Symp. zool. Soc. Lond. (1980) No. 45, 107–139

Patterns of Scent Marking with Urine and Faeces Amongst Carnivore Communities

DAVID W. MACDONALD

Zoology Department, University of Oxford, UK

SYNOPSIS

Carnivores deploy their urine and faeces (sometimes associated with glandular secreta) at varied sites and in diverse contexts. Recent field work has disclosed that the pattern and frequency of marking within some species varies with the individual's sex, social and reproductive status. In most cases the functions of urine and faecal marking remain largely unknown, but accumulating evidence suggests that many different messages are conveyed by these odours. It is stressed that the pattern of marking may show significant intra-specific variation when comparisons are made between populations inhabiting different habitats.

INTRODUCTION

In 1954 Konrad Lorenz suggested that a singing nightingale and a dog "cocking" its leg were engaging in functionally equivalent behaviour. The idea that avian song and mammalian scent marking were involved in territorial behaviour has been widely assumed for a long time; recently Krebs (1977) has proven that *one* function of great tit, *Parus major*, song is territorial defence, but what evidence has emerged concerning the role of scent-marking? I shall review this question for the Carnivora, especially concerning communicative functions of their urine and faeces. In particular, I shall consider whether the spatial distribution of these marks sheds any light on their functions.

Mammalian scent marking has been reviewed by Ralls (1971), Eisenberg & Kleiman (1972) and Johnson (1973) while Ewer (1968, 1973) and Mech & Peters (1977) have discussed many aspects of odour communication amongst carnivores. Kleiman (1966) reviewed scent marking by the Canidae and provided criteria for distinguishing marking from elimination. These include that the mark is (1) oriented to specific objects, (2) elicited by familiar landmarks and novel objects or odours and (3) repeated frequently on the same object.

Crook (1965) and Clutton-Brock & Harvey (1977) have used interspecific comparisons to derive ideas about the functional basis of differences in behaviour between species. Where possible I shall make comparisons between and within species from various ecological circumstances.

URINE

Although Kleiman never saw red foxes, *Vulpes vulpes*, urine marking in a zoo, urination by this species in the wild fulfils each aspect of her definition of scent marking. Foxes of both sexes frequently sprinkle a few drops of urine on visually conspicuous objects. I have studied this behaviour by combining observations on wild foxes by night, with experiments on tame foxes. From eight weeks of age, hand-reared foxes were walked throughout an area of similar size to a small wild fox territory. As the foxes matured they seemed to behave quite naturally during daily walks, so that urine marking and associated behaviour could be watched in great detail (Macdonald, 1979a). At about five months old vixens change from urinating during a few prolonged eliminations each day to leaving many small "token" marks. These tokens are directed towards visually conspicuous objects and, in contrast to the prolonged urinations, often involve leg-lifts or other postures apparently adopted to ensure that the urine is deposited on a chosen site. The behaviour of one vixen studied during 112 walks between November and March illustrates that very many such token sites are visited and marked. Figure 1 shows the pattern of token marks she left along woodland paths. Many sites were revisited daily during the study period and many were marked repeatedly. In midwinter the vixen consistently left over 100 token marks during each one hour walk, some sites being re-marked on each of over 70 days, and being marked more than once on any given day.

What factors influenced the distribution of token urine marks? A comparison of three measures (tokens/m, tokens/site, sites/m) for different parts of the fox's home range revealed that terrain influenced marking behaviour. Wild foxes often travel their home ranges along traditional paths and this applied to the experimental foxes too; sometimes they left the trail and crossed a field or woodland. Table I shows that token marking was less frequent off travel routes, although visually conspicuous sites were no less abundant.

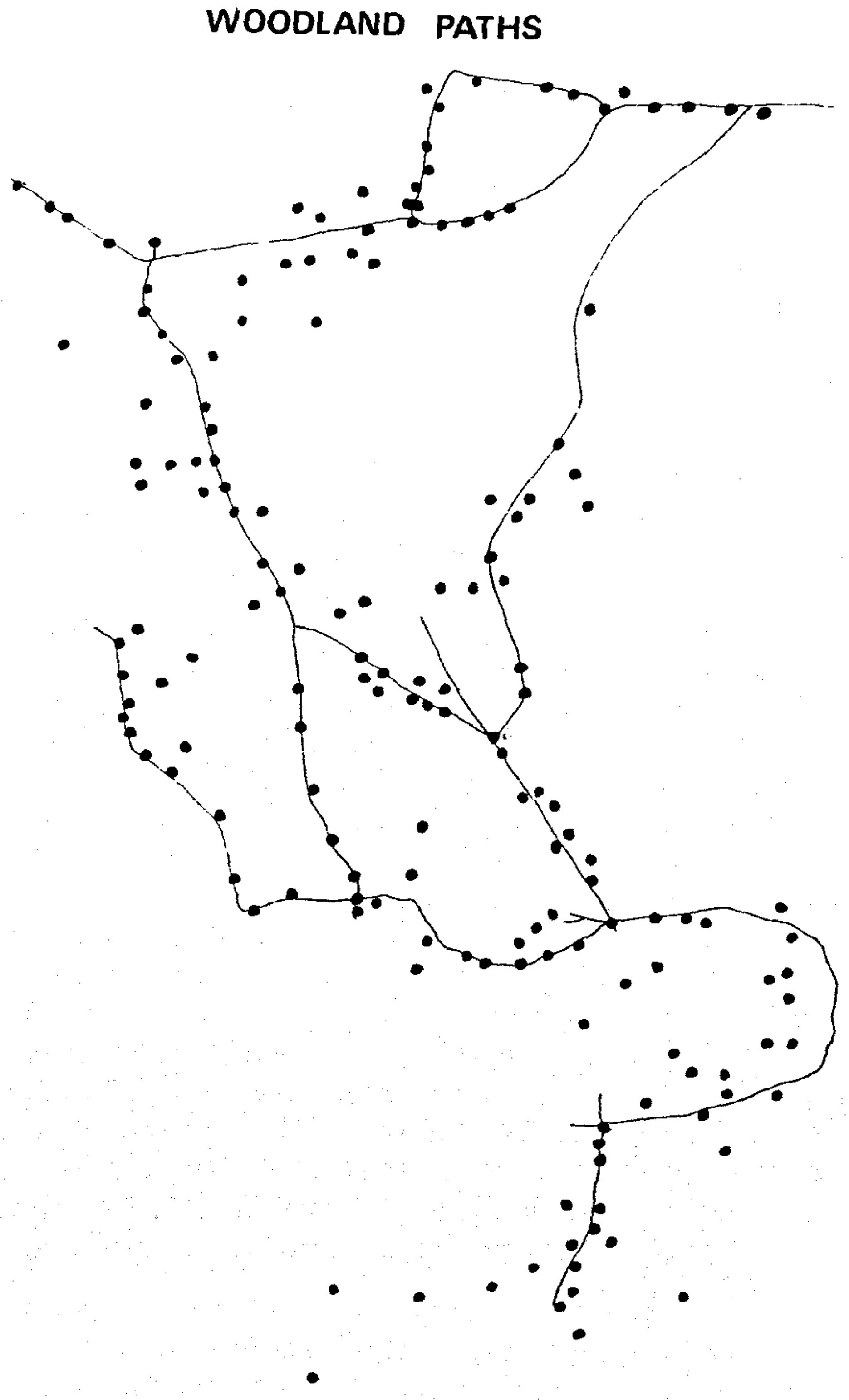

FIG. 1. Within the vixen's marking range she travelled a network of woodland paths. The figure shows the distribution of token marking sites along these paths.

In fact, the foxes were inclined to wend their way across the open field, while the "sites/m" were calculated from linear distances between sites. Hence, I estimate that the sites/m travelled off the path would be about a tenth of the value quoted (i.e. 0.71: 0.025 sites/m travelled). Another influence of terrain was the number of

TABLE I

Factors influencing the frequency of token urination by a red fox. More tokens were left on paths than off them. More sites were marked where prominent sites were available.

	Tokens per site	Sites per m
Terrain		
Rough ground	12.43	0.86
Flat ground	20.56	0.56
Paths		
Off a path	6.37	0.25
On a path	10.4	0.71

visually conspicuous sites available. Table I also shows that where sites were scarce each was marked more often. These differences aside, the vixen left token urinations along paths in numbers proportional to the frequency with which each path was travelled, irrespective of the location of the path within her home range.

Two captive vixens studied in detail both limited their token marking to a clearly defined area. At the edge of this area they frequently paused and spontaneously turned back. During three months a total of 1283 tokens was left by one vixen along a field edge leading to her "turning point". An analysis of these showed a rapid decline in the frequency of marking with proximity to the edge of her marking range (Table II). The marking range of one vixen gradually took on an identical configuration to that of the dominant vixen of her family group. The exact position of their turning point could be influenced by placing a sample of alien fox urine near the border. The fox would turn back when she smelled these samples, but did not turn back when she encountered her own, transplanted urine. In contrast, within her marking range a vixen overmarks samples of alien urine. Implicit in these results is an ability to discriminate between her own and other urine. Beauchamp (1973) showed that female guinea pigs investigate alien urine for longer than familiar

TABLE II

The "edge effect" towards the perimeter of a fox's marking range. The number of sites marked per metre declined rapidly to zero as the fox reached the border of her marking range.

Distance from edge (m)	Sites per m
100–235	0.95
70–100	0.26
35– 70	0.17
0– 35	0.17

urine; male tamarins, *Saguinus fuscicollis*, can recognize each other by urine and circumgenital gland odour (Ewer, 1973). Gorman (1976) and Rasa (1973) have shown that two species of mongoose can recognize individuals through glandular secretions, as can badgers, *Meles meles* (Ostborn, 1976) (see also Barash, 1974).

The exact configuration of each vixen's token marking range could be mapped by digging up a favoured marking site and moving it, by 10 m daily stages, across the countryside. The border to the area within which each vixen would mark her transplanted site could be determined very precisely, in some cases to the nearest 10 m. Many aspects of vixen behaviour (e.g. caching food) suggested that the token marking range corresponded to her territory. That token marking occurs within the territory does not demonstrate that it functions in territorial defence, but the above results certainly suggest this is probable. In addition, token urine marking by foxes clearly serves a variety of other functions, to which I will return below. First, I will compare these results with studies of other species.

Peters & Mech (1975) and Rothman & Mech (1979) have reported on an outstanding field study of scent markings by wolves, *Canis lupus*. Peters & Mech (1975) identified four kinds of scent mark while observing a captive pack, raised leg urination (RLU), scratching, squat urination (SQU) and defaecation. Each of these behaviours was seen several times as part of the assertive, agonistic and sexual behaviour, and SQUs were commonly associated with "friendly" interactions. Only mature, high ranking wolves (primary alpha animals) show RLUs, which seem to be analogous to foxes' token urinations. Amongst family groups of foxes, socially dominant vixens token mark more frequently than do their subordinates, and they also play a more active role in territorial defence (Macdonald, 1977). Peters & Mech (1975) used aircraft to find the tracks of members of 13 radio-marked packs and thereafter followed 240 km of trails in the snow. They found 583 RLUs, with frequencies ranging from 20 per km to 0 per 7 km (mean = 1 per 450 m). As with fox tokens, all but four of these RLUs were directed at visually conspicuous objects. These marks were often visited and sniffed later, as witnessed by nose-shaped indentations in the snow nearby. Peters & Mech point out that the elevated location of these marks (1) facilitates wind dispersal of the odour; (2) increases the evaporation surface as the urine trickles down; (3) minimizes the chance of the mark being covered by snow, and (4) produces visual contrast against the snow which is visible from several metres.

Peters & Mech (1975) studied the spatio-temporal features of raised leg urination and found a peak in frequency of 3.5 per km in February, falling to 1 per km in March. Again, the winter sees a peak in token marking by foxes, plunging to a minimum for vixens during oestrus (Macdonald, 1979a). Like foxes, wolves often travel well-used trails and leave a relatively large number of scent marks on these routes (Table III). Peters & Mech confirmed Seton's (1909) observation that many marks were left at junctions between trails; in fact 40% of RLUs were at junctions. Foxes too, frequently leave tokens at junctions (as both species do with faeces, see below), but not to the same extent as wolves (see Fig. 1). The influence of terrain, in addition to proximity to a path, is emphasized by the fact that all RLUs recorded on frozen lakes were on plants or rocks protruding through the ice.

TABLE III

Frequency with which members of wolf pack left different types of scent mark on fresh snow. Different types of scent mark were recognized by signs in snow to show their relative frequency (Peters & Mech, 1975).

	Signs per km
Raised leg urination	2.3
Squat urination	0.3
Faeces	0.5
Scratching	0.2

The most striking difference in the pattern of RLU marking was between the territorial borders and their interior (Table IV). The extent of this difference was not significantly influenced by the number of wolves in the pack, presumably because RLU marking is confined largely to the alpha pair. The scent profile of a pack's territory is like a doughnut, studded with "olfactory hotspots". The concentration of RLUs around the border arose from an increase in marking after direct or indirect encounters between packs.

Peters & Mech (1975) speculate on various functions of RLU and other scent marks and amongst these is territorial defence. While they do not have conclusive evidence of an aversive effect of alien RLUs on a pack's movements (as for foxes, see above) they do present powerful circumstantial evidence that supports this conclusion. For instance packs excursing into their neighbours' territory turn back under circumstances where scent marks are prime candidates as the aversive agent. Further, Jordan, Shelton & Allen (1967) report seeing a lone wolf cowering after smelling the recent marks of a resident pack in whose territory it was trespassing. These results come entirely from studies of territorial packs, but wolf populations

TABLE IV

Factors influencing the frequency of scent marking by members of a wolf pack. Wolves urine mark (RLU) more frequently near territorial borders. They mark more frequently on trails than off them, irrespective of the availability of suitable prominent sites (Peters & Mech, 1975).

	RLUs per km
Proximity to border	
Edge of territory	2.67
Centre of territory	1.27
Terrain	
Trails	3.4
Bush	1.7
Ice	0.4

also include itinerant "loners" of both sexes (Mech, 1970). These travelling loners sometimes meet and establish new pairs and Rothman & Mech (1979) have studied their marking behaviour, which provides a fascinating contrast to that of resident packs.

Newly formed pairs marked in a way more similar to pack wolves (see below) and in marked contrast to loners (Table V). In 72.2 km tracking of lone wolves Rothman & Mech (1979) found only one series of RLUs and no scratching, and these RLUs were away from travel routes. Loners neither overmark alien scent, nor do they mark in the vicinity of kills, both of which are heavily marked by resident packs. Furthermore, they consistently leave faeces away from trails. However, loners were no less interested in scent marks than newly formed pairs of pack wolves; all made three to four investigations per km along trails and loners discovered 0.9 scent marks per km. Furthermore, during 158 km of tracking, loners passed 52 trail junctions of which 14 were investigated. Similar, although less substantial, data have been presented for itinerant male foxes, who were never seen to token urinate, and for resident foxes who stopped token urinating while on excursions in neighbouring territories (Macdonald, 1979a). Outside their own marking range, foxes continue to visit and investigate suitable marking sites with the same frequency. P. Moehlman (personal communication) has seen silver-backed jackals, *Canis mesomelas*, urine marking near the perimeter of their territories and in the interior. She noted that some jackals had to travel up to 5 km from their territories to reach water, and that during these excursions they never urine marked.

Both wolves and foxes frequently re-mark particular sites with urine. Individuals of both these species (and many others, see below)

TABLE V

Comparison of location of faeces from lone wolves and newly-formed pairs. Lone wolves and newly-formed pairs select different marking sites. In particular, newly-formed pairs mark trails, which single wolves do not (Rothman & Mech, 1979).

Location	% of faeces	
	Single wolves ($n = 18$)	Pairs ($n = 20$)
Hills	16	5
Woods	50	30
Waterways	6	0
Roads and tracks	28	65

sometimes investigate a site they have previously marked, but do not re-mark it. How does the individual face the dilemma of to mark or not to mark? Peters & Mech (1975) showed that a RLU of only a few days' vintage was likely to stimulate overmarking, while those of nearer one month old did not. They concluded that the smell had probably faded from these old marks. If fresher urine generally provides a stronger stimulus for marking, there must be a maximum concentration at which the smell of an individual's urine inhibits further urination, or else marking would continue *ad infinitum*. Indeed, Peters & Mech (1975) found that sites revisited after one day were overmarked less than those revisited after a few days. Similarly, foxes walked along one path twice during one day with an 8–10 hour interval, urinated less the second time; when the interval was less than 1 h token marking was reduced to 30% of its previous level (Ostborn (1976) reported a similar result for badgers, *Meles meles*, subcaudal gland marking). However, on some occasions foxes seemed to get trapped in a vortex of overmarking, repeatedly walking a few metres from a site before hurrying back to mark it again. The maximum number of repeat marks by a vixen at one site within a few seconds was eight (Macdonald, 1979a).

Aside from artificial aspects of my fox study consequent upon captivity, one might speculate that differences in the temporal pattern of urine marking between foxes and wolves relate to differences in territory size, and the pattern of home range use; wolves reach every part of their territory at least once every three weeks, while in many habitats foxes travel every part of their territory at least once each night (Macdonald, 1977).

Since Kleiman's (1966) review of the subject, several studies have shed new light on carnivore urine marking. Perhaps because their anatomy and postures facilitate recognition of urination at some distance, most new information concerns canids. In a study of coyote, *Canis latrans*, social behaviour, Camenzind (1978) recorded 57 instances of urine marking (following Kleiman's 1966 definition). Of these, 68% were on territory boundaries; of the total, 40% involved females, 47% males and 13% animals of unidentified gender.

Camenzind (1978) found a seasonal pattern in urine marking with a minimum during September and October. Seasonal variation in frequency of urine marking has already been mentioned for wolves and foxes and seems generally applicable; in many cases the peak coincides with the period of pair formation and courtship and also, perhaps fortuitously, with the time of dispersal of non-resident juveniles. The phenomenon of double or overmarking in rapid succession by one animal on another's urine mark is widely reported during this period. Table VI summarizes Lamprecht's (1979) data for bat-eared foxes, *Otocyon megalotis*, and this behaviour has been recorded for golden jackals, *Canis aureus*, by Golani & Keller (1975), red foxes, *Vulpes vulpes*, by Macdonald (1979a), hunting dogs, *Lycaon pictus*, by Frame & Frame (1976), dingoes, *Canis dingo*, by L. Corbett (personal communication), and bush dogs, *Speothos venaticus* (Kleiman, 1972). It is also common knowledge that domestic dogs behave in the same way (Bekoff, 1979). The most detailed study of double marking is Rothman & Mech's (1979) on wolves. They found a high rate of RLU marking shortly after lone wolves of opposite sexes paired up. Frame & Frame (1976) reported members of a newly formed pair of hunting dogs urine marking together within 90 min of meeting. Rothman & Mech (1979) report an instance of increased RLU marking within five days of the first meeting between an incipient pair. Many of these RLUs were overmarks (or

TABLE VI

Seasonal patterns of urine marking by bat-eared foxes. Double marking showed seasonal variation in frequency amongst pairs of bat eared foxes (Lamprecht, 1979).

	Month (1972–73)										
	May	Jun	Sept	Mar	Apr	May	Jan	Jun	Oct	Nov	Dec
Observations of ♂	2	2	1	1	35	20	18	0	2	0	0
Overmarking partner's urine ♀	1	0	0	1	3	3	0	2	0	0	0
Minutes of observation	1331	325	245	5	215	241	116	21	27	372	60

within10 m of each other), and the rate of double marking decreased with the duration of the new pair bond. The urine of male mice can influence the reproductive condition of females (Whitten, 1956) so a similar process may be involved in double marking. Rothman & Mech (1979) suggest that, "behavioural and physiological synchronization of wolf pairs is accomplished via the visual and olfactory stimulus of the double mark", and quote four lines of evidence supporting this: double marking is (1) absent in pairs which subsequently fail to mate; (2) is associated with high rates of mutual investigation; (3) is at maximal frequency soon after pairing and (4) is performed largely by high ranking, breeding wolves. During the pairing season for foxes, males were only seen to follow and double mark with dominant vixens (who anyway do more token marking than subordinates) and only dominant vixens breed (Macdonald, 1979a, b). Furthermore, dominant vixens urine mark on members of their family group. The frequency of urine marking by oestrous females is known to increase in a wide variety of species, including various canids (Kleiman, 1966), zebra, *Equus zebra*, (Klingel, 1967), and Uganda kob *Adenota kob* (Buechner, Morrison & Leuthold, 1966).

Montgomery & Lubin (in press) have studied the foraging behaviour of crab-eating foxes, *Cerdocyon thous*, and double marking occurs between pairs outside the context of pairing. These foxes normally forage in pairs, whose paths frequently intersect. Neighbouring home ranges overlap widely. When the male urine marked, the female often overmarked the spot.

Camenzind (1978: 285) describes scent marking, presumably involving urination, along territory borders after clashes between neighbouring families and also around a denning area by coyotes whose pups had apparently been cannibalized by their neighbours. High frequencies of urination have also been reported following agonistic encounters both within and between groups for wolves (Zimen, 1976), golden jackals (Golani & Mendelssohn, 1971; Macdonald, 1979c) spotted hyenas, *Crocuta crocuta* (Kruuk, 1972), red foxes (Macdonald, 1977), and lions, *Panthera leo*, (Schaller, 1972), and is commonly seen to occur after encounters between males of both domestic dogs (see Doty & Dunbar, 1974) and house cats. Urine marking has also been implicated in territorial defence for mountain lions, *Felis concolor* (Hornocker, 1969), and kit foxes, *Vulpes macrotis* (Egoscue, 1962).

In addition to foxes and wolves many other species urine mark specifically on visually conspicuous objects, e.g. coyotes (Linhart & Knowlton, 1975), lions (Schaller, 1972), and cheetah (Eaton, 1973). Hornocker (1969) describes how puma, *Felis concolor*, scrape piles of vegetation together before urinating on them. Apart from odour disseminating properties, these elevated sites must be easy to locate and stress the probable visual components of many scent marks (e.g. collections of white faeces, scratches, urine on snow etc.). Kleiman (1966, 1972) has described the "handstand" urinating posture of female bush dogs; in this species male and female marks are consistently at different heights. Female red foxes and golden jackals occasionally do "handstands" while urinating (personal observation and Golani & Mendelssohn, 1971) and Kingdon (1978: 22) reports that hunting dogs do the same. Arctic foxes, *Alopex lagopus*, in summer sometimes urinate as often as once per minute in a way indistinguishable from red foxes (both species also leave faeces at similar sites (personal observation)).

Bobcats, *Lynx rufus*, urine mark throughout their territories at 3 times per 0.4 km (Bailey, 1974) as do other felids, e.g. lynx, *Lynx lynx*, 17–20 urinations per 1.6 km (Saunders, 1963) and tiger, *Panthera tigris*, 11 urinations per 30 min (Schaller, 1967, see also Sankhala, 1978). Fiedler (1957) described retromingent behaviour in many felids.

A completely novel explanation of urine marking by red foxes has been explored by Henry (1977) in a series of elegant field trials. Henry found that only 12% of sites were repeatedly urine marked during his observations. This contrasts with over 85% being marked more than once during my study. Henry explains this in the context that in his habitat (boreal forest/aspen parkland ecotone) foxes frequently hunt by investigating up to 220 spots on the forest floor per hour (the search strategy resembles that described by Macdonald (1980) for foxes hunting for beetles and earthworms). He hypothesises that foxes urine mark places where food has already been eaten, but where food odour or inedible food remnants remain. On subsequent investigation the urine odour signifies "no food" and hence acts as a form of "book keeping". In a series of field experiments Henry provided various combinations of food, miscellaneous odours and urine and measured the investigation times of foxes at each site. He demonstrated that sites with small quantities of food remains were investigated by a vixen for 6.8 ± 3.1 s while the investigation time decreased 1.24 ± 0.5 s when urine was added to the site. However, where lots of bait (30 g as opposed to 3 g) was added to a urine-marked site the "book keeping" signal was ignored, presumably because of the relative concentrations of food and urine odour.

Henry's study raises the interesting question of the possible relationships between scent marking and foraging behaviour: I suggest that the positive correlation between fox token urine marks and frequency of travelling a given route can transmit information on the pattern of home range use and L. Corbett (personal communication) has found a significant increase in faecal marking in preferred hunting areas of wild cats, *Felis silvestris*, and feral domestic cats, *Felis catus*. The idea that the pattern of resource exploitation underlies the distribution of various scent marks will be discussed below, while scent marking of individual prey items poses many puzzles: Korytin & Solomin (1969) believed foxes urine mark sites of caches to aid in discovering them subsequently. However, Macdonald (1976) has shown that caches are principally discovered through a precise memory of their location and identification of local landmarks may play a secondary role (viz. Tinbergen, 1965). Foxes do not urine mark on sites containing caches, but they often mark on the excavated cache sites once the food has been removed (Macdonald, 1976; Henry, 1977: 99). Furthermore, I have frequently seen foxes token mark large prey items before consuming them, or at the site where small prey, such as an earthworm, has narrowly escaped capture. Foxes rarely mark the capture sites of beetles or earthworms (perhaps these leave no confusing odour traces) but will mark on an excavated rodent burrow (which has also become a visually and olfactorily conspicuous object in the course of being excavated, as do many inedible prey remains in the course of being eaten). Henry does not state what prey his foxes were "scavenging" for, but presumably it was something which left detectable quantities of durable odour at its capture site. Kleiman (1972) notes that maned wolves (*Chrysocyon brachyurus*) urine mark on food (and faeces) and Ewer & Wemmer (1974) found captive civets rubbing on strong smelling food.

Urine is not always deposited alone; for instance Wemmer (1977) believes that the female genet, *Genetta tigrina*, deposits both urine and vaginal secretions when marking with its perineal gland. He states that around the oestrous period perineal gland marking sites become encrusted with urine. In addition, oestrous females sometimes urinated on these sites without perineal rubbing. The frequency of perineal and associated marking was minimal during the few days of oestrus, but was high previously and peaked two days after mating.

Wemmer (1977) states that captive adult genets generally directed their urine towards elevated objects. *Nandinia binotata* often urinated while walking slowly forward and in two other captive species *Paguma larvata* and *Civettictis civetta* males urinated in association with hindleg movements. *Paguma* scuffed its metatarsus in the urine, while the *Civettictis* kicked backwards when urinating (see also Dücker, 1971). Daubing the feet with urine has also been reported by Schaller (1972) and Bertram (1978) and there is a suggestion that anal gland secretion may sometimes be mixed with the urine (see Fig. 2). Binturong, *Arctictis binturong*, soaks both its tail and metatarsus while urinating. Kleiman (1974) describes metatarsus scuffing behaviour which presumably disseminates the odour and which was performed more commonly by males than females.

Bears also daub themselves with urine which is then transferred to specific marking sites: Lindemann (1954 in Lloyd, 1978) described how grizzly bears, *Ursus americanus*, roll in their urine and then rub their backs on marking trees, (see also Hediger, 1946 in Lloyd, 1978 and Tschantz, Meyer-Holtzapfel & Bachmann, 1970). Bears apparently lack specialized external scent glands (Davis, 1964 in Lloyd, 1978). Lloyd (1978) has recently studied bear marking trees in detail. Figure 3 illustrates the impact bears have on their marking sites (in this case a tree first marked in 1950 is still in use). Lloyd estimated the frequency of rubbing on these sites by noting the displacement of a length of fishing-line he fastened across the scar.

Lloyd found that one tree species, the amabilis fir, was marked preferentially (Table VII)(see also Schaffer, 1971 in Lloyd, 1978). All marked trees had straight trunks, with few branches below 1.5 m. The mean age of marking trees was 79 years, with a mean age of first scarring of 20 years. The average height of the highest scar was 139 cm. It has been suggested that the height of these scars (and of the elevated scent marks of other species) provides indirect information on the size and hence status of the signals. I doubt this since such a system would be too easily open to cheating.

Through analysis of the frequency with which his fishing line was displaced, Lloyd found that marking trees were used more often than tracking had suggested. Bear marking trees were largely confined at a density of 20 per km^2 or 3.4 per linear km of major watercourse. All were located near active bear tracks. F. Bunnell (personal communication) has suggested to me that the amabilis fir is selected because of its abundant pitch which might function in the retention and slow dissemination of odour.

Lloyd also describes ground marks apparently made by bears

TABLE VII

The selection of tree species for marking by bears. Bears select certain tree species for marking. They also choose trees of specific girth and structure (Lloyd, 1978).

	Observed	Expected
Amabilis fir	17	8
Others	1	10

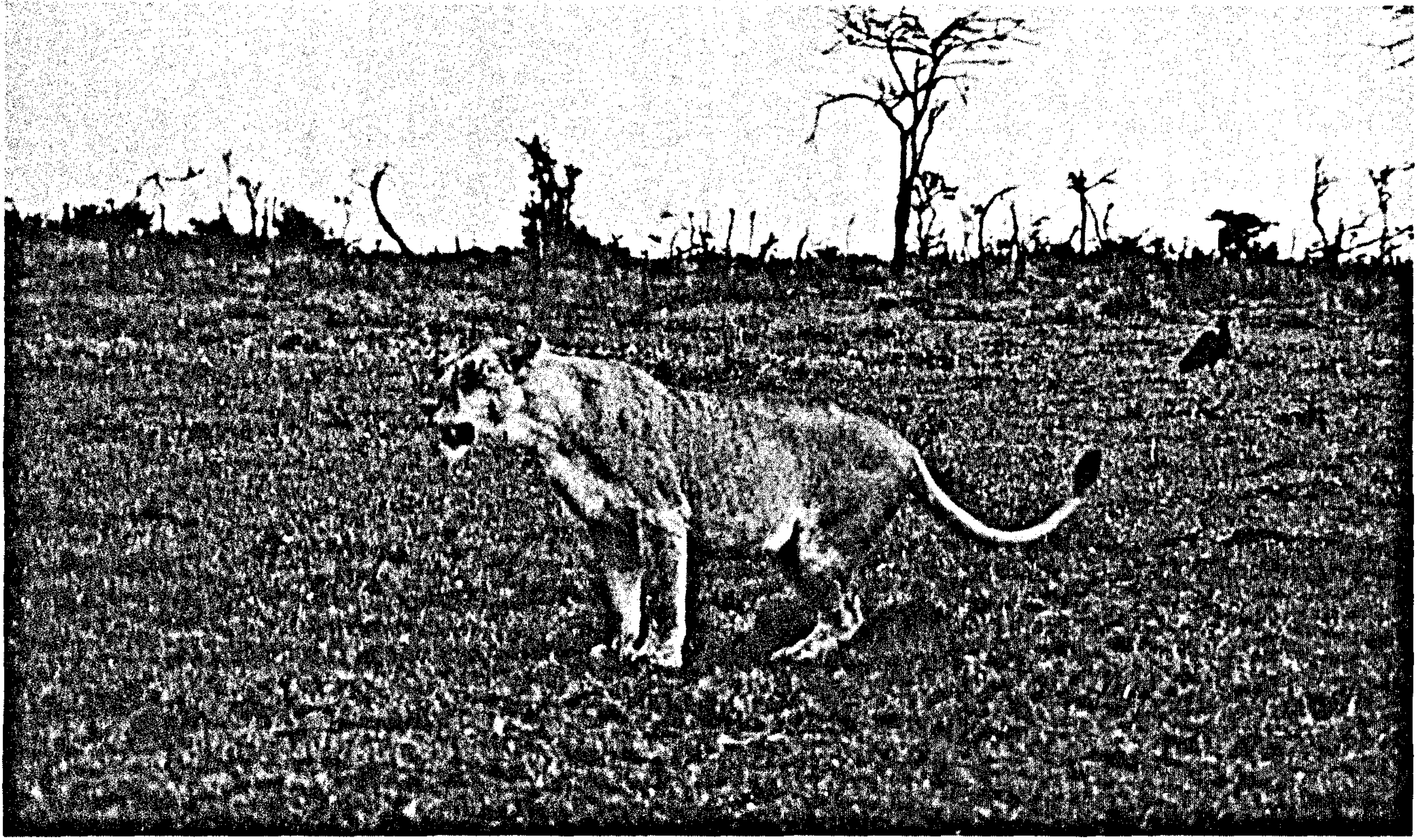

FIG. 2. A lioness treads with her hind legs as she urinates, so impregnating her paws with urine drenched mud (photo: B. C. R. Bertram).

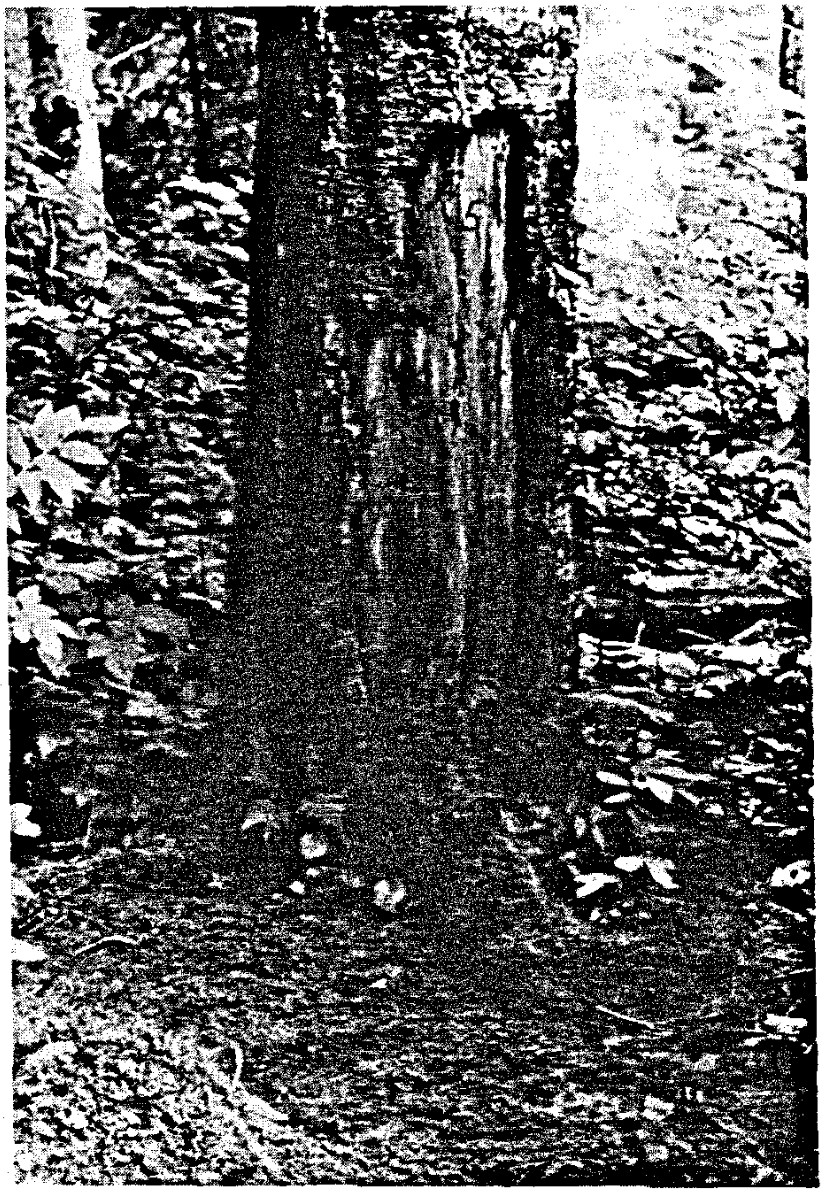

FIG. 3. Fir trees with mark stripped by bears. The scarred tree is rubbed with urine and mud (photo: K. A. Lloyd).

stamping on their trails which may serve as visual indicators of temporary foci of activity.

FAECES

At least in the respect that they can sometimes be more easily detected, faeces are more readily studied than urine. The few studies available suggest considerable inter-specific differences in the distribution of faeces (which may be coated in anal gland secretion) in an animal's home range, and in the number of faeces left at each site.

Inter-specific Comparisons

Table VIII indicates the frequency with which five species left faeces singly or in middens of various sizes. Red foxes left most faeces

TABLE VIII

Frequency with which faeces are left in groups of different sizes. A comparison of the frequencies with which faeces are deposited singly or in middens of various sizes by different species (Trapp, 1978; Macdonald, unpublished, 1978, 1979a).

	No. of faeces					
	1	2	3	4	>5	>10
Red fox	0.8	0.12	0.01	0.0	0.0	0.0
Grey fox	0.72	0.16	0.05	0.03	0.03	0.00
Cacomistle	0.56	0.07	0.04	0.05	0.28	0.28
Striped hyena	0.62	0.05	0.09	0.07	0.14	0.02
Golden jackal	0.44	0.04	0.03	0.09	0.15	0.23

singly, but two or three are sometimes found together. Red fox faeces are almost exclusively left on or near visually conspicuous objects, such as molehills; I have seen a fox standing on its front legs while defaecating on to a shrub. Although 5–10 faeces may often be found along 50 m or so of well used fox trail, I have only once seen any semblance of a midden when, in captivity, a dog fox left 13 faeces on one site.

Trapp (1978) has reported a concentration of grey fox, *Urocyon cinereoargenteus*, faeces around a fruiting tree (220 faeces in 10.7 x 19.7 m). Otherwise, the location of grey fox faeces seems to approximate to that of red foxes. Trapp found cacomistle, *Bassariscus astutus*, faeces were distributed along trails, on boulders or rocks, like foxes, but were also left in tree crotches and on horizontal boughs. In one attic the cacomistles left a heap of faeces 8 cm deep over an area of 45 cm x 45 cm (see also Trapp & Hallberg, 1975).

Kleiman (1972) contrasted bush dogs, *Speothos venaticus*, which scatter faeces, with maned wolves, which form middens. In a field study of maned wolves, J. Dietz (personal communication) found that faeces were predominantly left on elevated sites (e.g. termite mounds). Dietz also found that middens accumulate near resting places, and Kingdon (1978: 404) describes a similar phenomenon for cheetah.

Other species consistently leave their faeces in middens e.g. spotted hyenas, *Crocuta crocuta* (Kruuk, 1972), the palm civet, *Paradoxurus hermaphroditus* (Bartels, 1964), the pine marten, *Martes martes* (Lockie, 1966), the dwarf mongoose, *Helogale undulata* (Rasa, 1977), the long nosed mongoose, *Crossarchus alexandri* (Kingdom, 1978) and the African polecat, *Poecilogale* (Alexander & Ewer, 1959), raccoon dogs, *Nycterentes procyonoides*, (Ikeda, Eguchi & Ono, 1979), dholes, *Cuon alpinus*, and Simien foxes, *Canis simensis*, (J. Malcolm, personal communication), to cite but a few.

As Table VIII shows, even species using relatively enormous middens may also leave faeces singly. In some cases these single faeces probably have no communicative function (e.g. spotted hyenas in Ngorongoro, H. Kruuk, personal communication) but in others they may serve a different communicative function to faeces in middens. This appeared to be the case for a population of golden jackals, *Canis aureus*, where single faeces were more frequently left on conspicuous objects (such as shrubs) than were middens (44% of sites and 10% of faeces were singles)(see Fig. 4). The conspicuous single faeces were scattered within a group territory, while middens ringed the perimeter (see later, Macdonald, 1979c). Bailey (1974) found bobcat, *Lynx rufus*, middens scattered throughout territories and noted how rarely they were re-marked with fresh faeces. Other more solitary species, e.g. weasels, *Mustela frenata* and *M. rivalis*, also use middens, as do ferrets (Quick, 1951 and personal observation) but their distribution in terms of social spacing is unknown.

Figure 5 indicates the distribution of middens within territories of our contrasting species. The positions of the middens were plotted in terms of four annuli of equal width (and hence unequal area) between an approximately central den (otter, *Lutra lutra*, and badger) or the geometric centre of the territory (red fox and golden jackal) and the territory border. It might be more biologically meaningful to compare these figures corrected to per unit area of each annulus. These are given in the legend to Fig. 5 (for the jackals, single faeces are excluded from this analysis). In summary, while red foxes scatter faeces in all parts of their territories, coastal otters create middens near their lairs while golden jackals leave their middens like a string of beads around their territory. Badgers have both border middens and some near their setts. What differences in function underlie these broad descriptions and what ecological factors have given rise to them? To tackle this question I will look in more detail at the factors involved.

Kruuk (1978) describes a population of European badgers which was organized into social groups of 4—12 individuals, each maintaining territories which he differentiated by radio-tracking. By feeding the badgers at each sett with colour marked food and thereafter recovering the markers from middens, Kruuk demonstrated badgers were demarcating their territory borders with middens, many of which were linked by well trodden trails (0.72 middens per ha on border, 0.31 per ha on average). Kruuk also found that middens were located near certain landmarks more than predicted by chance (see Table IX) and that there were more defaecations/midden on the borders. In another study of radio-tracked badgers Macdonald &

FIG. 4. Single faeces of golden jackals are normally aloft prominent objects (a); jackals also use middens comprising many faeces (b) and these are associated with the territory border.

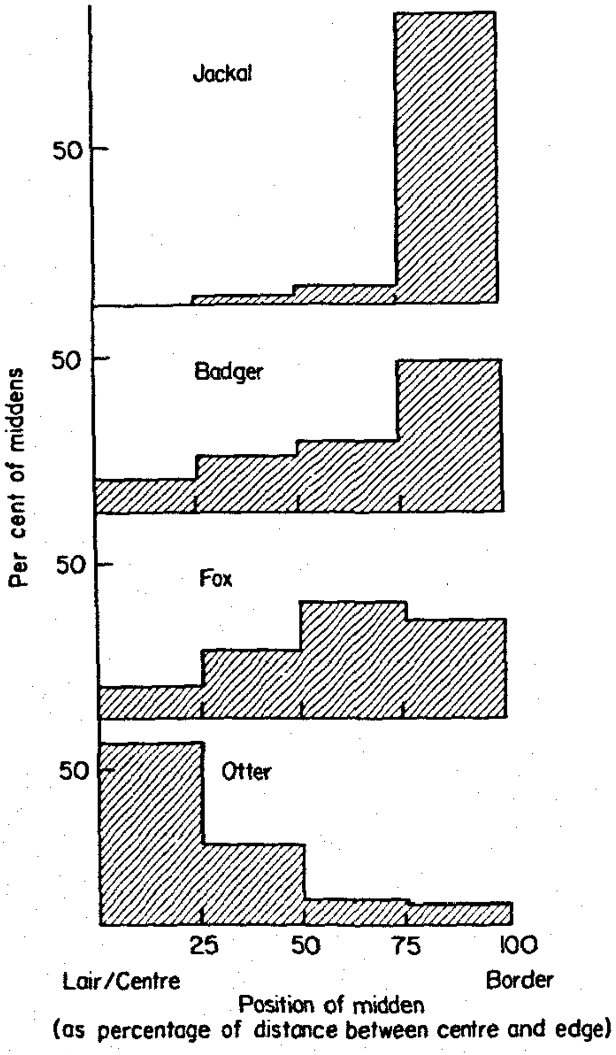

FIG. 5. Graphs of the proportion of faeces found in each of four annuli of equal width dividing home ranges. The figure shows how some species concentrate faeces near their borders, often near the centre of their ranges (see text). The data come from: jackal (Macdonald, 1979c, considering middens only); badger (Macdonald & Lindsay, unpublished); fox (Macdonald, unpublished) and otter (Kruuk & Hewson, 1978). As the annuli were of equal width they were of unequal area (in a ratio 1:3:5:7 from inner to outer). Correcting the figures to proportion of faeces per unit area of each annulus from inner to outer gives: jackal (0 :0.5: 0.08: 1.0); badger (1.5: 9.83: 0.6: 1.0); fox (2.2: 1.6: 1.7: 1.0) and otter (9.1: 4.0: 1.2: 1.0).

Lindsay (unpublished) also found middens along territory borders, but some long sections of boundaries had none (up to 25% of the perimeter); some of these stretches were across poor foraging habitat. Although there are differences in detail, a ring of middens similarly demarcates some spotted hyena territories (Kruuk, 1972) and some golden jackal territories (Macdonald, 1979c). In the case of the golden jackals this was also demonstrated using colour marked food. There was considerable variation in the size of jackal middens and some indications that middens were bigger along more frequently

TABLE IX

The influence of landmarks on the location of badger latrines. Badger latrines are found in association with landmarks more frequently than expected (Kruuk, 1978).

Type of landmark	% latrines (obs.)	% latrines (exp.)
Car track	39.6	11.0
Vegetation border	34.2	14.0
Fence	31.5	15.0
Conifer tree	9.0	0.0
Others	1.8	2.0
No landmark	31.5	69.0

contested stretches of border. The jackals, like the badgers and spotted hyenas, lived in large groups.

Kruuk & Hewson (1978) discovered that middens ("scats") of a population of coastal otters were more than twice as numerous within 100 m of holts than elsewhere. Several otters frequented each holt but foraged at sea up to 750 m away. These otters seemed to maintain linear territories along the coast, and so their middens were well away from territory borders.

Camenzind (1978) found 16 places where two to five coyote faeces were within 4 m^2 and Ozoga & Harger (1966) found 13 together, although coyote faeces are normally found singly. He also found one midden in a hayshed (500 faeces in less than 500 m^2) and reports another instance of a similar midden found beneath a bridge. The latrine which Camenzind found was not near a boundary, but was in a region where coyotes formed groups of three to seven adults.

Bearder & Randall (1978) have compared the size of latrines by two sympatric species, the spotted hyena and the African civet, *Civettictis civetta*. In their study area spotted hyenas live in territorial clans of about 12 adults. The civets normally moved solitarily, but several individuals occupied each assumed territory (see also Charles-Dominique, 1978). Bearder & Randall (1978) report how hyenas form temporary middens in the vicinity of large hills, from which the clan might feed for several nights. Some permanent feeding sites facilitate the build-up of big middens, e.g. a total of 295 faeces in three sites near a human settlement. In fact, all middens found away from a hyena trail were temporary, and 61% of long-term middens were at trail junctions (of the 25/57 remaining, three were near den sites and five at drinking places). These hyena latrines were more diffuse than those I have described for jackals (max. = 144 faeces per 800 m^2 as opposed to 105 per 2 m^2) and formed ellipses at trail junctions which extended further from the junction in the direction most frequently travelled by the hyenas. Middens near territory borders involved groups of hyenas as often as it did solitary ones, while middens in the interior were marked by solitary hyenas twice as often as by groups. In general, tracking revealed that hyenas passed middens at least three times for every twice they marked them. By transplanting faeces from a midden it was possible to show that the site, and not the faeces at it, stimulates fresh marking.

Most civet middens (civetries) were found throughout territories near trails of some type (61.6% along roads, 10.8% along game trails and 21.6% away from paths in the bush). Table X shows that civetries were located in clearings rather than in dense bush. Macdonald & Wise (in press) radio-tracked a Malay civet, *Viverra tangalanga*, which forged principally in clearings, and Charles-Dominique (1978) found that the African palm civet, *Nandinia binotata*, marks the fruiting trees from which it feeds.

TABLE X

Factors influencing the distribution of civetries and of perineal gland marking by African civets. Many different scent marks are often associated with middens, e.g. Randall (1977) showed that civet perineal gland marking was most frequent in trees near civetries, which in turn, were concentrated in clearings.

	% civetries per km	
1. Civetries and clearings	Clearing	Bush
Area I	74	26
Area II	71	29
2. Perineal gland marks along roads	No. checked	% marked
Trees	24	50
Rocks	7	28.6
Shrubs	31	19.4
Herbs	822	10.1

Ewer & Wemmer (1974) reported that African civets preferred to defaecate from heights, which corresponds to Bearder & Randall's (1978) observations that many civetries were in hollows and depressions. Similarly I found Malay civet middens filling up crevices between rocks, rather than on top of them as would be typical for many canids. Ratels, *Mellivora capensis*, tend to defaecate into holes and sometimes dig pits for this purpose (Kingdon, 1978).

Bearder & Randall (1978) listed considerable similarities in midden use by spotted hyenas and civets, including their location on trails, their longevity, pattern of use, distribution, and that they are used by several individuals who visit more often than they mark. Further, both species' middens act as foci for different sorts of marking; e.g. Randall (1977) has described the location of perineal gland marking on conspicuous sites near civetries (see Table X). In fact, middens of all species reported so far serve as foci for diverse sources of odour. Bearder & Randall also list differences between the two species, of which the most significant may be that civets always defaecate at civetries, while hyena often defaecate away from their middens.

Intra-specific Comparisons

Kruuk (1975) has reviewed the fast growing evidence that within the Carnivora species' social systems show considerable flexibility under various ecological pressures. If a species' organization alters between habitats does its scent marking behaviour also change? Several studies indicate that it does, and help to shed light on the ecological factors underlying certain patterns of scent marking.

Hyenas

Kruuk (1972) showed that spotted hyenas hunting stable, non-migratory prey populations lived in large stable matriarchal clans which defended group territories, the borders of which were delineated by collections of faeces. These middens were the focus of other scent markings too, e.g. anal gland pasting and scraping. In contrast, hyenas hunting migratory prey formed small ephemeral hunting groups, travelled relatively enormous distances and used small middens along trails. Bearder & Randall (1978) describe a third variant, with small clans in another habitat, feeding principally upon giraffe, probably defending territories and leaving middens largely at trail junctions.

The striped hyena, *Hyaena hyaena*, ranges solitarily over 44–72 km^2 of the Serengeti eating small, widely dispersed prey and leaving its faeces apparently randomly. In Israel, around stable feeding sites in the desert, the same species makes small middens in the vicinity of its feeding site and family groups remain in association at least until cubs are adult sized (Macdonald, 1978). For further comparisons see Kruuk (1975) and Mills (1978).

Jackals

Golden jackals, *Canis aureus*, in the Serengeti plains feed on small rodents, invertebrates, fruit and carrion. They are probably territorial, living either in pairs or in small family groups (van Lawick & van Lawick Goodall, 1970). J. Lamprecht (personal communication) rarely saw more than single faeces (invariably positioned in conspicuous sites) and while following silver backed jackals, *Canis mesomelas*, P. Moehlman (personal communication) similarly found only single faeces. In an area of highly clumped super-abundant food jackals formed large groups. They also used large middens, at least some of which delineated territorial borders (Macdonald, 1979c). J. Skinner (personal communication) has seen jackal middens in South Africa also.

Otters and mink

Studying otters, *Lutra lutra*, on inland waterways Erlinge (1968) found that they were territorial and that middens were predominantly associated with home range boundaries. Gorman (this volume p. 87) reports on the scattered distribution of otter scats around Scottish lochs, where they did not appear to be associated with territorial borders. Kruuk & Hewson (1978) studied otters along a coastline and found substantial overlap of foraging areas out to sea. In this habitat otter holts were rather evenly spread along the coast and middens were strongly associated with the holts and were rare at home range boundaries.

Mink, *Mustela vison*, also inhabit various aquatic habitats and establish middens. J. Birks (personal communication) finds that sprainting stones are frequently revisited around an eutrophic lake where mink ranges are contiguous. In contrast, along an oligotrophic stream he found large gaps between neighbouring ranges and found no evidence of repeated visits to marking sites.

Domestic cats

Cats, *Felis catus*, occupy a spectrum of habitats between complete dependence on man and independence. It is common knowledge that dependent house cats bury their faeces. In a detailed study of cats of various degrees of independence from man, L. C. Corbett (personal communication) has found considerable intra-specific variation in the pattern of faeces deposition within and between populations. For instance, dominant cats amongst a population of feral cats left faeces aloft conspicuous sites, especially along trails in the vicinity of dense or good hunting areas (of faeces on trails 92% were in good rabbit habitat, 39% were at multiple sites), whereas subordinate cats buried their faeces, often in the spoil heaps outside rabbit warrens. Furthermore a subordinate male utilized covered middens close to each of his three lairs. Liberg (in press) similarly found faeces left in conspicuous places by completely feral (independent) cats, but not by household (dependent) ones.

In mangrove swamps of Borneo, Malay houses are built atop of stilts above the water and houses are joined by intersecting cat-walks. I have seen neat piles of cat faeces along these walkways. Similarly, huge middens accumulate in cupboards and in other protected sites on industrial estates harbouring large populations of cats (R. Tabor, personal communication).

ECOLOGICAL BASES FOR INTER- AND INTRA-SPECIFIC VARIATION

Kleiman (1972) related differences between urine and faecal marking by maned wolves and bush dogs to the plains dwelling, solitary life style of the former and the forest dwelling, co-operative hunting of the latter (see also, Altman, 1972; Drewa, 1977). Kruuk & Hewson (1978) also suggest ecological explanations for intra-specific variation in otter marking behaviour: they suggest that inland territories which might be subject to invasion along well-defined routes could be best protected by border marking sites (viz. Erlinge, 1968) while middens near the holt could be most effective for coastal otters where intruders can land and trespass anywhere along the seafront.

Studies of this sort raise two specific questions: why use middens at all, and why concentrate them at the border or elsewhere (e.g. near the lair)?

Many species use middens but only European badgers, spotted hyenas and golden jackals have been found so far to use them for perimeter marking. In the study areas in question each of these species lived in large groups. But wolves and hunting dogs also live in large groups. Wolves occupy non-overlapping pack territories of over 125 km^2 (Mech, 1970) which may take three weeks to cover. Hunting dogs range over 1500 km^2 and overlap neighbouring ranges by 50% (Frame & Frame, 1976). The task of maintaining border middens to ranges of this size would be considerable, which might also explain why lions do not adopt the habit. Peripheral midden users are group livers who defend relatively small territories, in high density populations. They are also long-lived species with borders which may be stable for generations.

Non-peripheral middens are commonly associated with trails and junctions (e.g. civets, spotted hyenas, wolves) or lairs (e.g. badgers, dwarf mongooses, otters). For many species the lair is both a valuable resource and a focus of activity. It is hence an ideal site for information transfer both to other group members and to intruders. Middens close to the lair are frequent amongst animals that den communally e.g. badgers, meerkats, *Suricata suricatta* (Ewer, 1963), dwarf mongooses, *Helogale undulata* (Rasa, 1977). The localization of large numbers of faeces in one place may, at least for the mongoose, serve a sanitary function; A. Rasa (personal communication) found that putting faeces from another group onto a mongoose midden evoked no response. The distribution of middens by different species may be explicable in terms of the type of resources to be defended (if they have a defensive role), but insufficient data are available as yet. Where resources are distributed in stable patches one might expect these to be heavily marked, e.g. foxes and feral cats concentrate marks in favoured hunting areas. The more clumped the resource the more concentrated the marks can become, e.g. spotted hyenas establish temporary middens near big kills (Bearder & Randall, 1978) and 5–10 fox faeces are often found within 10 m of a sheep or deer carcase. Where resources are ephemeral concentrations of marks might be redundant.

FOCI FOR SCENT

Beauchamp, Doty, Moulton & Mugford (1976) point out that there are hundreds of volatile and non-volatile substances in urine, a sobering thought for those studying the functions of urine marking. Albone (1977) has reviewed the biochemical complexity of some glandular secretions, which may be further complicated by bacterial action (Albone *et al.*, 1977). While each odour source may convey considerable information by itself, a variety of odours is commonly left at one place. Spotted hyenas leave anal gland pastings at middens (Kruuk, 1972) and civets deposit perineal gland secretions near civetries (Randall, 1977). Wolves and coyotes often scrape after urinating (Peters & Mech, 1975; Bekoff & Diamond, 1976) which may involve odour from interdigital glands. Spotted hyenas and badgers also scrape at their latrines (Kruuk, 1972, 1978) and Bearder & Randall (1978) suggest spotted hyenas scrape and defaecate interchangeably. They found that spotted hyenas defaecated and scraped during 43% of active visits to latrines, scraped only on 30%, defaecated on 21% and pasted 6%. The ratio of faeces:scrapes varied from 165:185 in winter to 122:224 in summer, perhaps related to seasonal differences in the ground's hardness. Schaller (1967) describes a similar relationship between scrapes and faeces of tigers. Kruuk (personal communication) notes that badgers scrape at border latrines during seasons when they seldom defaecate at them. Anal and subcaudal gland secretions are also left at badger middens. To further complicate the issue, many carnivores share marking with, e.g., wolves and foxes, and striped hyenas and jackals may all defaecate at each other's sites.

Seventy per cent of red fox faeces may be on sites previously urine marked and foxes, silver backed jackals and maned wolves all urinate on faeces (Macdonald, 1979a; P. Moehlman, personal communication; Kleiman, 1966, 1974). In addition to urinating and defaecating at a site, foxes may deposit anal sac secretion, roll in the scent, or mark with interdigital glands. Sometimes vixen rub their richly glandular perioral region along the site (before and/or after urinating) and may drag grass stems or saplings through the corner of the mouth, trailing saliva (Fig. 6). I know of one fox who also occasionally scuffs with her hindlegs after token urinating. Each odour source may communicate different information, the interpretation of which may depend on which other combination of odours is present; also each (because of its volatility) may decay at a different rate, perhaps ensuring that the appropriate message is maximally effective at each interval after marking.

A COST TO SCENT MARKING – DETECTION BY PREY

In addition to conspecifics, other species can find and perhaps interpret scent marks. Hoskinson & Mech (1976) and Mech (1977) have shown how deer keep to the periphery of wolf territories. Kruuk & Sands (1972) suggest that aardwolves use middens to localize, and ensure the rapid disposal of, faeces which might otherwise alert their prey (they use anal glands for border marking). Recent trials exposing woodmice, *Apodemus sylvaticus*, to the faeces of weasels, *Mustela nivalis*, suggest the mice react more strongly to these odours than to odours not associated with predators (Macdonald, unpublished).

There is a need to distinguish functions and effects of scent marks: an effect of the fox's pattern of token urination may be to permit an intruder to chart a "safe" route through the territory avoiding the resident, but this would not be a function from the resident's standpoint (see also Montgomery's (1974) simulation study). Eaton (1970) suggested that cheetahs avoid each other's hunting trails through "reading" fresh urine marks.

CONCLUSION

Although much evidence from carnivores implicates urine and faecal marking in territorial maintenance, overmuch emphasis has been

FIG. 6. A red fox drags its mandibles across some grass stalks which it subsequently token marks with urine.

placed on attempting to fit urine or faecal marking into a role which stresses only their aversive functions. Demonstrating that urine or faecal marking only happens inside territories is not necessarily to say that they contribute to territorial maintenance. Territory marking is but one of a myriad functions that scent may serve and a broad spectrum of functions may operate simultaneously (see discussion of this point by Beauchamp *et al.*, 1976): similarly, Eisenberg & Kleiman (1972) have stressed that because marking is seen in aggressive contexts, this does not necessarily imply that the odour expresses aggression.

In addition to field experiments the solution to many questions concerning scent marking requires a reliable method for assessing an animal's internal state before and after discovering or depositing an odour. Holst & Kolb (1976) have attempted to use frequency of sniffing in this way. Biotelemetry may provide a powerful tool in this context.

Just as recent studies have pointed to the flexibility of carnivore societies, so we should expect the role that odours play to vary intraspecifically. Preliminary evidence suggests that the pattern of resource distribution in a given habitat and the influence of that pattern on a species' social organization, may underlie some features of the distribution of scent. Not only should we expect each scent to convey a diversity of information — we should expect its context and function to vary between individuals. The selective forces acting on each individual within a society are different and these will be reflected in their scent marking behaviour, as in all other aspects of their social life.

ACKNOWLEDGEMENTS

I am grateful to colleagues who have let me quote their unpublished studies, and use their photographs. N. B. Davies kindly criticised a draft of this paper.

REFERENCES

Albone, E. S. (1977). The chemical ecology of mammals — a new focus for chemical research. *Chemistry Britain* 13: 92–99.

Albone, E. S., Gosden, P. E., Ware, G. C., Macdonald, D. W. & Hough, N. G., (1977). Bacterial action and chemical signalling in the red fox, *Vulpes vulpes*, and other mammals. *Proc. Am. Chem. Soc. Symp.* 67: 78–91.

Alexander, A & Ewer, R. F. (1959). Observations on the biology and behaviour of the smaller African polecat (*Poecilogale albinucha*). *Afr. Wild Life* 13: 313–320.

Altman, D. von (1972). Verhaltensstudien an Mahnenwolfen, *Chrysocyon brachyurus*. *Zool. Gart., Lpz.* N.F. 41: 278–298.

Bailey, T. N. (1974). Social organization in a bobcat population. *J. Wildl. Mgmt* 38: 438–446.

Barash, D. P. (1974). Neighbour recognition in two "solitary" carnivores: the raccoon, (*Procyon lotor*) and the red fox (*Vulpes fulva*). *Science, Wash.* 185: 794–796.

Bartels, E. (1964). On *Paradoxurus hermaphroditus* (Horsfield 1824). *Beaufortia* 19: 193–201.

Bearder, S. W. & Randall, R. M. (1978). The use of fecal marking sites by spotted hyenas and civets. *Carnivore* 1: 32–48.

Beauchamp, G. W. (1973). Attraction of male guinea pigs to conspecific urine. *Physiol. Behav.* 10: 589–594.

Beauchamp, G. W., Doty, R. L., Moulton, D. G. & Mugford, R. A. (1976). The phenomena concept in mammalian chemical communication: a critique. In *Mammalian olfaction, reproductive processes and behaviour*: 143–160. Doty, R. (ed.). New York: Academic Press.

Bekoff, M. (1979). Scent-marking by free-ranging domestic dogs: olfactory and visual components. *Biol. Behav.* 4: 123–139.

Bekoff, M. & Diamond, J. (1976). Precopulatory and copulatory behavior in coyotes. *J. Mammal.* 57: 372–375.

Bertram, B. C. R. (1978). *A pride of lions*. London: Dents.

Buechner, H. K., Morrison, J. A. & Leuthold, W. (1966). Reproduction in Uganda kob with special reference to behaviour. *Symp. zool. Soc. Lond.* No. 5: 69–88.

Camenzind, F. J. (1978). Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. In *Coyotes*: 267–293. Bekoff, M. (ed.). New York: Academic Press.

Charles-Dominique, P. (1978). Ecology and social behaviour of the African Palm Civet, *Nandinia binotata*, in Gabon: with a comparison with sympatric prosimians. *Terre et Vie* 32: 477–528.

Clutton-Brock, T. H. & Harvey, P. H. (1977). Primate ecology and social organization. *J. Zool., Lond.* 183: 1–39.

Crook, J. H. (1965). The adaptive significance of avian social organization. *Symp. zool. Soc. Lond.* No. 14: 181–218.

Doty, R. L. & Dunbar, I. (1974). Attraction of beagles to conspecific urine, vaginal and anal sac secretion odours. *Physiol. Behav.* 12: 825–833.

Drewa, P. von (1977). Beobachtungen zur Gebart und naturlichen Aufzucht von Waldhunden (*Speothos venaticus*) in der Gefangenschaft. *Zool. Gart., Jena.* N.F. 47: 109–137.

Dücker, G. (1971). Gefangenschaftsbeobachtungen an Pardelrollern *Nandinia binotata* (Reinwardt). *Z. Tierpsychol.* 28: 77–89.

Eaton, R. L. (1970). Group interactions, spacing and territoriality in cheetahs. *Z. Tierpsychol.* 27: 481–491.

Eaton, R. L. (1973). *The world's cats*. 1. Winston, Oregon: World Wildlife Safari.

Egoscue, H. J. (1962). Ecology and life history of the kit fox in Toole County Utah. *Ecology* 43: 481–497.

Eisenberg, J. F. & Kleiman, D.G. (1972). Olfactory communication in mammals. *A. Rev. Ecol. Syst.* 3: 1–32.

Erlinge, S. (1968). Territoriality of the otter, *Lutra lutra*, L. *Oikos* 19: 81–98.

Ewer, R. F. (1963). The behaviour of the meerkat, *Suricata suricatta* (Schreber). *Z. Tierpsychol.* 20: 570–607.

Ewer, R. F. (1968). *Ethology of mammals*. London: Elek Sci. Press.

Ewer, R. F. (1973). *The carnivores*. The World Naturalist. London: Weidenfeld and Nicolson.

Ewer, R. F. & Wemmer, G. M. (1974). The behaviour in captivity of the African civet, *Civettictis civetta* (Schreber). *Z. Tierpsychol.* 34: 359–394.

Fiedler, W. (1957). Beobachtungen zur Markierungsverhalten einiger Säugetiere. *Z. Saügetierk.* 22: 57–76.

Frame, L. H. & Frame, G. W. (1976). Female African wild dogs emigrate. *Nature, Lond.* 263: 227–229.

Golani, I. & Keller, A. (1957). A longitudinal field study of the behavior of a pair of golden jackals. In *The wild canids*: 303–335. Fox, M. W. (ed.). New York: van Nostrand Reinhold.

Golani, I. & Mendelssohn, H. (1971). Sequences of precopulatory behavior of the jackal (*Canis aureus* L.). *Behaviour* 38: 169–192.

Gorman, M. L. (1976). A mechanism for individual recognition by odour in *Herpestes auropunctatus*, (Carnivora: Viverridae). *Anim. Behav.* 24: 141–145.

Henry, J. D. (1977). The use of urine marking in the scavenging behavior of the red fox (*Vulpes vulpes*). *Behaviour* 61: 82–105.

Holst, D. von & Kolb, H. (1976). Sniffing frequency of *Tupaia belangeri*: A measure of central nervous activity (arousal). *J. comp. Physiol.* 105: 243–257.

Hornocker, M. G. (1969). Winter territoriality in mountain lions. *J. Wildl. Mgmt* 33: 457–464.

Hoskinson, R. L. & Mech, L. D. (1976). White tailed deer migration and its role in wolf predation. *J. Wildl. Mgmt* 40: 429–441.

Ikeda, H., Eguchi, K. & Ono, Y. (1979). Home range utilization of a raccoon dog, *Nyctereutes procyonoides viverrinus*, Temminck, in a small islet in Western Kyushu. *Jap. J. Ecol.* 29: 35–48.

Johnson, R. P. (1973). Scent marking in mammals. *Anim. Behav.* 21: 521–535.

Jordan, P., Shelton, P. & Allen, D. L. (1967). Numbers, turnover, and social structure of the Isle Royale wolf population. *Am. Zool.* 7: 233–252.

Kingdon, J. (1978). *East African mammals* 3a. London: Academic Press.

Kleiman, D. G. (1966). Scent marking in the Canidae. *Symp. zool. Soc. Lond.* No. 18: 167–177.

Kleiman, D. G. (1972). Social behavior of the maned wolf (*Chrysocyon brachyurus*) and bush dog (*Speothos venaticus*): a study in contrast. *J. Mammal.* 53: 791–806.

Kleiman, D. (1974). Scent marking in the Binturong (*Arctictis binturong*). *J. Mammal.* 55: 224–227.

Klingel, H. (1967). Soziale Organisation und Verhalten freilebender Steppenzebras. *Z. Tierpsychol.* 24: 580–624.

Korytin, S. A. & Solomin, B. N. (1969). Materialy po etiologii provykh. *Trudȳ vses. nauchno-issled. Inst. Zhevotnogo Syr'ya Pevs Hiring* 22: 235–270.

Krebs, J. R. (1977). Song and territory in the great tit. In *Evolutionary ecology*: 47–62. Perrins, C. M. & Stonehouse, B. (eds). London: Macmillan.

Kruuk, H. (1972). *The spotted hyena:* A study of predation and social behavior. Chicago: Univ. Chicago Press.

Kruuk, H. (1975). Functional aspects of social hunting in carnivores. In *Function* *and evolution in behaviour*: 119–141. Baerends, G., Beer, C. & Manning, A. (eds). Oxford: Oxford Univ. Press.

Kruuk, H. (1978). Spatial organisation and territorial behaviour of the European badger, *Meles meles*. *J. Zool., Lond.* 184: 1–19.

Kruuk, H. & Hewson, R. (1978). Spacing and foraging of otters (*Lutra lutra*) in a marine habitat. *J. Zool., Lond.* 185: 205–212.

Kruuk, H. & Sands, W. A. (1972). The aardwolf (*Proteles cristatus* Sparrman) as a predator of termites. *E. Afr. Wildl. J.* 10: 221–227.

Lamprecht, J. (1979). Field observations on the behaviour and social system of the bat-eared fox, *Otocyon megalotis*, Desmarest. *Z Tierpsychol.* 45: 260–289.

van Lawick, H. & van Lawick Goodall, J. (1970). *The innocent killers*. London: Collins.

Liberg, O. (In press). Spacing patterns in a population of feral and domestic cats. *Oikos*.

Linhart, S. B. & Knowlton, F. F. (1975). Determining the relative abundance of coyotes by scent station lines. *Wildl. Soc. Bull.* 3: 119–124.

Lloyd, H.A. (1978). *Aspects of the ecology of black and grizzly bears in coastal British Columbia*. M.S. Thesis: Univ. Brit. Columbia, Vancouver.

Lockie, J. D. (1966). Territory in small carnivores. *Symp. zool. Soc. Lond.* No. 18: 143–165.

Lorenz, K. (1954). *Man meets dog*. London: Methuen.

Macdonald, D. W. (1976). Food caching by red foxes and some other carnivores. *Z. Tierpsychol.* 42: 170–185.

Macdonald, D. W. (1977). *The behavioural ecology of the red fox*, Vulpes vulpes: *a study of social organization and resource exploitation*. D.Phil. Thesis: University of Oxford.

Macdonald, D. W. (1978). Observations on the behaviour and ecology of the striped hyena, *Hyaena hyaena*, in Israel. *Isr. J. Zool.* 27: 189–198.

Macdonald, D. W. (1979a). Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes*. *Z. Tierpsychol.* 51: 1–22.

Macdonald, D. W. (1979b). Helpers in fox society. *Nature, Lond.* 282: 69–71.

Macdonald, D. W. (1979c). The flexible social system of the golden jackal, *Canis aureus*. *Behav. Ecol. Sociobiol.* 5: 17–38.

Macdonald, D. W. (1980). The red fox, *Vulpes vulpes*, as a predator upon earthworms, *Lumbricus terrestris*. *Z. Tierpsychol.* 52: 171–200.

Macdonald, D. W. & Wise, M. J. (In press). Notes on the behaviour of the Malay civet, *Viverra tangalanga*. *Sarawak Museum Journal*.

Mech, L. D. (1970). *The wolf*. New York: Nat. Hist. Press.

Mech, L. D. (1977). Wolf-pack buffer zones as prey reservoirs. *Science, Wash.* 198: 320–321.

Mech, L. D. & Peters, R. P. (1977). The study of chemical communication in free ranging mammals. In *Chemical signals in vertebrates*: 321–332. Müller-Schwarze, D. & Mozell, M. M. (eds). New York: Plenum.

Mills, M. G. L. (1978). The comparative socio-ecology of the Hyaenidae. *Carnivore* 1: 1–7.

Montgomery, G. G. (1974). Communication in red fox dyads: a computer simulation study. *Smithson. Contr. Zool.* No. 187: 1–30.

Montgomery, G. G. & Lubin, Y. D. (In press). Social structure and food habits of crab-eating fox (*Cerdocyon thous*) in Venezuelian llanos. *Acta cient. Venez.* 29 (5).

Ostborn, H. (1976). Doftmarkering hos grävling. *Zool. Revy* 38: 103–112.

Ozoga, J. J. & Harger, E. M. (1966). Winter activities and feeding habits of northern Michigan coyotes. *J. Wildl. Mgmt* 30: 809–818.

Peters, R. P. & Mech, L. D. (1975). Scent marking in wolves. *Am. Scient.* 63: 628–637.

Quick, H. F. (1951). Notes on the ecology of weasels in Gunnison County, Colorado. *J. Mammal.* 32: 281–290.

Ralls, K. (1971). Mammalian scent marking. *Science, Wash.* 171: 443–449.

Randall, R. M. (1977) *Aspects of the ecology of the civet,* Civettictus civetta *(Schreber, 1978).* M.Sc. Thesis: University of Pretoria.

Rasa, O. A. E. (1973). Marking behaviour and its significance in the African dwarf mongoose, *Helogale undulata rufula. Z. Tierpsychol.* 32: 449–488.

Rasa, O. A. E. (1977). The ethology and sociology of the dwarf mongoose, *Helogale undulata rufula. Z. Tierpsychol.* 43: 337–406.

Rothman, R. J. & Mech, L. D. (1979). Scent-marking in lone wolves and newly formed pairs. *Anim. Behav.* 27: 750–760.

Sankhala, N. (1978). *Tiger*. London: Collins.

Saunders, J. W. (1963). Movements and activities of the lynx in Newfoundland. *J. Wildl. Mgmt* 27: 390–400.

Schaller, G. G. (1967). *The deer and the tiger.* Chicago: Univ. Chicago Press.

Schaller, G. B. (1972). *The Serengeti lion: A study of predator-prey relations.* Chicago: Univ. Chicago Press.

Seton, E. T. (1909). *Life histories of northern animals* 2: 677–1267. New York: Charles Scribner and Son.

Tinbergen, N. (1965). Von den Vorratskammern der Rotfuchs, *Vulpes vulpes. Z. Tierpsychol.* 22: 119–149.

Trapp, G. R. (1978). Comparative behavioral ecology of the ringtail and the gray fox in Southwestern Utah. *Carnivore* 1(2): 3–31.

Trapp, G. R. & Hallberg, D. L. (1975). Ecology of the gray fox (*Urocyon cinereoargenteus*): a review. In *The wild canids*: 164–178. Fox, M. W. (ed.). New York: van Nostrand Rheinhold.

Tschantz, B., Meyer-Holtzapfel, M. & Bachmann, S. (1970). Das Informationssystem bei Braunbären. *Z. Tierpsychol.* 27: 42–72.

Wemmer, C. M. (1977). Comparative ethology of the large-spotted genet (*Genetta tigrina*) and some related Viverrids. *Smithson. Contr. Zool.* No. 239.

Whitten, W. K. (1956). Modifications of the oestrous cycle of the mouse by external stimuli associated with the male. *J. Endocr.* 13: 399–404.

Zimen, E. (1976). On the regulation of pack size in wolves. *Z. Tierpsychol.* 40: 300–341.