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The role of scent marking in a free-ranging, female black-footed cat (*Felis nigripes*)

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Abstract

A radio-collared, female black-footed cat (*Felis nigripes*) was followed for a total period of 575 hours, over seven observation periods spanning 18 months, in the Kimberley region of the Northern Cape Province, South Africa. Data on reproduction and scent marking were collected by direct observation. The predominant form of scent marking was urine-spraying, the frequency of which fluctuated during the year and seemed to be related to changes in the reproductive cycle. Marking frequency increased dramatically approximately one and a half months before mating, and conception of the first litter of the breeding season occurred at a low frequency during pregnancy, and was entirely absent when the cat was rearing young. This strongly indicates a primary function in the advertisement of female reproductive condition, although an additional role in the maintenance of social spacing is suggested. Scent marks were not restricted to the borders of the animal's range, but corresponded to those areas used most intensely during the year.

Key words: *Felis nigripes*, urine-spraying, reproductive status, home range, seasonal breeder

INTRODUCTION

Communication between conspecifics is important not only in social species but also in solitary species, to maintain social organization and ensure reproductive success (Clapperton, 1989). Intraspecific communication between solitary carnivores and between groups of social carnivores is achieved primarily by chemical means, most importantly urine and faeces (see review by Macdonald, 1980).

Field studies investigating scent marking among the larger felid species have relied primarily on indirect observations, owing to the difficulties of maintaining wild felids under continuous, direct observation (Saunders, 1963; Hornocker, 1969; Bailey, 1974; Sunquist, 1981; Robinson & Delibes, 1988; Smith, McDougal & Miquelle, 1989). This is, however, not a feasible method in species in which urine-spraying is the predominant form of scent marking, since evidence of urine sprayed on grass or small shrubs is almost impossible to detect by indirect methods. The difficulties are compounded in small species which may mark at high frequencies and do not use defined paths when moving through their home range. Thus, in small felid species, accurate data on patterns of scent marking can only be obtained by direct observation of their behaviour. The result is a dearth of information regarding spatial and temporal patterns of scent marking in the field. Geertsema (1985) recorded scent-marking behaviour in free-ranging servals (*Felis serval*) but could not confidently relate changes in frequency to the reproductive state of the female. Mellen (1993) investigated scent marking in 20 species of small (<20 kg), captive felids, and found that reproductively active felids generally displayed a higher rate of scent-marking behaviour. We feel that our observations will help to improve our understanding of the role of scent marking in the black-footed cat and small felids in general.

The black-footed cat (*Felis nigripes*) is a solitary, nocturnal felid endemic to the south-west arid zone of the Southern African Subregion. The species is listed in Appendix I of CITES and as rare in the South African Red Data Book. It is among the world's smallest felids, weighing 1–2 kg. Owing to its highly secretive nature, this cat is seldom encountered and thus little is known about its biology (Skinner & Smithers, 1990). Reproductive data obtained from cats in the wild are limited to observations that suggest seasonality of reproduction. A pregnant female with two foetuses was caught in November (Rautenbach, 1982), whereas no signs of pregnancy were found in a female caught in July (Smithers, 1971). Observations on captive black-footed cats suggest a relatively short oestrous period of 36 hours. The actual period of mating appears not to

exceed 10 hours, occurring at intervals of 20–50 min (Leyhausen & Tonkin, 1966). After a gestation period of 63–68 days, the female produces a litter of 1–3 young (Schürer, 1988).

In this study, a radio-collared, female black-footed cat was habituated and followed, allowing detailed information on scent marking and reproductive status to be obtained by direct observation.

MATERIALS AND METHODS

The study included 7 observation periods between 5 May 1993 and 25 October 1994. Data on reproduction, movement and scent-marking behaviour was obtained during a total of 575 hours of direct observation, over a distance of 402 km.

Study area

The study area was located on Benfontein (28°50′S, 24°50′E), an 11 400 ha game farm owned by De Beers Consolidated Mines. The farm is located approximately 10 km south-east of Kimberley in the Northern Cape Province, South Africa. Vegetation includes elements of 3 major ecosystems, namely Kalahari thornveld, pure grassveld and the Karoo, which converge in the Kimberley area (Acocks, 1975). Climatic conditions at this locality vary widely; winters (May–August) are cold and dry, with temperatures often dropping below freezing at night, whereas the average maximum temperature during summer (October–March) exceeds 30 °C. The area has an average annual rainfall of 431 ± 127 mm (Richardson, 1985).

Data collection

A female black-footed cat was trapped in a den, immobilized using a combination of ketamine hydrochloride (*c.* 10 mg/kg; Ketalar, Parke-Davis Laboratories, Isando, South Africa) and acetylpromazine (*c.* 0.2 mg/kg; Centaur Laboratories, Johannesburg, South Africa) and fitted with a radio-collar weighing 50 g. The collar had a range of approximately 800 m, depending on the terrain, using a Yaesu FT 290 R II receiver (Yaesu Musen Co., Tokyo, Japan) and two, 3-element Yagi type antennae. The cat was habituated, as described by Sliwa (1994), so that it could be followed in a 4-wheel-drive vehicle and it appeared to ignore the vehicle completely when followed at a distance of 10–15 m. Visual contact was maintained using the headlights of the vehicle and a spotlight. Each evening, the cat was located using radio-telemetry and followed for periods ranging from half an hour to her full activity period (sunset to sunrise). If the cat had already left her den, she was radio-tracked until found and followed from then onwards.

Initially, the cat's position was plotted relative to surveyed markers placed throughout the study area (Richardson, 1985; Anderson, 1994; Sliwa, 1994). However, early during the study this method was replaced with a Global Position System (GPS). This enhanced the quality and ease of data collection by reducing the possibility of overlooking individual scent marks, since time did not have to be spent identifying individual markers when determining the cat's position. The time, cat's position, and number of urine-sprays made since the previous observation were recorded at regular intervals (approximately 2–10 min) on a pocket dictaphone. The cat's path and individual urine-sprays were plotted on a grid consisting of 16 ha cells. Frequencies (sprays/h) were calculated using the total time during which scent marking was observed in each observation period. Time during which the cat was not directly visible was excluded from the calculation. The fluctuation in the frequency of urine-sprays was related to the cat's reproductive status.

Although the study focuses primarily on urine-spraying owing to the predominance of this form of scent marking, additional behaviours known to be associated with scent marking in the Felidae were observed and recorded. These comprised defecation, 'eliminative' micturition in a squatting position, cheek rubbing on grass tufts, bushes or termite mounds, rolling on her back, and clawing the substratum with the front paws.

RESULTS

Marking behaviour

Urine-spraying was the predominant form of marking behaviour, and was observed 1454 times during the study. The cat emitted a small amount of urine in a fine spray while lifting and vibrating her tail and simultaneously treading with her hindlegs. The spray was directed at small karroid bushes *Pentzia spinescens*, grass clumps and, rarely, termite mounds.

The number of recorded urine-sprays is certainly an underestimate, owing to the difficulties of observing this animal at night and the short duration of the marking behaviour. The frequency of urine-spraying fluctuated during the year and appeared to be related to the cat's reproductive state. First, urine-spraying was absent during periods in which the cat had dependent young. Second, spraying was observed during both pregnancies, although it occurred at relatively low frequencies (0.84 sprays/h and 0.95 sprays/h). Urine-spraying did not, however, accompany the entire pregnancy, but began after mating had taken place and ceased before the birth of the kittens. Third, during the June/July observation period, approximately one and a half months prior to the calculated mating and conception of the third litter (8–13 August 1994), the average frequency per night increased dramatically from 5.22 to 35.92 sprays/h within 15 days (Fig. 1). Urine-spraying frequencies as high as 40 sprays in 619 m and 41 sprays in 685 m were recorded. Data from May 1993 suggest that, before this increase, frequencies of urine-spraying were slightly

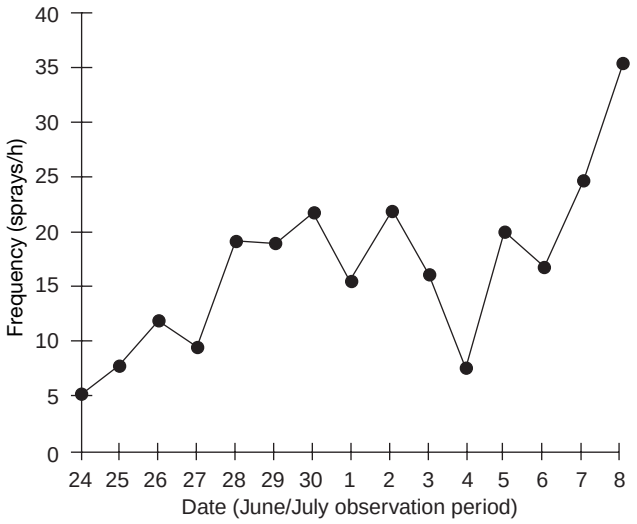


Fig. 1. Nightly increase in marking frequency during the June/July observation period from 24 June to 8 July 1994.

higher than those observed during pregnancy (avg. freq. 2.07 sprays/h). However, prior to the mating resulting in the conception of the second litter (15–20 December 1993), no marking was observed, probably due to the presence of the first litter.

The temporal variation in marking frequency is clearly illustrated in Fig. 2. The large number of urine-sprays observed during the June/July observation period (Fig. 2b) contrasts dramatically with the relatively low number observed during the remainder of the year (Fig. 2a). Urine-sprays were not restricted to the boundary areas of the range. Rather, areas in which higher densities of sprays occurred corresponded with areas that were used most intensely during the rest of the year (compare Fig. 2a and b). The cat travelled over a wider area each night than when she had dependent young. Kittens appeared to restrict the female to the general vicinity of the currently occupied den, since she repeatedly returned to the den to feed them.

Additional behaviours associated with scent marking in the Felidae were observed at low frequencies. Cheek-rubbing on grass tufts, bushes or termite mounds was observed on seven occasions, all of which occurred during the June/July observation period. Urination in a squatting position was observed 42 times, all during those periods in which the cat was not urine-spraying. On three occasions the cat urinated on top of a termite mound. Defecations were performed in a seemingly casual manner while travelling. Of the 19 defecations observed, only two were covered, and on both occasions this occurred close to the den that was being used by the kittens. No attention was paid to the faeces or the area in which they were deposited. Although the cat was not observed to defecate on prominent objects, scats were found on termite mounds. Neither defecation nor normal micturition was performed in combination with a scrape. The animal was seen to roll on her back on four occasions and clawing with the front paws was observed twice. Kittens were never observed to scent mark.

Reproductive status

Observation periods incorporated three stages in the cat's reproductive cycle, namely pregnancy, periods in which she had dependent young, and periods in which she was neither pregnant nor caring for kittens. Oestrus could not be identified through behavioural observation and no matings were observed. During the study the female produced three litters, although only the births of the second and third litters were observed. The female exhibited a seasonality of reproduction, producing two litters of two kittens each during the 1993/94 summer, and a third litter at the start of the following (1994/95) summer. The first litter was first observed on the 19 November 1993 and the kittens were estimated to be more than five weeks old, since the female was feeding them solid food (Estes, 1991; Olbricht & Sliwa, 1995). Parental care continued for approximately 10–12 weeks, from which time they were no longer observed with the adult. The male parent did not play any role in parental care and the kittens were left unaccompanied at the den while the female was hunting. The second litter was born on 20 February 1994 in a hollowed-out termite mound, and the third litter on 20 October 1994, during the following summer. Assuming a gestation period of 63–68 days (Schürer, 1988), the approximate mating periods for the two litters born in 1994 are calculated as 15–20 December 1993 and 8–13 August 1994, respectively. This indicates that the mating during

Table 1. Data obtained from approximately 575 hours of direct observation during seven observation periods from May 1993 to October 1995

Observation period	Total hours of observation	Distance ravelled (km)	Urine-sprays observed	Reproductive status
5–27 May 1993	33h58	27.60	49	Not pregnant, no young
17 Nov.–8 Dec. 1993	13h16	20.18	0	Dependent young
7–27 Jan. 1994	61h54	45.82	29	Pregnant
14 Feb.–5 March 1994	142h22	96.00	0	Birth 20 February 1994
5–15 April 1994	58h09	36.14	0	Dependent young
24 June–8 July 1994	104h49	62.96	1348	Not pregnant, no young
5 Sept.–25 Oct. 1994	161h05	113.60	28	Birth 20 October 1994
Total	575h33	402.29	1454	

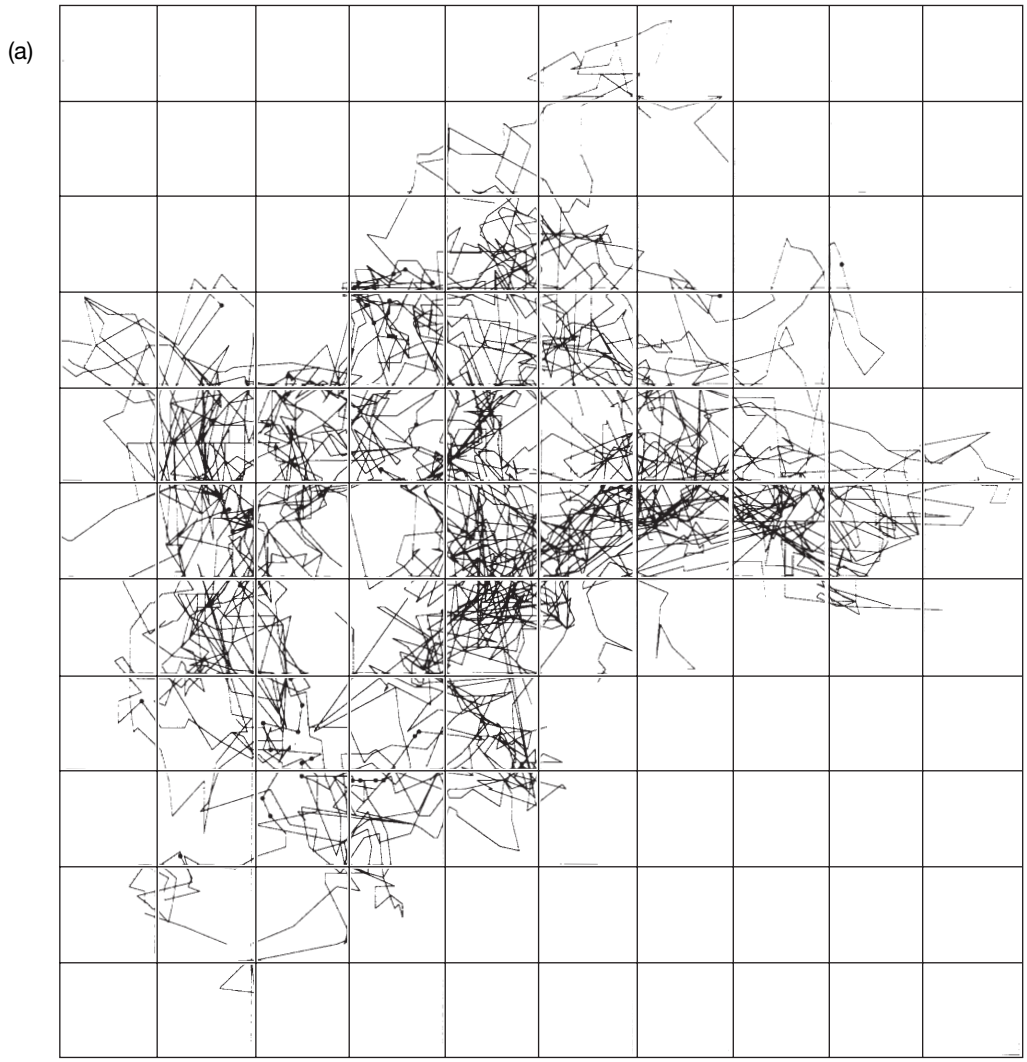


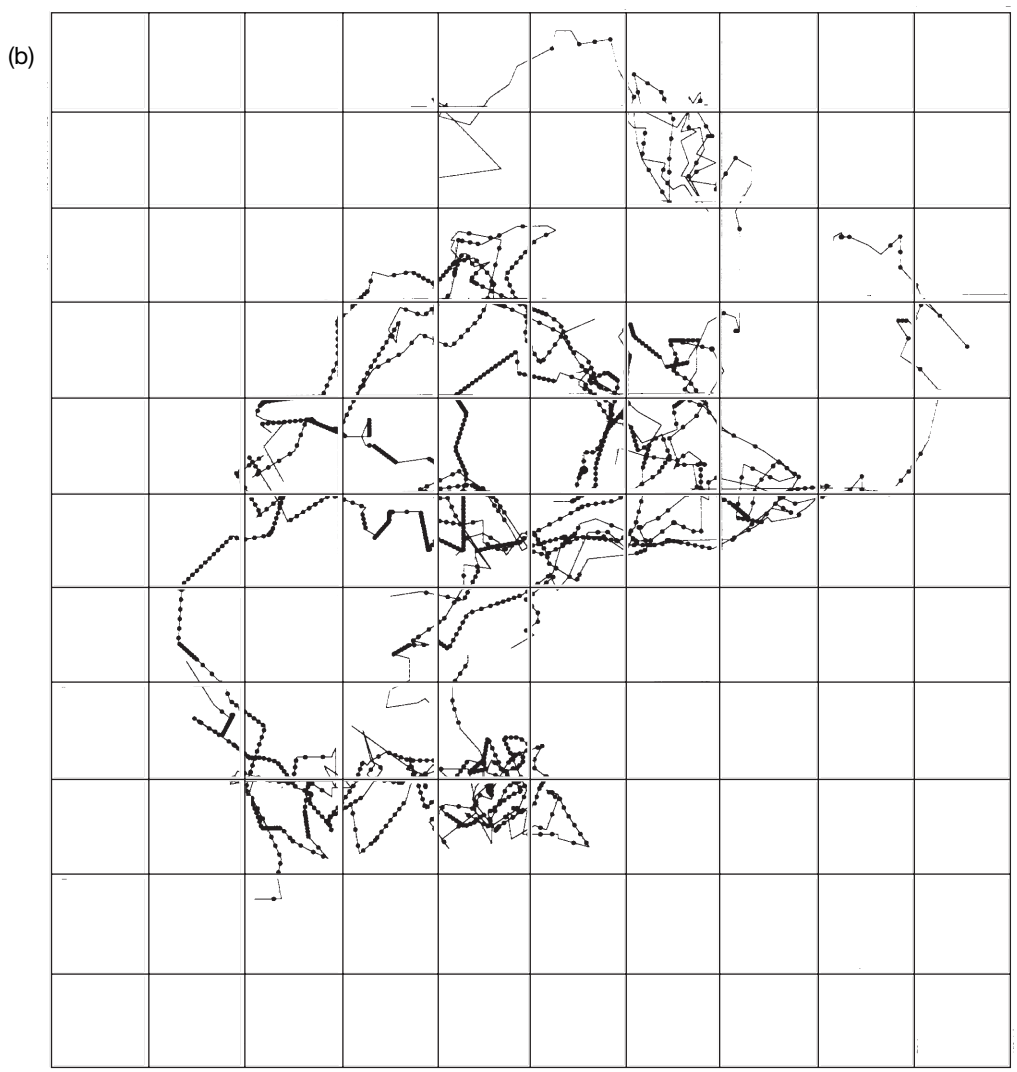
Fig. 2. Path followed by the cat (solid line) and individual urine-sprays (closed circles) plotted on a grid of 16 hectare blocks. (a) Data collected over 436 h 46 min, during five observation periods from 17 November 1993 to 20 October 1994, excluding the June/July observation period.

December occurred while the kittens from the previous litter were still in the care of the mother. In support of this, the female was observed together with the kittens, with an adult male on 6 December 1993. The male showed no interest in the kittens but followed the female. This was 9–14 days before the calculated period of mating and conception.

DISCUSSION

Function of urine-spraying

Scent marking may have numerous functions in any one species and different functions in different species (Johnson, 1973). Thus, for example, scent marks may be used to increase foraging efficiency in red foxes *Vulpes vulpes* (Henry, 1977; Harrington, 1981), as an indicator of sex and dominance status in wolves *Canis lupus* (Macdonald, 1985; Ryon & Brown, 1990) and during agonistic encounters in the domestic cat *Felis catus* (Panaman, 1981). A role in territoriality and the maintenance of social spacing is recognized in many species, although various hypotheses have been proposed to explain how scent marks function (Leyhausen & Wolff, 1959; Gosling, 1982; Richardson, 1993). Scent marks are also believed to play an important role in the advertisement of reproductive status. In solitary species, scent marks could assist a female's reproductive effort in two ways; first by informing males of her reproductive state and second by assisting a potential mate to locate her. There is a large amount of evidence to indicate that males are more attracted to odours of oestrous females than non-oestrous females and that the primary sources of these odours are urine and vaginal secretions (see review of Brown, 1979; Gorman & Trowbridge, 1989: 76). Within the Felidae, Verberne & de Boer (1976) have demonstrated that, in the domestic cat male, interest in urine eliminated by the female follows a cyclic pattern. Lions *Panthera leo* exhibit more flehmen



(b) Data collected over 104 h 49 min during the winter observation period from 24 June to 8 July 1994.

in response to urine of pro-oestrous females and male cheetah *Acinonyx jubatus* regularly sniff the ground where oestrous females have been lying, while ignoring non-oestrous females (Degenaar, 1977).

If the primary function of urine-spraying is the advertisement of female reproductive state, then a seasonal variation in frequency would be expected (Feldman, 1994). In this study, a dramatic increase in spraying frequency of the female black-footed cat was observed approximately 45 days before mating and conception of the third litter (8–13 August 1994; Fig. 1), compared to the absence and relatively low frequencies of urine-spraying at other times of the year (Fig. 2). Smith *et al.* (1989) and Sunquist (1981) observed that wild female tigers *Panthera tigris* exhibit a higher frequency of urine-marking prior to mating, resulting from an increase in marking during pro-oestrus. Similar observations were made in captive studies (Kleiman, 1974). Since it is a solitary animal, Sunquist (1981) believes that the higher frequency of marking between heats may ensure the presence of the male at the appropriate time. A similar strategy may be important in the solitary black-footed cat, since it has an extremely short oestrous period of approximately 36 hours, compared to at least six hours in the domestic cat *Felis catus* (Estes, 1991). If mating continues for only 10 hours, as observed in captive cats (Leyhausen & Tonkin, 1966), females would effectively have only one night in which to mate and conceive during each oestrous period. The fact that an increase occurred approximately one and a half months before mating and conception of the third litter, may reflect the occurrence of one or more periods of oestrus prior to conception. In this regard, it will be interesting to determine whether the spraying frequency fluctuates, possibly indicating multiple periods of oestrus, or remains high until conception occurs. Macdonald (1979) observed that the frequency of token urine marking in a tame red fox increased over winter and reached a peak, which was maintained, almost two months before mating, at which time it decreased dramatically.

Although they show great variability, intraspecific overlap of home ranges is the most common land tenure system within the Felidae (Sunquist, 1981). In this study, urine-sprays were not restricted to the borders of

the cat's home range but appear to be most dense in those areas used most intensively (Fig. 2a & b), thereby increasing the probability of a neighbouring male locating her within a shared range. During this period, the female is also able to distribute her odour over greater areas each night than when she has dependent young, since she is not restricted to the vicinity of the den.

Since this is a solitary species that inhabits an arid environment, an effective strategy for mate attraction and location, such as the extensive spatial and temporal pattern of scent marking seen before the breeding season, may be important in order to take advantage of favourable conditions for breeding during the summer. However, before conception of the second litter of the summer, no urine-spraying was observed. This may be due to the presence of the kittens, since urine-spraying was absent during all periods in which the cat had dependent young. Since the cat repeatedly returned to the den in order to feed the kittens each night, this may serve to minimize the possibility of predation of the kittens by, for example, black-backed jackal, *Canis mesomelas*. This is supported by the observations that, although generally left exposed, defecations made close to the den occupied by the kittens were covered, and both wild (Molteno, pers. obs.) and captive females (Leyhausen, 1979) regularly moved their kittens to new dens. It is therefore possible that urine-spraying assists the female to breed at the start of the breeding season, whereas later in the season a more important concern is to reduce the risk of predation of the kittens, since she has already invested substantial energy in rearing these offspring. This implies that scent marking constitutes a considerable risk to the kittens, outweighing the benefits of attracting a potential mate. Nevertheless, despite the absence of urine-spraying by the female, an adult male was observed with the female in the presence of the kittens before conception of the second litter.

The increase in the frequency of scent marking observed prior to conception of the third litter suggests a reproductive function. However, the fact that urine-spraying was observed during all periods in which the cat did not have dependent young (Table 1), albeit at a relatively low frequency, indicates that scent marks may serve an additional function in this species. Although infrequent, these scent marks may function in the maintenance of social spacing, as found in other felids (Hornocker, 1969; Eaton, 1970; Bailey, 1974; Sunquist, 1981), possibly through a mechanism of mutual avoidance (Leyhausen & Wolff, 1959). Thus, urine-spraying may function to minimize contact with conspecifics during most of the year, but facilitate attraction of opposite sex conspecifics during the mating period.

Types of marking

With the exception of the mountain lion *Felis concolor* (Seidensticker *et al*., 1973), urine-spraying is the most important form of chemo-communication within the Felidae, both in terms of reproductive advertisement and territory maintenance. The predominance of this form of marking indicates its importance in the black-footed cat. Although at a very low frequency, cheek-rubbing was also observed during the June/July observation period, suggesting a potential role in the advertisement of reproductive status. Cheek-gland secretions may contain information concerning female reproductive state, since male domestic cat interest in female cheek-gland secretion followed a cyclic pattern (Verberne & de Boer, 1976). In many felid species, faeces are believed to have a communicatory function in terms of social spacing, since they receive attention from conspecifics, are often deposited at prominent or conspicuous sites, and may be associated with scrapes made in the substratum (Saunders, 1963; Bailey, 1974; Corbett, 1979; Robinson & Delibes, 1988). Seidensticker *et al*. (1973) observed that adult male mountain lions deposited faeces on the pile of pine needles or soil made near the scrape. In this study, relatively few acts of defecation were observed while the cat was moving. As observed in the lion by Schaller (1972), who concluded that faeces were probably not involved in marking, the black-footed cat simply stopped, defecated and moved on. However, most of the observed defecations were left uncovered and, although not directly observed, evidence of scats deposited on termite mounds was found. A possible communicatory role of faeces needs further investigation. Urination in a squatting position is thought to have a primarily eliminative function (Corbett, 1979). This is supported in the black-footed cat by the fact that all eliminative urinations were observed during the periods in which the cat was not urine-spraying. Claw marks may serve as a visual signal in tigers, since different individuals recurrently marked and inspected the same trees (Smith *et al*., 1989). However, in this study, the cat did not repeatedly use a defined path when travelling, and the small number of claw scratches observed therefore appears not to have a communicatory function, but may rather be a comfort behaviour (Smith *et al*., 1989) or facilitate the removal of loose claw sheaths, as suggested by Mellen (1993).

In order fully to understand the role of various forms of scent-marking behaviour in this species, more information on temporal and spatial scent-marking patterns of both male and female cats, their use of home range, as well as the response to scent marks by neighbouring cats, is required. These aspects will be addressed as the study progresses and the number of study animals increases.

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