggest that faecal marking in wildcats is not influenced by seasonal parameters, such as mating or breeding. Furthermore, the fact that the faecal marking index did not vary between seasons could be related to the facultative specialist characteristic of the wildcats in the study area (PIÑEIRO & BARJA 2011). In this study, the seasonal consumption of small mammals depended on the ease of capture rather than their availability in the area (PIÑEIRO & BARJA 2011). Taking into account that small mammals are abundant all the year, with no difference among seasons, wildcats seem to defend their principal trophic resource throughout the year.

Wildcats have been described as nocturnal animals, being most active at dawn and dusk (CORBETT 1979). In dark environment conditions, mammals may utilise specific landmarks (e.g., scent marks which they deposit on physical structures) in their navigation (AVNI et al. 2006). This affirmation concurs with the high number of faeces with scent-marking function relative to those without it. Similarly, a study conducted in the study area showed that wildcats select conspicuous substrates as signal posts, facilitating the location of faecal marks (PIÑEIRO & BARJA 2012). On the other hand, the theory of feeding strategies (SCHOENER 1971) predicts that a predator should expend their time and energy only in the pursuit, handling, and consumption of prey, not on searching for it. In accordance, we would expect that wildcats deposit a greater number of faecal marks in habitats that contain a higher abundance of small mammals to minimise the forage time while simultaneously defending their principal trophic resource.

The difference among habitat types in terms of small mammal abundance is consistent with the selection of protective vegetation cover for reducing predation risk imposed by predators (KORPIMÄKI et al. 1996; PUSENIUS & OSTFELD 2002). In the study area, small mammals are present in the diet of several species (e.g., pine marten: ROSELLINI et al. 2008; wildcat: PIÑEIRO & BARJA 2011). So, to reduce the risk of predation, we could expect that small mammals should prefer safer, denser, and higher vegetation microhabitats, which offer shelter and escape possibilities. Thus, studies performed in scrubland habitats in the study area (BARJA 2005) and other areas (MORENO & KUFNER 1988; CAMACHO & MORENO 1989) showed a high abundance of small mammals in this habitat because it offers more refuges for these prey species (MUÑOZ et al. 2009). Additionally, the differences in the wildcats faecal marking index among habitats seems to be related to the habitat selection and abundance of their principal prey. Thus, wildcats in the study area deposited a greater number of faecal marks in scrubland areas, the habitat with a higher abundance of their principal prey, small mammals. These results were consistent with the economic approach to scent marking proposed by GOSLING (1981) for ungulates, which predicted a greater number of scent marks in locations where the preferred food is more abundant. Additionally, the results obtained in this study supported the hypothesis suggested by CORBETT (1979) that wildcats deposit a higher number of scent marks in resting areas and principal hunting areas. In addition, recent studies conducted on wildcat habitat selection in the Iberian Peninsula indicate that the felid is not a strictly forest species; wildcats prefer open fields made up of scrublands and pastures (LOZANO et al. 2007).

The higher number of faecal marks in deciduous forests than in pine forests could be related with that the pine marten prefers this habitat type in the study area (BARJA 2005), so wildcats could increase the deposition of faecal marks in deciduous forests to defend their main prey in the presence of an interference competitor, the pine marten.

The lower number of faecal marks detected in the pine forests of the study area appears to be related to the low prey availability in this habitat. This result is similar to that of a study performed by CORBETT (1979), who indicated that mature coniferous forests were rejected by wildcats. This study indicated that wildcats rarely use this habitat type due to the low abundance of prey caused by a lack of refuge for prey species. Additionally, the results of the present study are in concordance with those of habitat selection by wildcats in Europe (EASTERBEE et al. 1991).

On the other hand, the wildcats in the study area deposited a greater number of faeces on conspicuous substrates and at strategic sites (crossroads). This practice increased the efficiency of the scent marks and the probability of detection by other individuals, as indicated in other species of carnivores (EATON 1970; MACDONALD 1985; EMMONS 1988; ROBINSON & DELIBES 1988; BROOMHALL et al. 2003; BARJA et al. 2004; BARJA 2009). This result is supported by the second prediction of the economic approach to scent marking (GOSLING 1981), which indicates that scent marks should be placed on substrates that increase their efficiency and in zones of the territory where the probability of detection by competitors is higher, thus reducing the costs of resource defence and avoiding agonistic encounters between competitors (GOSLING & MACKAY 1990; AZEVEDO & MURRAY 2007).

The high number of faeces with a presumed marking function deposited by the wildcat in favourable hunting areas can also help to optimise the food search, a basic process assuring the survival of individuals. This scent-marking strategy advertises to other inter- and intra-specific individuals exploiting the same food resource that the resources at that location have been and are being exploited. In addition, according to the feeding strategies theory, the time required for a food search decreases, and the effort is centred on favourable hunting areas, which can be located using their spatial memory owing to the use of their scent marks as landmarks. In the present study, the faeces from males and females could not be distinguished; therefore, another possibility that can explain the defence of favourable hunting areas by wildcats is resource-defence polygyny (EMLEN & ORING 1977), where the female's choice of mate should be influenced both by the quality of the defending male and the resources under his control (EMLEN & ORING 1977). Taking this limitation into account, further studies are needed to determine whether the sexual variation in scent-marking patterns by wildcats is influenced by the availability of important resources.

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REFERENCES

- AHLBOM G.C & JACKSON R.M. 1988. Marking in free-ranging snow leopards in west Nepal: a preliminary assessment, pp. 25–49. In: Freeman H., Ed. Proceedings of the Fifth International Snow Leopard Symposium. *Dehra Dun, India: International Snow Leopard Trust and Wildlife Institute of India.*
- ALMEIDA D., BARRIENTOS R., MERINO-AGUIRRE R & ANGELER D.G. 2012. The role of prey abundance and flow regulation in the marking behaviour of Eurasian otters in a Mediterranean catchment. *Animal Behaviour* 84 (6): 1475–1482.

- AVNI R., ZADICARIO E & EILAM D. 2006. Exploration in a dark open field: a shift from directional to positional progression and a proposed model of acquiring spatial information. *Behavioural Brain Research* 171: 313–323.
- AZEVEDO F.C & MURRAY D.L. 2007. Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biological Conservation* 37: 391–402.
- BARJA I. 2005. Winter distribution of European pine marten *Martes martes* scats in a protected area of Galicia, Spain. *Mammalia* 69: 435–438.
- BARJA I. 2009. Decision making in plant selection during the faecal–marking behaviour of wild wolves. *Animal Behaviour* 77: 489–493.
- BARJA I & BÁRCENA F. 2005. Distribución y abundancia de gato montés (*Felis silvestris*) en el Parque Natural Os Montes do Invernadeiro (Galicia, NO de España): factores de hábitat implicados y relación con la presencia de zorro y marta. *Galemys* 17: 29–40.
- BARJA I. & LIST R. 2006. Faecal marking behaviour in ringtails (*Bassariscus astutus*) during the non-breeding period: spatial characteristics of latrines and single faeces. *Chemoecology* 16: 219–222.
- BARJA I., MIGUEL F.J & BÁRCENA F. 2004. Importance of the crossroads in faecal marking behaviour of the wolves (*Canis lupus*). *Naturwissenschaften* 91: 489–492.
- BARJA I., MIGUEL F.J & BÁRCENA F. 2005. Faecal marking behaviour of Iberian wolf in different zones of their territory. *Folia Zoologica* 54: 21–29.
- BROOMHALL L.S., MILLS M.G.L & DU TOIT J.T. 2003. Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. *Journal of Zoology* 261: 119–128.
- CAMACHO M. & MORENO S. 1989. Datos sobre la distribución espacial de los micromamíferos en el Parque Nacional de Doñana. *Doñana Acta Vertebrata* 16: 239–245.
- CORBETT L.K. 1979. The food of wild cats (*Felis silvestris*) and domestic cats (*Felis catus*) in Scotland. *Ph.D. Dissertation, University of Aberdeen, Scotland*.
- EASTERBEE N., HEPBURN L.V. & JEFFERIES D.J. 1991. Survey of the status and distribution of the wildcat in Scotland, 1983–1987. *Edinburgh: Nature Conservancy Council for Scotland*.
- EATON R.L. 1970. Hunting behavior of the cheetah. *Journal of Wildlife Management* 14: 56–67.
- EMLEN S.T. & ORING L.W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215–223.

- EMMONS L.H. 1988. A field study of ocelots (*Felis pardalis*) in Peru. *Revue d'Ecologie la Terre et la Vie* 43: 133–157.
- ERLINGE S., SANDELL M. & BRINCK C. 1982. Scent-marking and its territorial significance in stoats, *Mustela erminea*. *Animal Behaviour* 30: 811–818.
- ETIENNE A.S. & JEFFERY K.J. 2004. Path integration in mammals. *Hippocampus* 14: 180–192.
- GESE E.M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, and why. *Canadian Journal of Zoology* 79: 980–987.
- GESE E.M. & RUFF R.L. 1997. Scent-marking by coyotes, *Canis latrans*: the influence of social and ecological factors. *Animal Behaviour* 54: 1155–1166.
- GORMAN M.L. 1990. Scent marking strategies in mammals. *Revue Suisse de Zoologie* 97: 3–29.
- GORMAN M.L. & MILLS M.G.L. 1984. Scent marking strategies in hyaenas (Mammalia). *Journal of Zoology* 202: 535–547.
- GOSLING L.M. 1981. Demarkation in a gerenuk territory: an economic approach. *Zeitschrift für Tierpsychologie* 56: 305–322.
- GOSLING L.M. 1985. The even-toed ungulates: order Artiodactyla. Sources, behavioural context and function of chemical signals, pp. 550–618. In: Brown R.E. & Macdonald D.W., Eds. *Social odours in mammals*. Oxford: Oxford University Press.
- GOSLING L.M. & MCKAY H.V. 1990. Scent-rubbing and status signalling by male mammals. *Chemoecology* 1: 92–95.
- GOSLING L.M. & ROBERTS S.C. 2001a. Scent-marking by male mammals. Cheat-proof signals to competitors and mates. *Advances in the Study of Behavior* 30: 169–217.
- GOSLING L.M. & ROBERTS S.C. 2001b. Testing ideas about the function of scent marks in territories from spatial patterns. *Animal Behaviour* 62: 7–10.
- GURNELL J. & FLOWERDEW J.R. 1994. Live trapping small mammals, a practical guide. London: The Mammal Society.
- HARRINGTON F.H. 1981. Urine-marking and caching behavior in the wolf. *Behaviour* 76: 280–288.
- HENRY J.D. 1977. The use of urine marking in the scavenging behavior of the red fox (*Vulpes vulpes*). *Behaviour* 61: 82–105.

- JEDRZEJEWSKI W., SCHMIDT K., OKARMA H. & KOWALCZYK R. 2002. Movement pattern and home range use by the Eurasian lynx in Bialowieza Primeval Forest (Poland). *Annales Zoologici Fennici* 39: 29–41.
- KITCHENER A. 1991. The natural history of the wild cats. *Ithaca: Cornell University Press*.
- KITCHENER A. 1995. The wildcat. *London: The Mammal Society*.
- KORPIMÄKI E., KOIVUNEN V. & HAKKARAINEN H. 1996. Microhabitat use and behavior of voles under weasel and raptor predation risk: Predator facilitation? *Behavioral Ecology* 7: 30–34.
- KRUUK H. 1992. Scent marking by otters (*Lutra lutra*): signalling the use of resources. *Behavioral Ecology* 3: 133–140
- KRUUK H., CARSS D.N., CONROY J.W.H. & DURBIN L. 1993. Otter (*Lutra lutra*) numbers and fish productivity in two areas in North East Scotland. *Symposia of the Zoological Society of London* 65: 171–191.
- LOZANO J., MOLEÓN M. & VIRGÓS E. 2006. Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. *Journal of Biogeography* 33: 1076–1085.
- LOZANO J., VIRGÓS E. & CABEZAS-DÍAZ S. 2013. Monitoring European wildcat *Felis silvestris* populations using scat surveys in central Spain: are population trends related to wild rabbit dynamics or to landscape features? *Zoological Studies* 52: 16.
- LOZANO J., VIRGÓS E., CABEZAS-DÍAZ S. & MANGAS J.G. 2007. Increase of large game species in Mediterranean areas: Is the European wildcat (*Felis silvestris*) facing a new threat? *Biological Conservation* 138: 321–329.
- MACDONALD D.W. 1985. The carnivore: Order Carnivora, pp. 619–72. In: Brown R.E. & Macdonald D.W., Eds. Social odours in mammals. *Oxford: Clarendon Press*.
- MAHER C.R. & LOTT D.F. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* 49: 1581–1597.
- MANFREDI C., SOLER L., LUCHERINI M. & CASANAVE E.B. 2006. Home range and habitat use by Geoffroy's cat (*Oncifelis geoffroyi*) in a wet grassland in Argentina. *Journal of Zoology* 268: 381–387.
- MOLTENO A.J., SLIWA A. & RICHARDSON P.R.K. 2006. The role of scent marking in a free-ranging, female black-footed cat (*Felis nigripes*). *Journal of Zoology* 245: 35–41.
- MORENO S. & KUFNER M.B. 1988. Seasonal patterns in the Wood Mouse population in Mediterranean scrubland. *Acta Theriologica* 33: 79–85.

- MÜLLER C.A. & MANSER M.B. 2007. Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew. *Ethology* 114: 174–185.
- MUÑOZ A., BONAL R. & DÍAZ M. 2009. Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem. *Basic and Applied Ecology* 10: 151–160
- PANAMAN R. 1981. Behaviour and ecology of free-ranging female farm cats (*Felis catus*). *Zeitschrift für Tierpsychologie* 56: 59–73.
- PETERS R.P. & MECH L.D. 1975. Scent-marking in wolves. *American Scientist* 63: 628–637.
- PIÑEIRO A. & BARJA I. 2011. Trophic strategy of the wildcat (*Felis silvestris*) in relation to seasonal variation in the availability and vulnerability to capture of *Apodemus* mice. *Mammalian Biology* 76: 302–307.
- PIÑEIRO A. & BARJA I. 2012. The plant physical features selected by wildcats as signal posts: an economical approach to fecal marking. *Naturwissenschaften* 99: 801–809.
- POWELL R.A. & PROULX G. 2003. Trapping and marking terrestrial mammals for research: integrating ethics, performance criteria, techniques, and common sense. *Institute for Laboratory Animal Research Journal* 44: 259–276.
- PULGAR I. 2004. Guía da flora do Parque Natural Montes do Invernadeiro. *Consellería de Medio Ambiente, Xunta de Galicia, Orense*.
- PUSENIUS J. & OSTFELD R.S. 2002. Mammalian predator scent, vegetation cover and tree seedling predation by meadow voles. *Ecography* 25: 481–487.
- RABINOWITZ A. & NOTTINGHAM B. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology* 210: 149–159.
- REMONTI L., BALESTRIERI A., SMIROLDO G. & PRIGIONI C. 2011. Scent marking of key food sources in the Eurasian otter. *Annales Zoologici Fennici* 48: 287–294.
- RICH T.J. & HURST J.L. 1998. Scent marks as reliable signals of the competitive ability of mates. *Animal Behaviour* 56: 727–735.
- RICHARDSON P.R.K. 1993. The function of scent marking in territories: a resurrection of the intimidation hypothesis. *Transactions of the Royal Society of South Africa* 48: 195–206.
- ROBINSON I.H. & DELIBES M. 1988. The distribution of faeces by the Spanish lynx (*Felis pardina*). *Journal of Zoology* 216: 577–582.
- ROPER T.J., BUTLER C.J., CHRISTIAN S.E., OSTLER J. & SCHMID T.K. 1993. Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland use. *Behaviour* 127: 289–307.

- ROSELLINI S., BARJA I. & PIÑEIRO A. 2008. The response of European pine marten (*Martes martes* L.) feeding to the changes of small mammal abundance. *Polish Journal of Ecology* 56: 497–504.
- SCHAUENBERG P. 1981. Eléments d'écologie du chat forestier d'Europe *Felis silvestris* Schreber, 1777. *Revue d'Ecologie la Terre et la Vie* 35: 3–36.
- SCHMIDT K. & KOWALCZYK R. 2006. Using scent-marking stations to collect hair samples to monitor Eurasian lynx populations. *Wildlife Society Bulletin* 34: 462–466.
- SCHOENER T.W. 1971. On the theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369–404.
- SHERWIN C.M. 2006. Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour* 71: 245–253.
- SHETTLEWORTH S.J. 1998. Cognition, evolution, and behavior. *New York: Oxford University Press*.
- SHINN K.J. 2002. Ocelot distribution in the Lower Rio Grande Valley National Wildlife Refuge. *Ph.D. Dissertation, University of Texas-Pan American, Texas*.
- SILLERO-ZUBIRI C. & MACDONALD D.W. 1998. Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *Journal of Zoology* 245: 351–361.
- SUNQUIST M. & SUNQUIST F. 2002. Wild cats of the world. *Chicago: The University of Chicago Press*.
- URRA F. 2003. El gato montés en Navarra: Distribución, ecología y conservación. *Ph.D. Dissertation, Universidad Autónoma de Madrid, Spain*.
- ZUB K., THEUERKAUF J., JEDRZEJEWSKI W., JEDRZEJEWSKA B., SCHMIDT K. & KOWALCZYK R. 2003. Wolf pack territory marking in the Bialowieza primeval forest (Poland). *Behaviour* 140: 635–648.

Table 1. ANCOVA results examining the effects of the abundance of small mammals, habitat type, and season on the faecal marking index (number of faeces with a marking function in each cell/km surveyed) in wildcats. No significant interaction between factors was found.

Factors	β	F	df	P
Number of small mammals	0.19	5.68	1	0.019
Habitat type		6.14	2	0.003
Pine forest	-0.42			0.049
Deciduous Forest	-0.60			0.091
Scrubland	0 ^a			0 ^a
Season		1.75	3	0.162
Winter	0.14			0.513
Spring	0.08			0.722
Summer	-0.50			0.069
Autumn	0 ^a			0 ^a

0^a. This parameter is set to zero because it is redundant.

Fig. 1. Variation in the proportion of small mammals captured and in the index of faeces with a presumed marking function and without a presumed marking function in relation to habitat type.

