

## Methods of scent marking in the domestic cat

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Carnivores use various scent-marking methods. Semi-feral domestic cats (*Felis silvestris catus*) were observed to use the same means as their wild counterparts. Adult males performed most urine spray marking. Cats scratched tree bark, producing a visual mark, and probably used trees both as markers and for claw sharpening. Most scratching trees were located along frequently used paths rather than along territorial boundaries or scattered randomly throughout a home range. Bark consistency affected the tree species that were scratched, with soft bark preferred. Although deposition of faeces and urine was recorded, there was no clear evidence for their use as territorial markers; cats primarily eliminated away from the core area of the home range. Most faeces were buried, although exposed deposits were also observed. Cats also rubbed against objects, probably using glandular secretions from the face and tail areas to scent mark. Males rubbed objects more than females, and males scent marked more. Individual males may use different means of scent marking. Scent marking in this study supports the idea that cats do not defend territories, instead patrolling and reinforcing marks throughout a looser home range. The suggestion has been made that different forms of marking may serve separate signalling functions.

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Les carnivores utilisent différentes méthodes de marquage. Chez des Chats domestiques (*Felis silvestris catus*) semi-sauvages, les méthodes de marquage utilisées sont les mêmes que celles d'animaux sauvages correspondants. Les mâles adultes marquent les objets en y vaporisant de l'urine. Les chats grattent l'écorce des arbres, produisant ainsi une marque visuelle; ils utilisent probablement les arbres à la fois comme marqueurs et comme substrats pour s'aiguiser les griffes. La plupart des arbres marqués se situent le long de sentiers fréquentés plutôt que le long de frontières territoriales ou en des points dispersés au hasard à l'intérieur du domaine vital. La nature de l'écorce est un facteur important du choix de l'espèce d'arbre à gratter et les arbres à écorce souple sont les préférés. Les fèces et l'urine sont utilisées, mais il est impossible de déterminer leur rôle comme marqueurs territoriaux; les chats urinent ou défèquent surtout loin du centre de leur domaine. La plupart des fèces sont enfouies, bien que certaines restent découvertes. Les chats se frottent également sur les objets, les marquant probablement ainsi d'odeurs provenant de sécrétions glandulaires faciales ou caudales. Les mâles se frottent sur les objets plus souvent que les femelles et les marquent aussi plus souvent de leurs odeurs. Différents individus peuvent utiliser différentes méthodes de marquage. Le marquage au moyen d'odeurs tel qu'observé dans cette étude corrobore l'hypothèse selon laquelle les chats ne défendent pas de territoires, mais patrouillent plutôt certains points marqués qu'ils marquent de nouveau à l'intérieur de domaines aux limites peu définies. Il se peut que différentes méthodes de marquage transmettent des signaux différents.

[Traduit par la Rédaction]

### Introduction

Most terrestrial mammals use olfaction as a primary means of communication, and this is particularly conspicuous in carnivore species (Gorman and Trowbridge 1989). Odours are produced by most organs that secrete externally, including the sebaceous and apocrine sweat glands of the integument (Adams 1980; Gorman 1980; Gorman and Trowbridge 1989), salivary glands (Ewer 1968; Adams 1980), and accessory eye organs (Adams 1980). Urine, vaginal secretions, and faeces are also used in many species (Smith 1977; Adams 1980; Gorman 1980; Macdonald 1980, 1985). In felids, the vomero-nasal organ, a specialized chemoreceptor, may help to discriminate urine and other closely smelled odours; exercising all olfactory organs, it is possible for cats to detect low levels of complex mixtures, and even to distinguish individual odours by their varying composition (Dodd and Squirrel 1980).

Domestic cats provide a valuable model for examining the form and function of scent marking in felids. The variable composition of secretions may allow the encoding of a range of information, including the marker's age, sex, reproductive state, and individual identity (Ewer 1968; Reiger 1979; Passanisi and Macdonald 1990). Additionally, there is the potential for transfer of information regarding status and

residual tenure. These signals facilitate the social interactions between individuals, in both group-living and more solitary populations, allowing a complex network of social and spatial relationships.

Scent-producing organs in the cat are located on the cheeks, abdomen, and paws, above the tail, and near the anus (Ewer 1968, 1973; Gorman 1980; Macdonald 1985; Gorman and Trowbridge 1989); secretion is controlled by the endocrine and nervous systems (Adams 1980). Scent marking involves placing secretions on prominent objects and other individuals (Smith 1977; Gorman 1980; Macdonald 1980). There are several mechanisms by which cats scent mark; domestic cats, like many felids, are retromingent and urinate posteriorly (Ewer 1968, 1973; Corbett 1979; Macdonald 1980). This allows the deposition of urine mixed with either vaginal or anal-gland secretions (Macdonald 1980). A second common way to deposit odour is through scratching objects while exuding odorous secretions from paw glands. A third, less common, way is rubbing the face or body against objects, leaving behind glandular secretions.

The function of scent marking is not fully established. Different forms probably function in separate, sometimes reinforcing ways, given the variation in secretion constituents, location and time of marking, and identity of the marking animal. This investigation is the first to examine the different forms of scent marking in a single population of cats. The few

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previous studies have concentrated on urine spray and faeces deposition; there are few data on rubbing and scratching patterns in carnivore species. Four forms of marks were considered in this study and are elucidated below: urine spray, elimination (urine and faeces), scratching, and rubbing.

Anal and vaginal secretions may be relatively pungent and long-lasting, suitable for relating sex, reproductive state, and possibly status and individual identity information. In addition, more persistent traces, such as exposed faeces, could act as territorial markers, both spatial and temporal, e.g., the placement of badger latrines at borders (Gorman 1980). There is little evidence that scent marks actively deter intruders from entering an area (except in foxes and wolves; Macdonald 1985), but they could act as a warning mechanism, predisposing an intruder to yield in an encounter with the resident. Matching scent marks with their owners may allow intruders to assess potential competitors. Territory holders likely have dominant status and act to maintain resources, therefore it might be advantageous for intruders to relinquish claims in the presence of known residents (Gosling 1982; Gorman and Trowbridge 1989). In addition, territory holders, by identifying themselves with scent marks, may benefit from non-escalated aggression whenever possible. This may offer a partial explanation for the common observation of scent marking during agonistic encounters in many carnivore species (Dards 1979; Macdonald 1980; Gosling 1982). Both urine and skin-gland secretions of females may contain pheromones that advertise reproductive state to investigating males (Verberne and de Boer 1976; Gosling 1982).

Urine spray should show seasonal variation if it functions to indicate reproductive condition. If it also signals status, older cats should mark more than younger ones, while females and males may show differences due to social context. Faeces marking a territorial area should correspond to range borders and be left exposed.

In comparison, scratching leaves an obvious visual marker and probably has some olfactory element; while some individual information may be relayed by the secretions from interdigital glands, scratch marks likely act as territory markers. Marking patterns may elucidate the degree of species-specific territoriality. The distribution of scratched trees offers information about their function relative to the question of whether cats have territories (perimeter marking) or home ranges (path marking).

Rubbing on objects and the spreading of facial secretions are likely to function on a smaller scale, conveying details about the individual animal, such as identity, status, and familiarity. Rubbing may differ between males and females and between adult and younger cats, indicating a status-signalling function. There may also be differences between individuals, denoting identity.

This study examined marking behaviour in two groups of feral cats. The general visibility of individuals allowed detailed examination of activities such as object rubbing and scratching. Different types of scent marking are considered separately, including urine spraying, tree scratching, deposition of faeces, and object rubbing. These actions were considered to potentially convey information to conspecifics about territorial boundaries, home-range use, or reproductive state. By examining the spatial and temporal distribution of the different types of marks, as well as age and sex

differences, the functions of scent marking can be elucidated for the domestic cat.

## Methods

The study was conducted from January 1988 to April 1989 at the Sub-Department of Animal Behaviour at Madingley, Cambridge. An area of 1600 m<sup>2</sup> was fenced off from the surrounding farm fields and woodlands, but was otherwise left without interference. This outdoor enclosure was divided into two separate areas by a high fence. One mature male and five breeding females were released into each half of the enclosure in April 1987 (Feldman 1993). The two populations were allowed to grow naturally, and cats born into the groups were feral. Daily provisioning ensured a plentiful and stable supply of food and water; the cats were regularly observed to hunt and capture live prey in addition to the food provided.

Behaviour was recorded for all adult and juvenile cats over the 16-month period using focal animal sampling. Only those individuals present at the start of 1988 were used as focal animals, including adult males ( $N = 2$ ), adult females ( $N = 11$ ), and juveniles born in 1987 ( $N = 9$ ). All occurrences of urine spraying, tree scratching, and object rubbing were recorded during the focal sampling (Hinde 1973; Altmann 1974). Individuals were observed daily, using a random schedule of names. No cat was observed more than once each day, and individuals contributed 17–80 focal watches, varying with visibility and age (juveniles contributed fewer observations than adults). If a cat was not in sight, the next visible individual was observed. Each focal period was 34 min; a total of 619 h of focal data was collected. Deposition of faeces and urine was recorded for all cats from November 1988 to March 1989. For each elimination, individual identity, location, and several other variables were noted, including whether the animal sniffed the deposit and whether any attempt was made to bury it.

### Urine spray marking

Urine spraying is considered the predominant method of scent marking in canids and many felids, including the domestic cat and tiger (Smith et al. 1989), as it can be performed rapidly and leaves apparently persistent olfactory cues. Spray marking can be distinguished from elimination by orientation to a specific object and repetition on the same object (Macdonald 1980; Bateson and Turner 1988). In cats, it can also be recognized by its characteristic form, in which the marking individual backs up to an object, lifts its tail vertically, and directs a fine spray between its hind legs; this is accompanied by an intense quivering movement of the tip of the tail (Ewer 1968; Corbett 1979; Dards 1979; Leyhausen 1979; Bateson and Turner 1988). Anal-sac contents may be mixed with the urine (Dards 1979) to create a characteristic and pungent concoction that can be distinguished from ordinary eliminated urine; the anal sacs are paired organs found on either side of the anus and opening to the rectum, which hold apocrine and sometimes sebaceous secretions (especially prevalent in domestic cats, lions, and tigers) (Macdonald 1985; Gorman and Trowbridge 1989).

### Tree scratching

Two possible distribution patterns for the scratched trees were considered: along the perimeter of the enclosure or along the heavily used paths throughout the enclosure. Detailed descriptions and species names were gained through consultation with P. Heavens (personal communication) and Mitchell (1988). Seven distinct species of tree were growing in the enclosure, with four species making up the majority of trees. Including both sides of the enclosure, there were 167 trees in total, ranging in size from young saplings (from 1 in. (1 in. = 25.4 mm) in diameter and 6 ft (1 ft = 0.3048 m) in height) to mature trees (with trunks several metres in girth). The majority of trees were completely unmarked by scratches, but most of those used as "scratching posts" showed severe damage to the bark. Bark damage was scored on a 5-point scale, where 0 was no scratch damage, 1 was mild damage, 2 was moderate damage, and 3 and 3+ were severe damage.

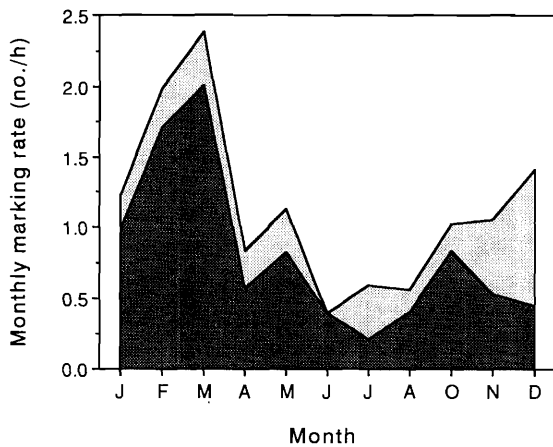


FIG. 1. Mean rate of scent marking by month, from January to December (there are no data for September). The dark area indicates urine spray marking; the lighter area indicates object rubbing.

Tree species were assessed on their bark characteristics. The common ash (*Fraxinus excelsior*) has pale grey bark, which is very smooth on young trees and acquires thick, interwoven ridges in old trees. The English oak (*Quercus robur*) has pale grey bark, closely fissured into short, narrow, vertical plates. *Alnus cordata*, the Italian alder, has pale brown-grey to dull grey bark; the texture is smooth but blistered, with shallow, wide vertical fissures. Ash, oak, and alder trees were classified as "hard-barked." The English elm (*Ulmus procera*) has dark brown bark that is deeply cracked into small square plates, and has small sprouts spreading from numerous burrs. The common beech (*Fagus sylvatica*) has smooth, silvery grey bark, often slightly roughened and less often with rippled patches or a fine network of ridges. *Salix pentandra*, the bay willow, shows brown-grey bark, finely fissured by narrow orange-buff cracks. The decorative pale-grey-barked cotoneaster (*Cotoneaster frigidus*), originally from the Himalayas, is short-boled, often leaning, with long vertical sprouts growing from the bole. Elm, willow, and cotoneaster were grouped as "soft-barked."

**Results**

*Urine spray marking*

A total of 679 spray marks were delivered by the cats during focal animal samples. Only 4 of these were performed by females and the remaining 675 (99%) were made by males; this was a statistically significant difference across all individuals ( $U = 1.5, Z = -3.94, p < 0.001, N = 7$  males, 15 females). All spray marks were made by adult cats ( $\geq 18$  months old). Group A contributed nearly three times as many spray marks to the sample than group B (497 to 182), despite the larger group size and the greater preponderance of males in B; however, this difference was not significant across all individuals ( $U = 47, Z = -0.94, ns; N = 10$  in group A,  $N = 12$  in group B). When only the two adult males were considered, the group A male sprayed much more frequently ( $\chi^2 = 179.14, df = 1, p < 0.001$ ), contributing 9.2 spray marks per hour to the group B male's 2.8. Spraying rate varied through the year (Fig. 1), with a marked increase during the mating period in late winter and early spring.

*Scratching*

All trees and stumps were examined for a pattern in the distribution of scratched trees. The location of a tree was important in determining its use for scratching (Fig. 2a). Trees along perimeters were compared with those along paths and

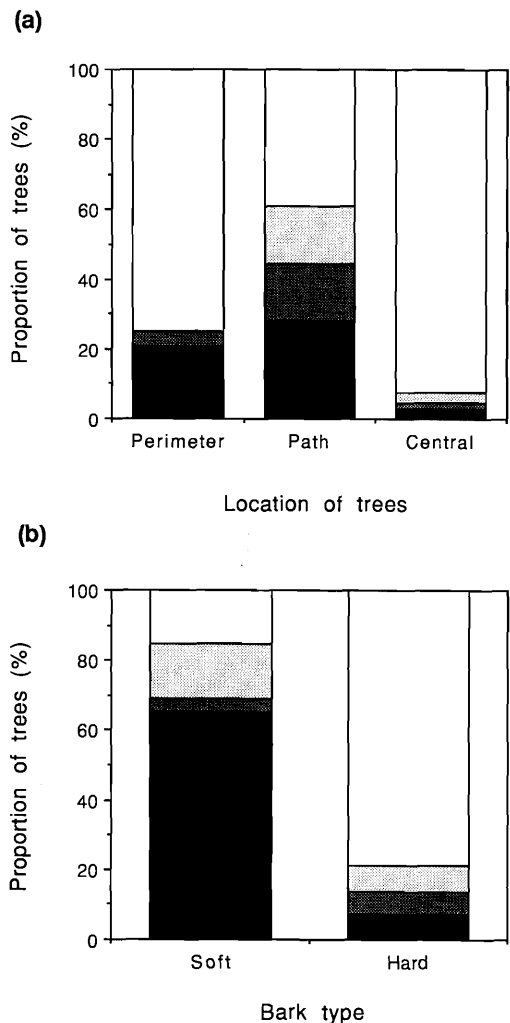


FIG. 2.(a) Tree location and scratch marks. Trees in each of three locations were rated according to the degree of scratching ( $n = 50$  perimeter, 47 path, and 67 central trees). (b) Bark types and scratch marks. Trees were grouped by species and bark type into "soft" and "hard" categories, then rated according to the degree of scratching ( $n = 26$  soft- and 138 hard-barked trees). The degree of scratching is indicated by shading: white shows no damage, light shading shows mild damage, darker shading shows moderate damage, and black shows severe damage.

in central regions for each enclosure. Heavily scratched trees were located primarily along well-defined and much-used routes, and only rarely at outer boundaries or in central non-path areas. When perimeter trees ( $< 2$  m from the boundary fence) were distinguished from central trees ( $> 2$  m from the boundary fence), both areas were scratched equally, whether any scratching is considered ( $\chi^2 = 0.0003, df = 1, ns; N = 51$ ) or just the severe rates ( $\chi^2 = 0.0003, df = 1, ns; N = 27$ ). While the borders were scratched in the same proportions as the central region, scratched trees were more densely located along heavily used pathways ( $\chi^2 = 44.52, df = 1, p < 0.001$ ), as were the severely scratched trees ( $\chi^2 = 30.00, df = 1, p < 0.001$ ).

Not all trees along the paths were scratched; several unmarked trees were intermingled with heavily scratched ones. The species and bark type of the trees might have influenced the choice of scratching posts. Individual trees of all species had a range of scratch damage and contributed to

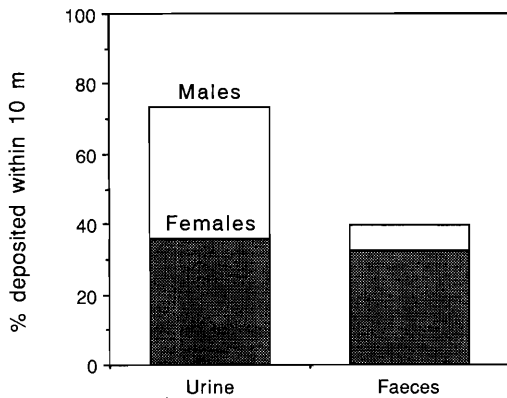


FIG. 3. Placement of urine and faeces deposits by adult male (white bars) and female cats (dark bars). Observations were examined with respect to distance from a stable food source.

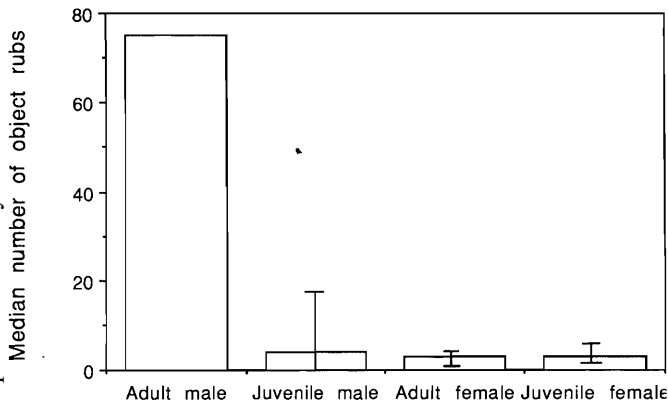


FIG. 4. Object rubbing by animals of different age and sex classes. Median numbers of rubs are given, with interquartile ranges indicated by bars. The interquartile ranges were equal to the median for adult males, so this column has no error bar.

the full range (0–3+) for several species. Using Friedman's test (Zar 1984) with tree species as blocks and scratching as the matched factor, the differences were significant in the amount of scratching across tree species ( $\chi^2 = 23.64$ ,  $df = 7$ ,  $p < 0.01$ ,  $N = 8$ ). When compared using  $2 \times 2$  contingency tables (Zar 1984), hard-barked trees (ash, oak, alder) showed significantly less damage than soft-barked trees (elm, *Salix*, cotoneaster) ( $\chi^2 = 38.39$ ,  $df = 1$ ,  $p < 0.001$ ). When only scratched trees were considered, significantly more soft-barked trees showed rates of scratching in the severe damage category ( $\chi^2 = 7.56$ ,  $df = 1$ ,  $p < 0.01$ ). These results support the hypothesis that differential scratching is due, in part, to differences in the type of bark of the tree species (Fig. 2b). Tree species were widely dispersed with reference to their location along perimeters and paths and in central areas. Owing to the non-normal distribution of the data, it was not possible to do an analysis of variance to separate the effects of location and bark type. All cats, regardless of sex or age, contributed to the scratch damage seen in the study.

#### Faeces and urine elimination

In total, 55 defaecations and 44 urinations were observed over a 5-month period. Adult males contributed 20% of faecal deposits and 18% of urinations; adult females accounted for

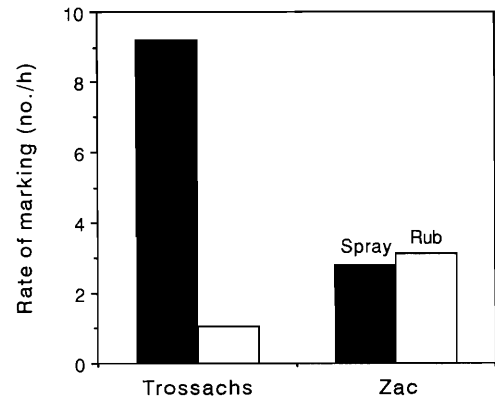


FIG. 5. Scent-marking rates for Trossachs and Zac, two adult males. The solid bars represent urine-spray rates and the open bars represent object-rub rates.

73% of defaecation and 82% of urination; the remaining defaecations were performed by young non-focal animals (7% of faeces). Over all animals and including both urine and faeces, 70% of elimination occurred farther than 10 m from the food area (Fig. 3). A total of 14 scats (25%) were deposited within 10 m of the central provisioning area (by adult females and juveniles only). All cats primarily defaecated outside a 10-m radius of the food area, and this was significantly different from random deposition ( $\chi^2 = 13.25$ ,  $df = 1$ ,  $p < 0.001$ ). Proportionately more urine deposits were made within the 10-m radius (36%) by both adult males and females. This distribution was not significantly different from random deposition ( $\chi^2 = 3.27$ ,  $df = 1$ , ns). Over half of all observed urine deposits were left completely exposed, and the majority of these were not sniffed after deposition. Faeces were usually sniffed (98% of scats), and in most cases a small attempt was made to scratch over the scats, leaving them partially exposed. Only two scats were left completely exposed, both by males.

#### Object rubbing

Overall, 240 rubs were observed, 193 of which were performed by males (80%). When all cats were considered, there was no significant difference between males and females ( $U = 32$ ,  $Z = -1.46$ , ns;  $N = 7$ , 15). However, when only adults were compared, males performed significantly more rubs than females ( $U = 0$ ,  $Z = -2.20$ ,  $p < 0.05$ ;  $N = 2$  males and 11 females). Most rubs were made by adults, both female and male, with juveniles offering only 23% (55 of 240) (Fig. 4). The majority of juvenile rubs were made in the period when young males were reaching maturity and beginning to display adult scent-marking behaviour. When the two adult males were compared in terms of rubs delivered, the group B male was found to rub objects significantly more than the group A male ( $\chi^2 = 32.67$ ,  $df = 1$ ,  $p < 0.001$ ; Fig. 5).

#### Discussion

Females rarely spray marked in this study (see also Macdonald and Apps 1978; Dards 1979; Kerby and Macdonald 1988), although males did so frequently. This result is consistent with other studies, which report that adult male cats spray frequently, often while walking along the paths and boundaries of their range (Liberg 1981; Macdonald et al. 1987; McFarland 1987) and while hunting (Corbett 1979); adult females have been occasionally observed to spray, also while hunting and travelling along paths, but much

less frequently than adult males (Panaman 1981; Natoli 1985). Spray marks are often directed onto conspicuous objects, such as grass tussocks (Corbett 1979), projecting twigs (Gosling 1982), and tree stumps (this study), supporting their function as spatial markers. This study did not examine the chemical nature of different forms of scent marking; however, several recent studies have shown that adult cats can distinguish the urine of familiar and unfamiliar conspecifics (Natoli 1985; Passanisi and Macdonald 1990). Males sniff longer at the urine of oestrus females (Verberne and de Boer 1976), and fresh spray is smelled for longer periods than older marks (de Boer 1977).

Urine spraying in this study showed some seasonal patterning (Fig. 1), suggesting a link with reproductive state or stimuli. Individual differences in the rate of urine spraying (2.8–9.2 sprays/h, Fig. 5) were similar to those seen by Corbett (1979). It is possible that this variation reflects differences in either “status” or “territoriality.” If marking frequency is linked to high dominance status, through the influence of androgens (Gosling 1982), then the group A male might appear to be the more dominant of the two males. Alternatively, he could be a more territorial individual in the presence of a neighbouring potential competitor.

Various carnivore species scratch and gnaw the bark of trees, leaving a visually discernible area of damaged wood. Wild cats are known to use “claw-sharpening” trees, which can serve as both visual and olfactory markers (Ewer 1968; Corbett 1979; McFarland 1987). Felid species that regularly display this behaviour include the domestic cat, African and European wildcats, bobcat, and leopard; it has also been reported, to a lesser extent, in tigers, lynx, and pumas (Hediger 1950; Ewer 1973; Smith et al. 1989). The same tree may be used repeatedly over time (Ewer 1973; Smith et al. 1989) by different individuals. In this study, trees along paths were scratched more than trees along the perimeter or in the general area of each side of the enclosure (Fig. 2a), which provides little support for the idea that territories are defined by scratch marking along perimeters (as with sprays, as reported by Panaman 1981). Instead, it confirms that domestic cats are similar to other carnivore species with overlapping home ranges and mark within their range along habitual paths (Gorman 1980).

Tree characteristics also influenced the distribution of scratches; soft-barked trees were scratched more than hard-barked trees (Fig. 2b). Species with hard, smooth bark might be less suitable for visual marking, since they probably offer increased resistance to shredding forces, as opposed to those with softer bark, as this yields more readily to claws, and patches are clearly discernible. This supports a dual function for tree scratching; claw maintenance (Hediger 1950; Bateson and Turner 1988) and home-range marking.

Many carnivore species mark with faeces (Gorman and Trowbridge 1989); in felids, this is less thoroughly documented, but has been suggested for the Scottish wildcat (Corbett 1979), Spanish lynx (Robinson and Delibes 1988), and lynx, puma, and bobcat (Macdonald 1985). In this study, cats tended to urinate and defaecate away from the feeding areas (>10 m) (Fig. 3), ultimately minimizing contamination effects. This could be particularly important because of the prevalence of parasitic worms in feral populations.

Deposition of faeces was quite concentrated along the perimeters of the enclosures, perhaps corresponding to

functional range borders, due to middens (“dungheaps” used by several individuals) near the perimeter. Young cats contributed to these communal latrines, which were relatively close to the common or core areas. Other studies of feral cats have reported faecal deposition along well-used paths and in several middens (Corbett 1979; Fitzgerald and Karl 1986), and similar latrine areas used by the African wildcat have been seen (Stuart 1977). With relatively limited space, elimination outside the core may necessitate some clumping of faeces nearer the perimeter.

Home-based cats tend to cover or bury faeces, especially close to the core area (Liberg 1980; Panaman 1981), but may leave them exposed, although not prominently displayed (Macdonald et al. 1987). Macdonald (1980) suggested that dominant and subordinate individuals differ, with dominants leaving more exposed scats. In this study, cats were not observed to leave faeces entirely exposed; however, there were deposits in exposed sites prior to the focal period of 5 months (personal observation) in both conspicuous (along paths and in latrine areas) and inconspicuous locations. Faecal deposits were rarely left without being sniffed (Macdonald et al. 1987), consistent with the suggestion that faeces are territorial markers; however, no clear pattern was discernible in this study. In general, there is less support for the use of faeces as markers by domestic cats (Dards 1979).

Males contributed few deposits, owing to their small numbers, so conclusions are necessarily biased by the predominance of females. Also, one female suffered from chronic diarrhoea, and skewed both total numbers and that of exposed scats. Although these results are inconclusive for determining whether faeces are used in home-range marking, cats appear actively to avoid defaecating in feeding areas.

The tendency of cats to rub themselves on objects, other cats, and people has been widely described (Reiger 1979; Bateson and Turner 1988; Kerby and Macdonald 1988). Rubbing on conspecifics was considered a contact behaviour and was not included in this analysis. Cats rubbed their cheek, lip, and chin regions along prominent objects such as twigs, stumps, wooden shelter structures, and the perimeter fence. Secretions from these facial regions are high in fats, are richly scented, may include saliva, likely have characteristic individual odours, and probably vary with reproductive state (Ewer 1968; Reiger 1979). Secretions rubbed onto conspecifics may not be marks, acting instead as a means by which the odours of known individuals are detected and become familiar (Gorman and Trowbridge 1989; Smith et al. 1989). Males rubbed more than females (Fig. 4), perhaps reflecting the overall lack of female home-range defence in this population of cats. Adults rubbed more than juveniles, supporting the use of rub marks as territorial or status indicators. In one case, an adult female rubbed a tree; moments later, the adult male sniffed the rubbed place and then rubbed it himself. Females seem particularly interested in smelling skin-gland secretions rather than urine marks (Verberne and de Boer 1976). Saliva, transferred to the fur and paws during grooming, might also be a scented form of self-anointing, reinforcing individual identification (Gosling 1982). Reiger (1979) suggests that social (e.g., group-living) carnivores may scent rub more than solitary ones, supporting the contention that rubbing should be treated as a form of social interaction. Social groups may produce a common group odour, based on a mixture from all members, especially

in the presence of allomarking (particularly rubbing in cats) and the marking of objects in common (Gorman 1980; Gorman and Trowbridge 1989).

Individual adult males differed in their rates of spraying and object rubbing (Fig. 5). Several explanations can be given: (i) the differences are due to individual variation and have no communication function; (ii) the two adult males differed in "territoriality," and spraying reflected differences in the degree to which the individual males were motivated to demarcate a home range; (iii) the two forms of marking have different characteristics and convey separate messages (which may or may not be related to either dominance or territoriality).

The composition of the odorous substances produced by the different organs involved in spraying and rubbing is likely to influence such aspects as the longevity and potency of the marks; observers have noted the strong, pungent smell of spray, even to the relatively insensitive human nose. Rub marks, however, have evoked little response or notice in researchers, perhaps because of the difficulty of distinguishing rubs through odour or visual cues.

Male cats may perform different types of marking on similar objects, e.g., on the walls of shelters containing females and their kittens (Corbett 1979; this study). Occasionally, cats have been seen to spray an object after rubbing it (Corbett 1979; Dards 1979; Panaman 1981), but never in the reverse order. A further possibility is that spraying and rubbing have distinct functions, and are therefore unrelated. Object rubbing may also have simple grooming functions at times (e.g., the relieving of itches or removal of ectoparasites), but these are probably better performed through self-scratching, as part of grooming behaviour.

Overall, relatively little support was found for the hypothesis that marking plays a role in territory maintenance in domestic cats. Cats have rarely been seen to leave or avoid an area after investigating marks, suggesting that the marks serve as information markers rather than as an active method of deterrence (Bateson and Turner 1988). Males did not appear to maintain exclusive access to their ranges through aggressive exclusion of others.

Furthermore, the pattern of marks was not concentrated at the periphery of the ranges, as one would predict if territory marking were the primary function of spraying, exposed faeces, scratching, and(or) rubbing. Rather than territories, cats hold loose, non-exclusive home ranges, which may be reinforced by marking.

There was some evidence supporting a "spatial defence" function for scent marking, including: (i) the arrangement of some "latrines" near the perimeter, (ii) occasional aggression between the two adult males, and (iii) one male's habit of pacing the dividing fence. The pattern of male dispersal in feral cats observed in this study and others (Dards 1979; Liberg 1980; Kerby 1987) also supports "territorial" behaviour in male cats. Almost all of these observations can be explained by the placement of groups in adjoining limited areas in full view of each other; males may simply have acted as if an intruder were often present near the core area with the food source. Patterns of dispersal, range use, and "territoriality" in males probably have functions beyond mere competitive exclusion from food sources. Reactions to an intruder were mainly observed when a strange feral cat (adult female) living near the study site investigated the study cats;

this sparked strong agonistic displays both from the adult male and from adult females, and seemed more indicative of a potentially resource-guarding response.

Domestic cats share many characteristics with wild felids, including the variety of different scent-marking patterns. The sociality seen in group-living feral cats may allow them to occupy home ranges rather than exclusive territories. The social signalling function of marking is likely to be similar for both small and large cats. Felids have intricate social interactions, and scent marks probably play an important role in establishing and reinforcing social systems in these species.

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