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Some Observations and Field Experiments on the Urine Marking Behaviour of the Red Fox, *Vulpes vulpes* L.

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With 9 figures

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Abstract

Some red foxes, *Vulpes vulpes*, urinate very frequently on conspicuous sites. This paper describes such 'token' urine marking in detail from observations in the wild (around Oxford, England and Ein Gedi, Israel) and on leash-walking, tame foxes. Field experiments show that token urination occurs at specific sites and in particular areas. A leash-walked vixen reacted differently to her own urine marks than to experimental ones of alien urine, and her reaction was influenced by where she encountered the marks. Token urine marks are most frequently made by socially dominant foxes and are seen in a variety of contexts, including courtship and aggression.

Wafts of fox urine can often be smelled repeatedly in the same places; TINBERGEN (1965) mentions a discarded boot on which he detected fox urine regularly for over three years. By watching wild foxes through infra-red binoculars, I have seen that they urinate very frequently. A vixen and a dog-fox watched in February marked 1.2 and 1.0 times per min respectively; the same foxes watched in April urine marked 0.5 times per min and 0.1 times per min. Another dog-fox tracked across snow in April urinated 14 times in 200 m. Yet, on other occasions foxes of both sexes may not urinate for hours on end. What determines whether or not foxes will urine mark, how frequently they do so, and the location of their marks? Answers to such questions are crucial to a proper understanding of fox social behaviour, since:

“... one could hardly claim to understand a mammal's social system until that person gains a detailed knowledge about the species' olfactory signaling” (MECH and PETERS 1977).

The carnivores are prolific in their use of odours, and the roles these play in their social behaviour have been reviewed by GORMAN (1979) and MAC-

DONALD (1979 a). KLEIMAN (1966) has reviewed scent marking amongst the Canidae and detailed studies within this family include those on wolves, *Canis lupus*, (PETERS and MECH 1975; ROTHMAN and MECH 1979), foxes, *Vulpes vulpes*, (HENRY 1977) and jackals, *Canis aureus*, (MACDONALD 1979 b).

The red fox, *Vulpes vulpes*, is territorial in many habitats, defending areas varying between under 20 ha and over 1000 ha. Territory size seems to be determined largely by food availability and distribution. Between 2—6 adult foxes, comprising one ♂ and several related vixens, may occupy each territory. Group size is probably also related to food supply. Where several vixens comprise a group only the more dominant ones generally breed. Other foxes are itinerant and are attacked by resident foxes on whose territories they trespass. The following account of urine marking can be considered in the context of this summary (from MACDONALD 1977a) of fox social behaviour.

Methods

Scent marking by a wide-ranging mammal like the fox is not amenable to study under confined laboratory conditions. In order to study scent marking under semi-natural circumstances while maintaining some opportunity for detailed observation and experimental manipulation, I have used hand-reared foxes walking within an area with which they were thoroughly familiar, and following routes of their own choice. This approach had already been used to study aspects of the fox's feeding behaviour (MACDONALD 1976, 1977b). Once ideas have been generated and partly tested with these tame animals I have tried to corroborate them by observing wild foxes' behaviour and so to minimize the risk of attaching importance to anomalies resulting from captivity. Field observations on wild foxes were made at Boars Hill, Oxford, and Ein Gedi, Israel, where their social organization was essentially the same (MACDONALD 1977a). It is hard to be confident that leash walking foxes behaved exactly like wild ones, but their behaviour seemed indistinguishable from that of wild foxes; wild foxes have not yet been observed behaving in a way which casts doubts on the validity of any observation made during leash walking.

Fox cubs were hand-reared and trained to walk on a leash from 8 weeks of age. They were walked through the same area day after day to familiarize them with it, in the same way that field observations suggest that wild cubs gradually become familiar with the area further afield from their earth. The foxes were allowed to walk where they pleased, but all foxes show a predisposition for keeping either to paths or the borders of fields, and so it was comparatively easy to either anticipate or manipulate the routes which these leash-walking foxes would take and so to plan field experiments. The study area measured about 20 ha, equivalent to a small wild fox territory.

Ontogeny

Reactions to Experimentally provided Urine

For 7 vixens (between 1974—1977) field observations began with leash walks in the countryside when they were 8 weeks old. In addition to recording each vixen's response to wild fox odour, on 13 occasions I positioned 0.5 cc samples of fox urine along routes taken by Vixen I (born March 1974).

Until the vixens were about 14 weeks old their response to wild fox urine involved overt submission; they reacted to the odour with the same behaviour with which they might greet an adult fox. By 4 months old they only paused to sniff the urine before continuing. During 8 of 9 trials until she was 20 weeks old, Vixen I 'submitted' to the experimental urine. She never showed this response subsequently.

Posture and Token Marking

Until 5—6-months-old vixens urinated by pausing to squat and then urinating for between 7—25 s (mean 9.9 ± 4.75 S.D., $n=20$). This posture was named the 'squat' for urination by dogs (SPRAGUE and ANISKO 1973). Squat urinations were not preceded by active sniffing nor were they directed at particular sites or noticeable landmarks.

In addition to one squat urination, Vixen I adopted a new posture at 157 days old when she sprinkled a few drops of urine at each of two different sites (Fig. 1). These 'token' urinations were distinguished by their brevity and their sites. Visually conspicuous tussocks of grass were marked. There was also considerable preliminary sniffing before each urination.

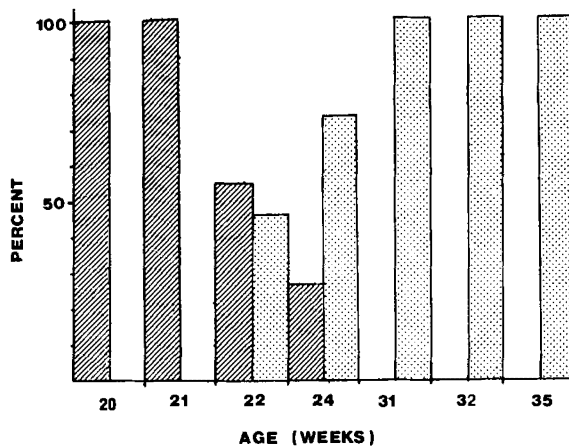


Fig. 1: The percentage of urinations during leash-walks which were 'tokens' (dotted) as opposed to prolonged 'squats' (cross-hatched) as the vixen grew older. Data are represented for only those weeks when the vixen marked during three or more walks and when there were no experimental manipulations

The ontogeny of each vixen's token urination behaviour followed a similar course. For example, Vixen II was born in March 1975 and was walked daily during July and August. She did not token mark until 21st August (5 months old). She left 21 tokens on 21st August, having only squat urinated until then.

Detailed Analysis of Token Urine Marking

In addition to observations on 7 vixens, detailed data were collected on Vixen I during 1974—1975—1976, and on Vixen II (Vixen I's daughter) during 1975—1976. The history of 2615 sites token marked by these vixens was analysed. Each site on which they urinated was marked (at a distance) with a numbered stake, together with a strip of reflecting paper (since much of the experimental work was done at night). All urinations during this period were tokens. Some sites were revisited daily by both vixens, while others attracted only cursory attention as their physical features changed: a clod of soil visited almost daily might lose its appeal as it disintegrated through weathering, an annual plant might wither prematurely through repeated dousings in urine and cease to be visited as it faded from the landscape. Vixens token marked throughout the year (Table 1). The leash walking foxes wove a network of paths through the long grass of the meadow, woodland and field borders. Token sites were mainly along these ramifying paths, but some were

Table 1

Monthly mean number of token urinations (\pm S.D.) each walk for 2 vixens. Mean urinal manipulations. The mean monthly figures for the 2 foxes are not strictly comparable: rate reflects the fact that she was loath to leave the enclosure

	July	Aug	Sept	Oct	Nov	Dec
	n = 5 N = 2	n = 17 N = 5	n = 16 N = 10	n = 14 N = 17	n = 4 N = 6	n = 0 N = 0
Vixen II	0	11.6* \pm 7.0	40.8 \pm 19.3	63.8 \pm 28.4	104.2 \pm 20.7	-
Vixen I	5.0 \pm 1.4	4.0 \pm 1.4	17.8 \pm 7.1	21.2 \pm 7.5	16.3 \pm 3.7	-

* Vixen II; mean \pm S.D. for walks after 20th August

n = sample size for Vixen II

N = sample size for Vixen I

in places only rarely visited — for instance, a molehill or donkey's faeces found and marked while hunting or playing off the paths. These isolated sites were rarely revisited and hardly ever re-marked, but those on the network of trails were marked repeatedly.

The pattern of marking is illustrated by Vixen I's behaviour from 8th November 1974 — 2nd March 1975, on 112 walks (approximately 1 h duration) during which she token marked 615 sites (Fig. 2).

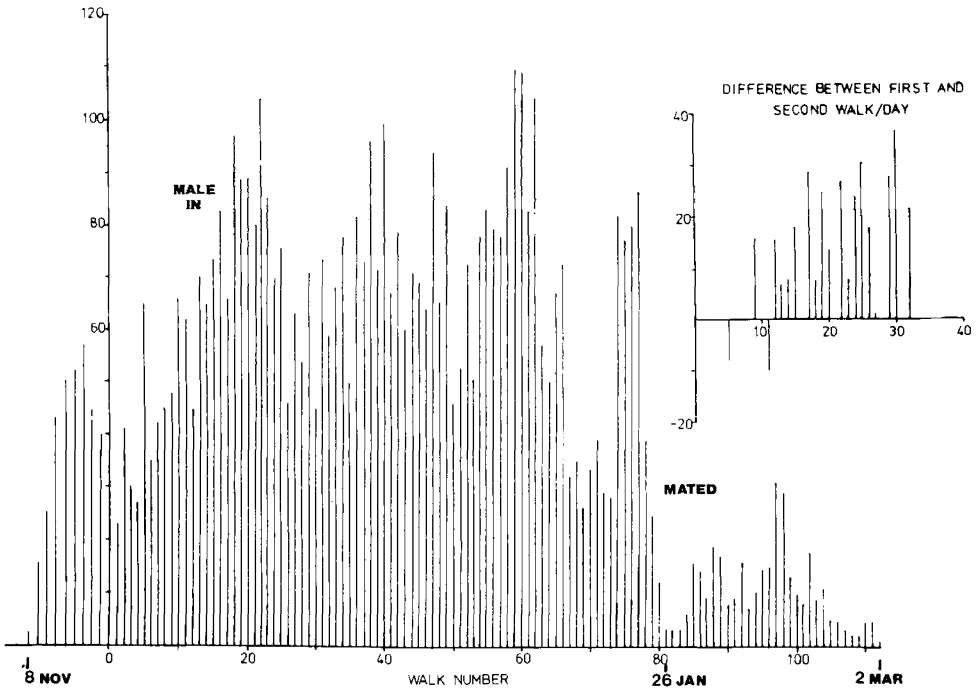


Fig. 2: Total sites urine marked during each walk. 9 walks on the left of the abscissa occurred before tokens were individually numbered and hence not included in the analysis. On some days there were two walks, the inset shows that both walks involved similar numbers of sites being marked, although more were generally marked during the first walk. Minimum intervals between first and second walks was 6 h, and between the second walk and the first one of the next day, about 16 h

Table 1

marking frequencies have been calculated using only those walks which involved no experience, Vixen I marked only 4–5 times during walks in April and May but this low for more than a few min when her cubs were still small

	Jan	Feb	March	April	May	June	July	Aug
	n = 1 N = 2	n = 4 N = 4	n = 3 N = 3	n = 9 N = 9	n = 12 N = 1	n = 7 N = 1	n = 0 N = 1	n = 0 N = 1
Vixen II	114.0 ±0.0	95.2 ±13.0	94.3 ±21.1	20.6 ±16.2	5.2 ±5.7	40.4 ±22.5		
Vixen I	25.5 ±0.7	19.5 ±11.3	18.0 ±2.6	6.0 ±2.0	4.0 ±0.0	5.0 ±0.0	76.0 ±0.0	37.0 ±0.0

A. The Spatial Organization of Sites

Although Vixen I token marked a total of 615 separate locations, there were areas where she walked regularly but never urinated (Fig. 3).

Table 2: The stake numbers at junctions between major paths are shown in Fig. 2. The averaged marking parameters for these sections are summarized on this table. The path running between stakes 271–420 was wide (5 m) and the fox would walk down one or other side of it on a given walk; hence, the data for both sides are presented separately. The data for 422–440 has been split from 422–461 since the former stretch of path traversed a different habitat, i.e. a lawn and flowerbed. Finally, Keeble's field edge (see Fig. 2) 463–615 has been split into 5 sections of increasing proximity to the marking border

Stake Nos	Path length	Total tokens	Total sites	Mean tokens / site	Mean tokens/m	No. Walks equivs.	Sites / m	Path. dist. from enclosure
1 - 38	40	416	38	10.95	10.4	146	0.95	20
39 - 48	12	86	10	8.6	7.16	112	0.83	46
49 - 61	18	41	13	3.15	2.28	46	0.72	49
62 - 75	22	69	14	4.93	3.13	52	0.636	69
77 - 81	17	11	5	2.4	0.65	15	0.29	63
82 - 90	12	55	9	6.1	4.58	69	0.75	58
93 - 109	20	109	15	7.2	5.45	91	0.75	74
112 - 116	9	11	5	2.2	1.22	15	0.55	90
117 - 129	34	83	13	6.38	2.44	112	0.38	79
136 - 155	38	148	20	7.4	3.89	112	0.52	103
156 - 270	150	1383	114	12.2	9.22	146	0.76	196
271 - 420	136	1173	149	7.87	8.62	146	1.09	389
Side I	136	770	84	9.2	5.6	(146)	0.62	389
Side II	136	403	65	6.2	2.96	(146)	0.48	389
422 - 440	32	370	18	20.56	11.56	146	0.56	
422 - 461	55	631	39	16.18	11.47	146	0.71	439
463 - 591	135	1203	128	9.4	8.91	146	0.95	562
592 - 599	30	51	8	6.37	1.7	146	0.26	
604 - 609	35	17	6	2.83	0.48	146	0.17	
610 - 615	35	12	6	2.0	0.34	146	0.17	
Field	125	204	32	6.37	1.63	146	0.25	
463 - 615	275	1283	152	8.91	5.46	146	0.65	562

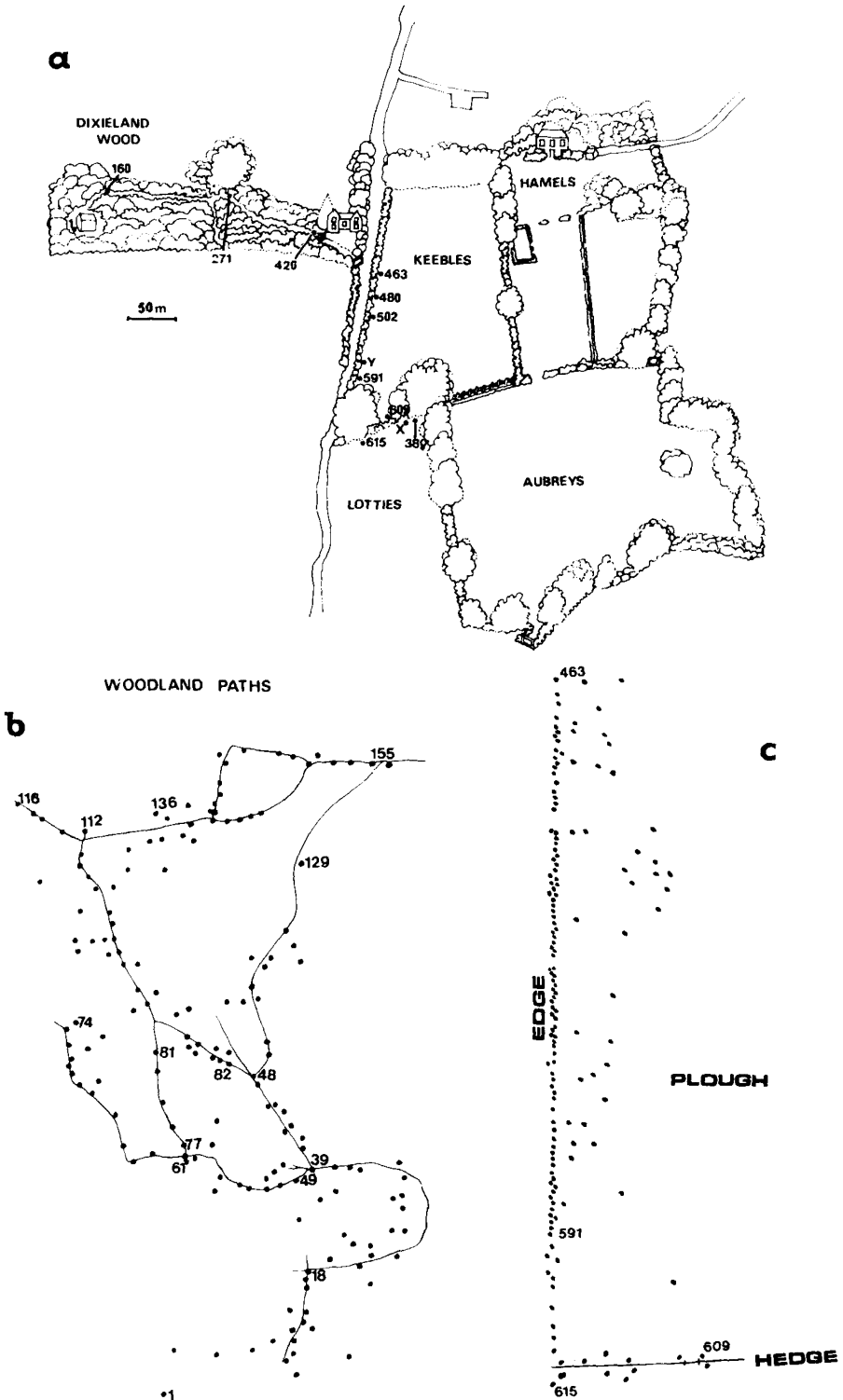


Fig. 3: Map of urine study area (a). Numbers apply to token urine marking sites specifically mentioned in the text. Maps (b, c) picture all the token marking sites along paths in a small area of woodland and along the edge of a ploughed field

I defined a perimeter zone including all sites outside stake no. 591 (see Fig. 3), choosing this site as the innermost point at which the vixen showed a tendency to turn back to the centre of her range (see below). For the area within site no. 591 I have divided the woodland paths into a number of sections based on obvious junctions and intersections (Table 2). During the 112 walks the different paths were travelled a different number of times: for instance, while several paths ramified through the woodland immediately adjacent to the fox's enclosure, eventually they all channelled together into a main track running down a wooded hillside. The fox invariably went down this main path but also travelled along any one or more of the subsidiary trails. The number of tokens per m increased with the number of walks along a given path ($t = 3.64$, $df\ 11$, $p < 0.05$). There is a strong correspondence between the number of tokens per site and the number of walks per path ($t = 5.73$, $df\ 11$, $p < 0.001$).

The computation of the number of times a path was travelled presents some complications, not only because the fox sometimes made detours off regular paths, but more especially because sections of the path might be travelled in two directions, i.e. the outward and the return journey during any one walk. Simply to double the number of 'walks' is incorrect because fewer urinations were left on the return journey (see Fig. 4) along a path, and some of these were 'duplicates' on the same sites which had already been visited on the way out. In general, the total number of return urinations was 30% of the outward number of urinations on any one walk (regression analysis $y = 0.33x - 1.68$; $t = 26.22$, $df\ 11$, $p < 0.001$) and I have used this as an approximate correction factor for those paths visited twice during any one walk (i.e. 112 walks in both directions take a value of 146 walk-equivalents [Fig. 5]). This correction improves the correspondence between tokens per site and number of walks ($t = 5.735$ becomes $t = 6.295$, $df\ 11$, $p < 0.001$), (first order polynomial [$df = n - (k + 1)$] was best in each case, testing goodness of fit with a t-test).

While the average number of urinations per site increases linearly with the number of walks along each path, the number of sites per m reaches a

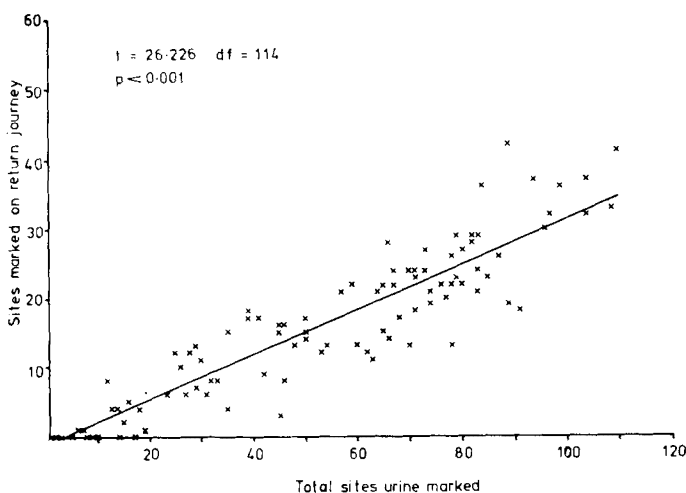


Fig. 4: Relationship between total sites urine marked and number marked during return walk. When a path was travelled twice during one walk (i.e. normally, during 1 h) considerably fewer tokens were left on the return journey

plateau after an initial increase. Two factors that could jointly contribute to this plateau are first, that there are only a limited number of suitable sites, and second that a site once visited gains considerably in attractiveness over other sites not yet visited. These factors may together explain why after only 18 days, 50% of the total 615 sites ever to be token marked had already been marked.

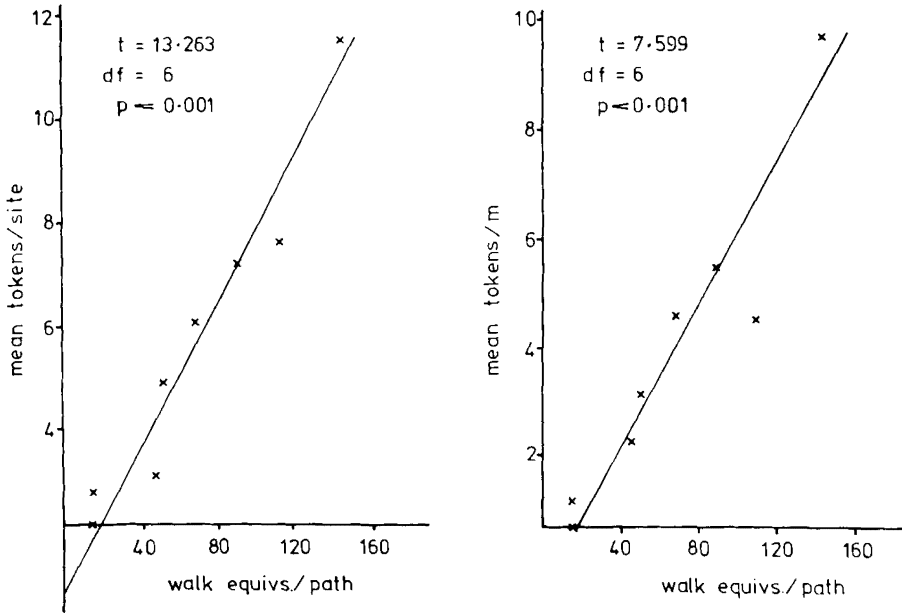


Fig. 5: Spatial features of token urine marking. The relationship between two measures of marking frequency (corrected for the fall in marking on return visits to the same path during each walk) using the *mean* figures for all paths walked the same number of times

i. Influence of Terrain

To discover whether the number of sites influences the pattern of marking, a detailed comparison was made between two paths representing markedly different habitats. (1) The path ran through a garden between flowerbeds with several visually prominent and odourous objects, such as a lavender bush, an *Antirrhinum* and a *Hydrangea*, which were marked during 42, 28, and 47 walks¹). (2) The path crossed rough, unkempt grass. The figures for these two sections of the path were:

Paths	Tokens / m	Tokens / Site*	Sites / m*
1	11.56	20.56	0.56
2	11.34	12.43	0.86

While fewer sites (34.9% fewer) were visited in the garden than in the immediately adjoining rough ground, each site was marked more frequently so that the average number of tokens per site is 65.4% greater. The two different paths received the same number of tokens per m during the three months of study and both sections of path were travelled the same number of times.

¹) A useful field sign when tracking wild foxes is the yellow, withered leaves of habitually marked plants.

ii. Influence of Paths

Comparing the vixen's behaviour along a field border path, and in the adjacent ploughed field, gave the following results over three months of study:

	Tokens / m*	Tokens / Site	Sites / m*
Field centre clods:	1.63	6.37	0.25
Field edge path:	7.4	10.4	0.71

* indicates a significant difference at greater than 0.05, testing mean tokens/m and mean tokens/site with a students t-test and mean sites/m (comparing 7 one-week sample periods) with a Wilcoxon matched pairs test.

Each measure of marking frequency is lowered in the open field compared to the field edge path and to both paths 1 and 2 mentioned above.

Notwithstanding the differences of attractiveness of clods of soil compared to grassy tussocks from the fox's viewpoint, these data suggest that marking rate is depressed off regular paths and my impression in the field supports this conclusion, which also tallies with PETERS and MECH's (1975) finding for wolves.

iii. Edge Effect

The fox's behaviour differed along the apparently contiguous terrain running down the field border between 463 and 615 with a transition point at stake 591 (the innermost 'turning point'). A continuous strip of field boundary between stakes 463 to 615 (Fig. 3), runs the length of Keeble's field along the bottom and through the gate into Lotties field. A total of 1283 token urinations was left on 152 sites down this stretch during 112 walks. This gives overall figures of 5.46 tokens per m, 8.91 tokens per site. However, these average figures mask a gradual decay of marking frequency:

Table 3

Sites No.	Tokens / m	Tokens / Site	Sites / m
463 - 615	5.46	8.91	0.65
463 - 591	8.91	9.4	0.95
592 - 599	1.7	6.37	0.26
604 - 609	0.48	2.83	0.17
610 - 615	0.34	2.0	0.17

Thus over the most peripheral 200 m of the fox's marking range, there was a gradual decrease in the frequency of tokens per m, tokens per site and sites visited and marked per m, which culminated at site 615 outside of which tokens were never left. The frequency of sniffing at suitable sites was maintained at a high level beyond site 615 and throughout the study area.

What is the function of the self-imposed limit on token marking? The following three series of experiments are an attempt to answer this question, by investigating the vixen's behaviour within and outside the marking area.

Experimental Investigation of Edge Effect

1. Fox urine experiments

Method: Along the different sections of path, both within and beyond the self-imposed marking border, I selected sites that resembled those that the fox token marked. Urine from freshly dead foxes acquired for post mortem examination was sprinkled on these sites and the fox's behaviour towards them that day, and subsequently, was recorded.

Result: 16 sites were treated with urine during 11 experimental days between 24th November 1974 and 20th January 1975. Three of these sites

were outside the normal marking range of the vixen while the remaining 13 sites were either in the woodland or field borders along which the vixen customarily left tokens. All the experimental sites were carefully sniffed by the vixen and each of the 13 within her marking range was token marked, while none of the three outside was marked. The intensive sniffing that the vixen typically showed as she approached these experimental sites, which began 2 m away, was accompanied by other changes in her behaviour; the area surrounding the experimental site was investigated, often with a slightly crouched body, tail curved and ears flicking backwards (postures associated with unease), and she might return to the site several times, sometimes urinating for a second or third time. Her behaviour during 1–2 min following discovery of the urine was 'excited', running between the next few of her own regular token sites continuing to sniff intensively.

None of the experimental sites had been marked before by this vixen. In every case those within her normal marking area were marked, and all but one were marked on subsequent days as well.

2. Site moving experiments

Method: Particularly favoured sites that had already been marked several times by the vixen were carefully dug up and moved both within and outside her marking range.

Result: Two sites were chosen for the site moving experiment. Both sites were in woodland well within the marking range and had already been marked several times. Both were token marked in their normal positions on 24th November and thereafter moved back and forth across the border of the vixen's marking range during 57 experimental walks. Both were invariably marked on all 35 trials within her marking range, but never during 22 trials outside it. The line defining whether or not she would mark was no more than 20 m wide.

During the first night of the experiment the fox swerved off the woodland track to each of the 'empty' transplanted sites and sniffed intensively around them. She spent 35 and 20 s digging at the leaves and sniffing around the area before trotting off without marking (compared with $3.1 \pm \text{S.D. } 1.9$ s spent sniffing at 20 token sites prior to marking). Arriving at the transplanted tussocks the vixen spent 80 and 20 s sniffing at them and urinated and defecated. Both were within her marking range. Subsequently she stopped making detours to the 'empty' sites but continued to visit the tussocks in their new locations. When sites were transplanted outside her marking range her behaviour was different: on approaching the site X in Lotties (outside her marking range, Fig. 3), she scented it at over 2 m range and leaped towards it in a frenzy of sniffing, running quickly all around the tussock and back and forth, but not marking. X was not marked for a further 15 walks, when, fearing that the tussock might have lost its odour, I moved it back to its original site which had not been marked for 16 walks. On the next walk the fox sniffed, for 25 s, at this tuft and marked it. After the walk I transferred the tussock back to site X where it remained, again sniffed daily but never marked until six walks later when I replaced it in its original location whereupon the fox again marked it and continued to do so subsequently.

3. Straw heap experiments

Method: Straw from the vixen's enclosure, smelling strongly of her own urine, was left at regular intervals along paths within and outside her marking range in small heaps of about 15 cm diameter.

Result: Summarized results of the third experimental technique also show that marking declined towards the periphery of the fox's marking range, and never occurred outside that range. 28 out of 31 piles were marked in the woodland, 14 out of 23 between 463 and 601 in the field corner and 1 out of 20 on the Keeble-Lotties border.

Reaction to Urine Marks outside Marking Range

Turning point

Throughout most of each walk Vixen I was keen to proceed, except when she reached the periphery of the area within which she token marked, where she often turned back. This prompts the question of whether alien urine outside her own marking range made any observable difference to her behaviour, and specifically to the turning point. To investigate this, urine from strange vixens was left in the vicinity of the turning point and Vixen I's behaviour was observed.

On 25th November 1974, 5 drops of vixen urine (♀38) were positioned 40 m into Lotties. Later that day, the vixen walked into Lotties and along the field edge sniffing each prominent tussock of vegetation although not marking any of them. Just short of the experimental site she began sniffing into the breeze and leant forward cautiously until her nose touched the urine-sprinkled blades of grass; she wheeled around and, sniffing audibly, trotted back into her marking range. This result was obtained with urine from two other vixens, suggesting that the vixen was less inclined to venture outside her range when she encountered alien urine. However, her own urine, left in similar locations, had no effect on her turning point (see above).

The following account describes subsequent days of the experiment begun on 25th November 1974:

Her turning point remained at exactly the spot of ♀38 urine for three walks, after which I sprinkled 5 drops of ♀38 urine on a tussock before the original ♀38 urine site. During the next walk she trotted along the border of the field until she came to the new sample of ♀38 urine, whereupon she turned back at once. On the following day she again turned back after sniffing the nearer sample of ♀38 urine. Samples of ♀38 urine left within the vixen's marking range did not evoke this response.

In March 1975 Vixen I was moved to a new enclosure to have her first litter. She was not walked again till June, and by July had established another marking range with well-defined turning points, and beyond which she would not token urinate (Fig. 6).

During the autumn and early winter of 1975 Vixen II marked over a wider area than her mother, Vixen I, including places outside the area with which she was most familiar. On 1st January 1976, Vixen II walked for 4.5 h during the night when she marked 224 different sites. The frequency of marking dropped from 1/10 m to 1/40 m on similar terrain outside her normal range, but increased again to 1/16 m on return. However, as the winter progressed, Vixen II's marking range became progressively circumscribed; this was monitored by straw heap experiments (as described above).

By mid-January 1976 Vixen II's behaviour had changed: she began to pause and sometimes to turn back towards Hamels from the vicinity of stake no. 7 (see Fig. 6). In March and April every walk was punctuated by a prolonged pause along the east hedgerow of Aubreys, which has a commanding view of the fields to the west. Vixen II would sit, watching over the area, sometimes for 10 min or more before turning and heading back towards Hamels. She also became nervous if forced to continue further. At the end of

Area token marked throughout summer

Token marks during one walk, mid September

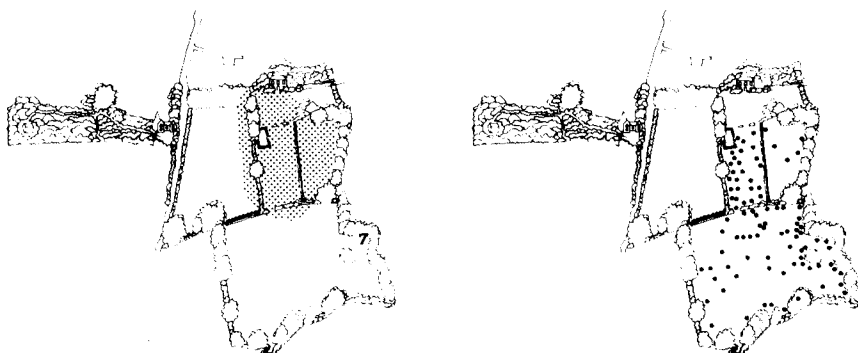


Fig. 6: Study area for urine marking experiments during 1975—1976. Stippled area shows extent of Vixen I's token marking range, while stars (right map) show individual tokens during a single walk in September

April 1976 and throughout May, Vixen II's 'turning point' became inflexible and by May she was unwilling to leave Hamels field at all. For the first time since the previous autumn she began to squat urinate occasionally, and always turned back after stake 145. The subordinate Vixen II's marking range thus came to have the same borders as that of her dominant mother, but the limits were defined in spring (age 12 months) compared to Vixen I who the previous year had restricted her marking range by autumn (about 8 months). Vixen I had her second litter in March 1976, but the subordinate Vixen II did not breed. Each vixen marked on the other's token sites when these were inside its marking range. Neither vixen token marked every site she discovered bearing the other's urine even when they were fresh, and outside the area of overlap they visited and carefully sniffed each other's sites.

A period of plasticity

In September 1975 and 1976 the self-imposed border of Vixen I's marking range seemed to break down temporarily, e.g. on 15th September 1976 Vixen I marked 93 times, including 64.5 % outside her normal marking range (Fig. 6). Two days later she marked 108 sites, with 75.0 % outside her old area. Perhaps late summer is a period of plasticity when readjustments are incorporated into territorial boundaries after the breeding season.

Token marking by dog-foxes

Data were collected on the urine marking behaviour of one leash walked dog-fox during 1976/1977/1978 and another during 1978/1979. The following points summarize their behaviour:

1. The dog-foxes did not token urinate until mid-January 1977, when they were about 10 months old.
2. From mid-January until the end of the month they token marked on conspicuous objects approximately 1/min. They double-marked every token mark of dominant vixens.
3. Thereafter they continued to token mark throughout the year, but at a much lower frequency.
4. They marked within the enclosure and when leash walking, within 40—50 m of their enclosures, but never marked when walking further afield.

B. Temporal Features of Token Marking

Some sites were visited and marked with tokens repeatedly. Only 615 separate sites were visited during the total period from November 1974 until March 1975. Fig. 7 is a histogram of the distribution of total numbers of tokens on individual sites. Some sites have been marked consistently over 5 years. After 6 weeks' enforced absence from one field, Vixen II marked 114 sites, of which only 41.5% were new, in spite of considerably altered vegetation.

i. Blanket Coverage

Was the vixen's entire marking range marked every night or was the 'blanket' coverage only accumulated during the study period? Vixen 1 token marked at least 1/min (and often 4/min) everywhere she travelled within her marking range, unless distracted (e.g. by prey). Towards the end of February the area covered by this blanket marking started to contract to the immediate neighbourhood of the enclosure. As her spontaneous marking range contracted so did her tendency to mark during straw pile experiments. Ultimately, on 2nd March, she left only one token urination, which was beside the enclosure. Nightly variations in the pattern of marking were dependent on such vagaries of Vixen I's interest as whether she wanted to look at a cached food item or to play.

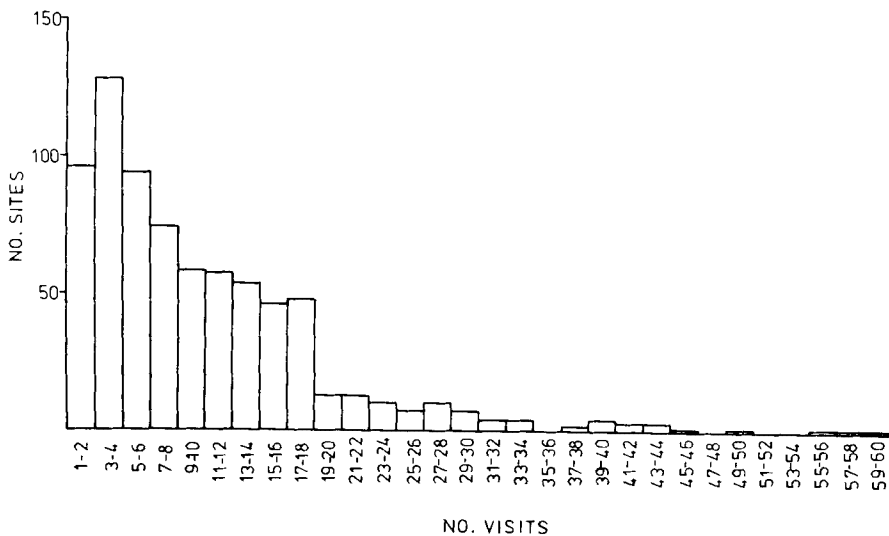


Fig. 7: Total marking visits per site (during 112 walks)

Token marking involved continual 'topping-up' of particular marking sites often through deliberate detours. Wild foxes make similar marking detours, including trips where the scent station is downwind of the fox.

ii. Causal Mechanisms

Over half of the sites ultimately to be marked more than 9 times had been initiated during the first 10 walks.

Sites which were visited on the homeward journey (Fig. 4) were called 'returns'. Some 'returns' were 'duplicates', i.e. marked on both the outward and homeward journeys. The total number of 'duplicates'/walk increased with

the total number of sites marked/walk (regression analysis, $y = 0.09x - 0.674$; $t = 14.19$, $df 114$, $p < 0.001$). 'Duplicates' similarly increased with 'returns'. This might suggest that the 'returns' were made with no reference to the outgoing marks so that on a random model the number of duplicates would increase linearly with the total number of sites marked. However, the fox's behaviour did not look random; some sites marked on the outward journey were sniffed carefully and marked with 'duplicates', others were not re-marked after equally protracted sniffing. The causal basis of how the fox faces the dilemma of to mark or not to mark is unknown.

C. Wild Fox Scent Marks

Field observation on urine marking behaviour outside a fox's territory are infrequent since residents make excursions so rarely. Fig. 8 (top) shows the position of all observed token urinations by members of two family groups watched at Ein Gedi, Israel. The sites marked by members of any one group overlapped each other widely, but the sites marked by individuals from the two groups did not overlap but were delineated by the territorial boundary established on the basis of both radio tracking and observation of inter-group encounters. This was understandable as members of the two groups rarely trespassed far into each other's domain. Nevertheless no tokens were left by foxes during ten observations of trespassing in their neighbours' territory in Israel (see Fig. 8 bottom).

Food hoarding

Other than the foxes' reluctance to mark outside their territory, their behaviour, including sniffing at likely marking sites, was often similar inside and outside the territory. Foxes were more easily startled outside their marking range, but systematic measures of this insecurity were elusive. One demonstrable behavioural difference within and beyond marking borders concerns food caching behaviour.

i. Field Experiments

Method: During September and October 1975 Vixen I was presented with small rodent prey in the field during eight separate trials. In four trials the prey were positioned within her marking range, while in the other four they were positioned outside her marking range. I recorded the number of caches made during each trial and the direction in which the food was carried prior to caching.

Results: Of 29 mice found outside her marking range 75.8% were carried approximately south-west for up to 100 m and into or towards the fox's marking range. In contrast, the 13 mice found within her marking range were distributed evenly between the four cardinal points, only 23% being carried in a south-westerly direction. Mouthfuls of 5–7 mice were carried back to her marking range, where they were then systematically scatter-hoarded (see MACDONALD 1976).

ii. Field Observations

Comparable data on wild foxes were collected by noting the location of caches made by individually recognisable foxes around three subsidiary feeding sites at Ein Gedi, Israel (see Fig. 9). Site A was inside the territorial boundary of group I. Site B was in group II's territory south of the track

that formed part of the boundary between the two groups, and site C was well inside group I's territory. During two months' observation I saw foxes make 112 caches which confirmed that members of the two groups carried food for caching into the area which they urine marked. One exception to this occurred on 4th January 1976:

Thin ♀ and Small Head ♀ (both group I) had been competing over food, running to and from site A as they hurriedly made caches (food caching is sometimes a mechanism for saving time, MACDONALD 1976). As Small Head ♀ approached, Thin ♀ fled with a mouthful of food, crossing the territory border and penetrating about 50 m into group II territory. Thin ♀ dropped some food and was unable to pick it up again since her mouth was full and so she hastily buried it, before trotting in a wide arc back to her territory where she buried the remaining food. Later, as she trotted down the track towards the feeding site, Thin ♀ suddenly veered southwards and returned to the cache she had made 50 m south of the feeding site and in group II territory; she unearthed this cache and carried the contents well into group I territory where she eventually buried it.

D. Social Status and Token Marking

PETERS and MECH (1975) show that RLU marking by wolves is almost exclusively confined to high status animals and links between the dominance of individuals and either the frequency of marking or the intensity of odour production have been widely reported (see RALLS 1971; EISENBERG and KLEIMAN 1972). After agonistic encounters a victorious fox usually token marks (pers. obs.) but outside this context, is the token marking behaviour of a vixen related to her status within the group?

i. Field Observations

Of three vixens in a family group studied at Ein Gedi (Israel), one was clearly subordinate, and she was seen to token mark a third as often as the other two vixens. In a neighbouring group the most subordinate vixen token marked only once compared to two more dominant vixens who were seen to token mark 31 and 13 times. Another, rather subordinate vixen marked 10 times.

During the winter of 1974/1975 in Oxfordshire a sub-adult vixen was severely harassed by adult members of her family group (MACDONALD 1977a, p. 311) and token marking was conspicuously absent from her behaviour. Nevertheless older subordinate vixens in the same group did token mark. So, token marking may be reduced in subordinate vixens, but it is not the sole prerogative of the dominant vixen.

ii. Observations in Captivity

Two captive family groups were maintained, each comprising one dog-fox and several related vixens, and thus mirroring the composition of wild groups in some habitats. In one group only the dominant vixen token urinated, while two other adults always squat urinated. As the role of dominance changed from one year to the next, so the new dominant would begin to token mark and the displaced dominant would begin prolonged urination. Within the litter of 5 vixen cubs from which this group grew, all except the most subordinate had begun token marking at 5 months old. Two relatively dominant vixens from this group were released with radio-collars. As they were tame it

was possible to watch them at close quarters in the wild, in one case for over two years. The more dominant of these two soon began to token mark again while the subordinate was never seen to.

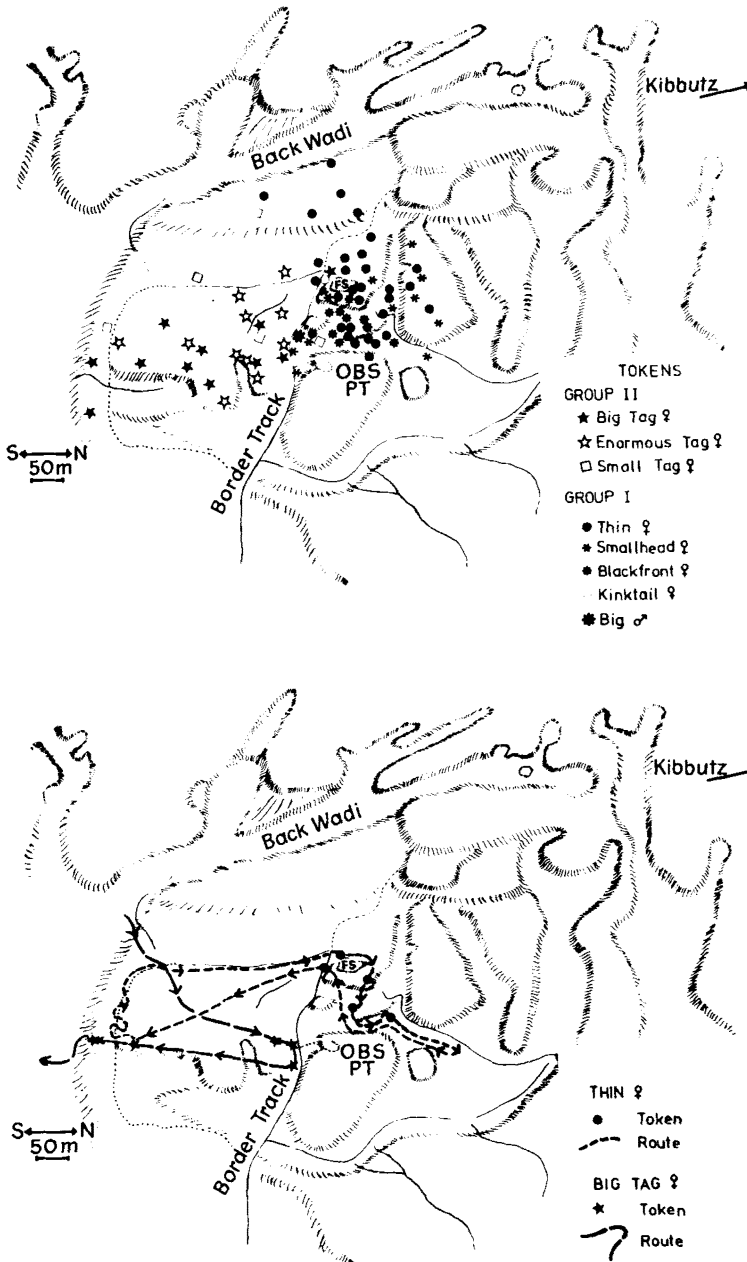


Fig. 8: (top) Distribution of token marks left by members of two neighbouring family groups, whose territories met along a border track. My observation point (obs.pt.) and the feeding site (FS) are shown. (bottom) Routes taken by two foxes who marked only within their group's territory. Thin ♀'s, group I, excursion south of the border track took 6 min. On return to her territory she urinated 4 times in 1 min. 10 min later Big Tag ♀, group II, appeared and urinated 5 times in 2 min, including at one site where Thin ♀ had sniffed, but not marked

In the second enclosure, the most subordinate vixens never token marked. Both Vixen I, the dominant, and Vixen II, the second in the hierarchy, marked at high frequencies. One reflection of dominance amongst vixens is the opportunity to breed (MACDONALD 1980) and in Site A this enclosure only the most dominant vixen bred. Reproductive vixens invariably token mark at high frequencies, but not all vixens which token mark breed.

iii. Allomarking

Dominant vixens and dog-foxes were often observed to token mark on group members. This was most frequently seen when the dominant animal approached a sleeping subordinate, sniffed at the prostrate animal and token marked its head or shoulder. Allomarking sometimes involved 'mouthing' (see below).

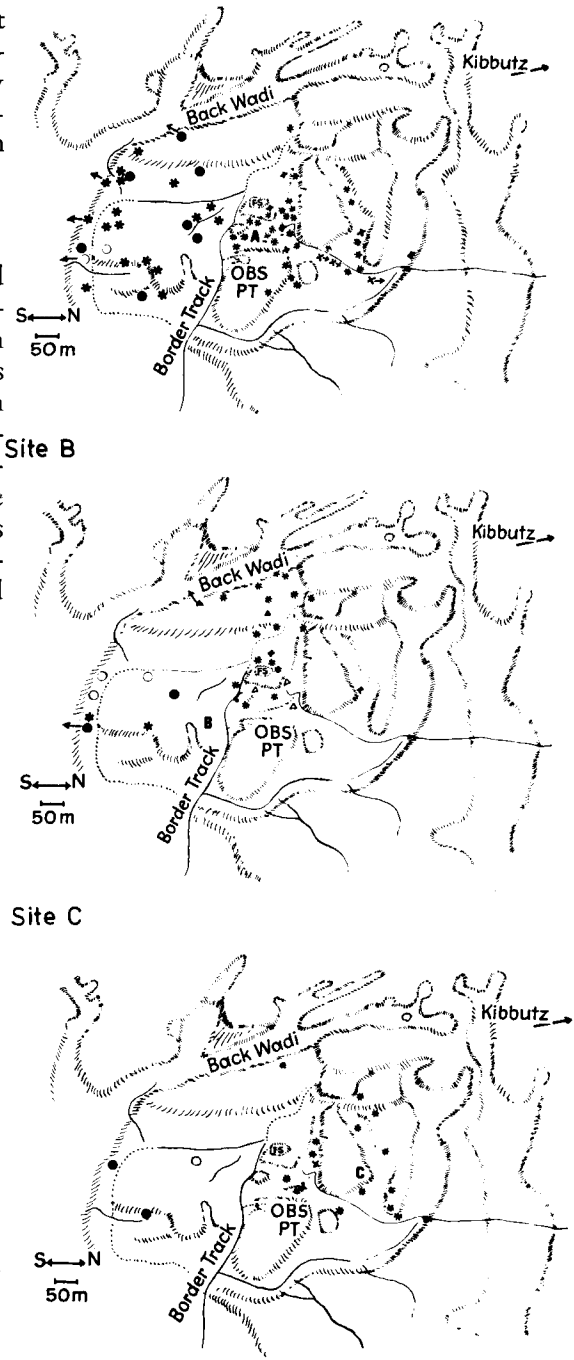


Fig. 9: Location of caches made by foxes (symbols for each individual as Fig. 8) when food was provided in each of three feeding sites (A, B and C). Food was always carried back into each fox's group's territory for caching

iv. Agonistic Encounters

After both inter- and intra-group aggressive encounters the victor token marks at a high frequency for 1—2 min. Several detailed examples are given in MACDONALD (1977a).

E. Behaviour Associated with Urine Marking

i. Multiples

Sometimes foxes leave more than one token urination on a given site during one visit. This typically involves sniffing at the site, marking, continuing to sniff, marking again, or perhaps moving a few feet away and then returning to the site and marking it for the third time. These *multiple tokens* most frequently involve only one additional urination on a given site, but sometimes there were more (maximum 8).

ii. Rubbing and Mouthing

Many of the same sites that attracted multiples, also elicited 'rubbing'. For Vixen I this behaviour appeared on 28th November 1974 (age 8 months) and was already infrequent again by the end of January 1975, not to recur until the same time in subsequent years. During the winter, both the frequency and intensity of rubbing increased to a peak in December. Rubbing was invariably accompanied by at least one token and involved sliding the chin and perioral region of the head along vegetation, often the upright trunks of saplings or hedgerows. Rubbing both preceded and followed urination and the two behaviours often alternated. At its most intense, 'rubbing' also involved 'mouthing', during which the fox opened its mouth and wedged the branch or vegetation into the angle of its jaws and then dragged it through, visibly trailing saliva. Mouthing was also directed towards other foxes as well as onto vegetation. Histological examination showed that foxes have enlarged perioral sebaceous glands, especially near the angle of the jaw (pers. obs.).

iii. Faeces

BURROWS (1968) has pointed out that fox faeces are commonly found on top of visually prominent objects and so fall within KLEIMAN's (1966) definition of scent marks. Typically they are left on mole hills or tussocks of grass or even high up in astonishing locations such as the top of gorse bushes. While foxes normally stand beside or on top of objects they defecate onto, I have seen them defecate while standing on their forelegs with their hind legs raised above them on some object, so that the faeces were deposited aloft.

Between 18th November 1974 and 2nd March 1975 Vixen I defecated 135 times during 112 leash walks. At least 95 faeces (70.3%) were positioned on sites that she had previously urine marked. It is possible that because of their visually prominent qualities the same sites were independently attractive for both urine and faecal marking and that the positioning of faeces on sites already urine marked, was a coincidence resulting from the general saturation of all suitable sites with urine.

I do not know what proportion of faeces were tainted with anal sac secretion, which is critical to further interpretation of their communicative function (ALBONE et al. 1978). Faeces, like urine marks, were distributed throughout fox territories and not, for instance, concentrated around the peri-

meter. Certain paths may temporarily be heavily marked with faeces (and urine) by wild foxes over a period of weeks. In some cases these paths are near sleeping places and hence often travelled. In other cases they appear to be 'barking trails' and may be associated with vocal advertisement of territories (in prep.).

Discussion

Acknowledging limitations of sample size and methodology, these results support the suggestion that the token marking area may correspond to a territory and that *one function* of token marking may be concerned with the spatial organisation of fox populations. Marking with urine and faeces has been ascribed a territorial function for many animals (see EWER 1968). The few experimental investigations of this all reveal considerable complexity (e.g. LEUZE 1977). SCHENKEL (1947) assumed that scent marking was involved in the maintenance of wolf, *Canis lupus*, territories. Many urine marks and faeces are found at the junctions of wolf paths (SETON 1909; MECH and FRENZEL 1971). Although MOWAT (1963) suggested that wolves urine mark at a line of sites around the territorial border, PETERS and MECH (1975) have elegantly shown that through urine marking ". . . the entire range is studded with olfactory 'hotspots'". The Raised Leg Urinations (RLUs) of dominant wolves seem analogous to token urinations by foxes, both being directed at visually conspicuous sites. PETERS and MECH (1975) point out that having demonstrated that RLUs are distributed throughout the wolf pack's territory (although in their case more frequently at the borders), it is necessary to discover whether one pack's RLUs cause aversion on the part of their neighbours. They quote convincingly indirect evidence to suggest that this is the case. In the present study the manipulation of the vixen's turning point by foreign urine directly demonstrates an aversive effect. The main limitation of this study was the absence of direct encounters with other foxes at territory borders and the uncontrolled presence of wild foxes in the study area. Perhaps coincidentally, part of the border of the captive vixens' marking range was also the known border between wild fox territories.

For comparison with PETERS and MECH's (1975) findings, I compared the frequency of token marking at different distances from Vixen I's enclosure (taken as her activity centre). A slight trend ($t = 2.68$, $df 11$, $p < 0.05$) suggested an increase in marking frequency towards the periphery of the *core* area (i.e. excluding the border of her marking range). However, this trend was an artefact of the particular ramifications of paths that were frequently travelled.

PETERS and MECH (1975) also describe the temporal pattern of RLU marking, with wolves being inclined to re-mark fresh RLU sites rather than old ones. As they point out, this resulted in 'sign' of the resident pack being particularly dense in areas they visit frequently, which is again the case for foxes. While the spatial pattern of token urinations may provide information affecting the behaviour of trespassing neighbours and potentially invading itinerants, the temporal pattern of marks within the range could, in addition, provide useful information for other group members. It is not yet proven whether foxes can recognize individuals from their scent marks, but badgers and mongooses are known to have this ability (ÖSTBORN 1976; GORMAN 1976). Dog-fox urine is known to contain a compound absent in vixen urine (JORGENSEN et al. 1978). Some sites are visited and sniffed every day yet they were not marked every day. Possibly the cumulative concentration of odour had to

be kept at a certain level, but was allowed to decay without re-marking as long as it remained above that threshold or was not overmarked by other foxes. Since tussocks that have previously been ignored are marked repeatedly after their first marking, the causal trigger for marking may be fresh urine. However, there must be some 'switching off' mechanism if only to avoid the vortex of a fox walking back and forth past one site repeatedly and marking *ad infinitum*. A mechanism inhibiting marking one's own very fresh urine would explain PETERS and MECH's finding that wolves re-mark RLU sites more often when the sites are several days old than when they are one day old. There is still no adequate explanation for why foxes should token mark so many sites so frequently within their territories, nor is there information on how this rate varies between territories of different sizes. The marking rates recorded in leash walks may be high, but snow tracking sometimes reveals comparable rates by wild foxes.

I have never seen excursing residents urine mark, although one dispersing radio-collared vixen token marked during a period of temporary residency (N. HOUGH in prep.). Casual observations suggest that sub-adult vixens are reluctant to token mark outside their familiar area when they first start marking, e.g. at 5 months old Vixen I token marked on four consecutive days in her familiar range, but during the next eight consecutive walks in an unfamiliar area she only squat urinated during the first four. The following four walks involved two squats and 12 tokens. On return to the familiar area she left one squat and four tokens during each of her first two walks, but no urinations during the next walk, through some adjacent but unfamiliar fields.

It seems probable that urine marking serves many functions, communicating different types of information within and between groups, varying from territory maintenance to pair formation. HENRY (1977) proposed that urine marking aids the fox in saving time by avoiding scavenging in areas already harvested, a principle suggested by CHARNOV et al. (1976). While I have not seen this 'book-keeping' by wild foxes in my habitats, places where invertebrates had been captured (or missed) were occasionally token marked. Inedible food remains are frequently marked, for instance decayed sheep carcasses may accumulate as many as a dozen fox faeces. Similarly, fox faeces and the smell of urine are commonly found around the entrances to rabbit warrens. Large edible food items are so frequently both token marked (and defecated) upon that the practice probably has a particular function; perhaps these sites take on temporary olfactory conspicuousness and are marked like any other conspicuous object, or perhaps scent marking is a way of safeguarding food items too big to be cached readily. Whatever the explanation, it is clear that urine marking communicates diverse messages within fox communities.

Summary

1. Token urine marks were distinguished from squats by their short duration and small volume, by posture (often involving a cocked leg) and their location. Token marks were normally on conspicuous objects and at nose height. Sometimes vixens climbed backwards up trees to mark. Both sexes may cock their hind legs, but vixens normally have a more convex back and elevated tail while doing so.

2. Two adult tame vixens only token marked within a clearly defined area, which could be divided into a large core surrounded by a narrow peripheral belt over which the frequency of token marking rapidly declined. Wild

foxes have not been seen to token mark outside their territories and so the marking range of leash walking foxes is interpreted as analogous to territory.

3. Within the core, paths on similar terrain were marked with a frequency proportional to the number of times they were travelled. For two sections of the path, travelled equally often, the number of marks/m were the same. On the section with fewer, but more conspicuous sites, this was achieved by marking each site more often. A comparison between marking frequency on and off fox paths suggests that it is higher on paths.

4. A vixen responded to her own and strange urine marks differently within and beyond the peripheral belt, and so demonstrated that she could distinguish between her own and other urine. A fox often chose not to venture beyond the limits of her marking range and the point at which she turned back was influenced by the presence of conspecific urine.

5. Foxes knew the position of many sites from memory and made detours to reach them.

6. In general, subordinate vixens token marked less than dominant ones. In one case, the token marking range of a subordinate vixen eventually took the same configuration as that of the dominant vixen of her group. Sometimes the two vixens overmarked each other's tokens, but sometimes they did not and no pattern could be recognised in their response.

7. Vixen cubs begin token marking at about 5 months old and initially mark in any area they are familiar with. There are indications of a second period of plasticity in the configuration of the marking range in succeeding autumns. A subordinate vixen continued to mark over a wide area for four months longer than her dominant mother.

8. Vixens token marked everywhere they travelled within their marking range every night.

9. Food caches are more commonly made within the marking range.

10. Token marking is also seen in the context of agonistic encounters, courtship, allomarking, and in association with other forms of scent marking, such as 'mouthing' and defecation.

Zusammenfassung

Urinmarkieren läßt sich vom Harnen durch die kurze Dauer, die Stellung (oft mit angewinkeltem Bein) und den ausgesuchten Ort (oft ein auffälliges Objekt in Nasenhöhe) unterscheiden. Beide Geschlechter können dabei das Bein heben, aber Fähen tun es mit stärker gebogenem Rücken und erhobenem Schwanz.

Zwei zahme Fähen markierten nur in einem ganz bestimmten Gebiet, am meisten in dessen mittlerem Teil, immer weniger zum Rand hin. Auch wilde Füchse markierten nie außerhalb ihres Reviers. Marken werden am häufigsten auf den Wechsellinien gesetzt, um so häufiger, je öfter diese benutzt werden; gibt es dort weniger geeignete Stellen, werden diese um so häufiger benutzt. Eine Fähe reagierte auf eigenen und fremden Urin (im Revier und außerhalb) verschieden, konnte also beides unterscheiden. Sie und ein Rüde machten jeweils vor fremden Marken kehrt.

Füchse haben viele Markierungsstellen im Gedächtnis und machen Umwege, um dorthin zu gehen. Rangtiefe Fähen markieren weniger als dominante; manchmal meiden sie die Markierungsstellen der dominanten, manchmal nicht. Jungfähen beginnen mit 5 Monaten zu markieren, zuerst in vertrauten Gebieten. Im folgenden Herbst scheinen sich die markierten Gebiete noch zu ver-

schieben. Fähen markierten jede Nacht dort, wohin sie auf ihren Streifzügen (in ihrem Gebiet) kamen. Das Markieren schien einem gewissen Rhythmus zu folgen.

Futterverstecke werden bevorzugt im markierten Gebiet angelegt. Urinmarkieren kommt auch in verschiedenen sozialen Kontexten vor.

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